PUPAL ECOLOGY AND ROLE OF PREDATORS AND PARASITOIDS IN NATURAL POPULATION REGULATION OF GLOSSINA PALLIDIPES AUSTEN (DIPTERA : GLOSSINIDAE) AT NGURUMAN, KENYA.

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BY

DELPHINA ABA ADABIE, B.Sc (UST, Ghana), M.Sc. (UG, Ghana).

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DECLARATION

I, THE UNDERSIGNED, DECLARE THAT THIS THESIS IS MY OWN ORIGINAL WORK AND HAS NOT BEEN SUBMITTED FOR ANY DEGREE IN ANY UNIVERSITY. ALL SOURCES OF MATERIALS USED HAVE BEEN DULY ACKNOWLEDGED.

AUTHOR'S SIGNATURE.

DEDICATION

TO MY FAMILY ESPECIALLY MY CHILDREN, KWAMENA AND AUDREY, THEIR PERSEVERANCE WAS A CONSTANT SOURCE OF ENCOURAGEMENT AND THEIR LOVE AND UNDERSTANDING MADE THE TASK WORTHWHILE AND PLEASANT,

AND

TO ALL WHO HAVE DEVOTED THEIR LIVES AND SERVICES TO THE FIGHT AGAINST CROP PESTS AND INSECT VECTORS WHICH ARE RESPONSIBLE FOR HUNGER AND DISEASES IN THE WORLD.

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ABSTRACT

A two-year programme was carried out at Nguruman in the Kajiado District of the Rift Valley Province of Kenya, to identify the characteristics of larviposition sites, quantify pupal mortality rates, determine predators and parasitoids of *Glossina pallidipes* Austen and to provide data on mechanisms of population regulation through the actions of predators and parasitoids.

Pupal sampling was done using hand searching for two man-hour per site. The efficiency of this technique was measured and found to be 60%. The larviposition sites were usually found in dense shade under bushes. This is the first description of *G. pallidipes* breeding sites in the Nguruman area. Though puparia were found in a wide range of soil types, they occurred more frequently in loamy-sand soils and showed a marked tendency to be aggregated in shade underneath big horizontal branches. In general, larvae pupate near the surface of the soil where and when it is very wet or covered with a thick carpet of leaf debris, but were found deeper in the soil when it is very dry or has no leaf debris cover.

There was evidence that seasonal variations in relative abundance and distribution of puparia resulted partly from a seasonal shift in breeding sites from low-lying sites to sites on hilly slopes during the rainy season when most riverine habitats were flooded.

Rainfall over 80mm per month increases pupal mortality through flooding and waterlogging of the larviposition sites. Adverse climatic factors caused 15.9% mortality through degeneration and/or decomposition

of puparia. The survivorship curve from pooled age data indicated a mortality rate of up to 4% a day. An index of overall pupal loss rate (log number of pupae found - log number of tenerals caught in biconical traps in the following month) was plotted against the log number of pupae found. The strong linear relationship indicates that the overall pupal loss rate is density dependent, and thus serve to regulate population size. Part of this mortality could be quantified by holding field-collected pupae in the laboratory till emergence. The causes of non-emergence were identified as developmental failures (mean = 18.0%), emergence failures (mean = 24%); parasitism (mean = 12.3%) and fungal infections (mean = 33.7%). None of these was density dependent. Predation estimated from empty puparial cases showed that an average of 24.0% had arthropod-induced damage. Parasitism rates by Exhyalanthrax lugens Lw. and E. beckerianus Bezzi (also known as Thyridanthrax. argentifrons Austen) were usually below 10.0% and apparently inversely density dependent with a delayed density dependent component.

The Agar gel double immuno-diffusion technique developed to detect tsetse meal in guts of arthropods and to identify the natural predators of G. pallidipes, proved very sensitive and specific for Glossina. The length of time a tsetse meal remained detectable in gut of predators varied from a minimum of 6 h for the gryllid Liogryllus bimaculatus to 48 h for another gryllid Phaeophillacris sp. Positive results were identified in 288 of 1,702 (16.9%) arthropod predators tested. Asiliidae, Gryllidae, Hymenoptera and Odonata were numerous and consistently had high proportions of positive results, indicating that they were the most important natural predators of G. pallidipes at

Nguruman, Kenya. However, no numerical response could be demonstrated between these predators and tsetse numbers.

Laboratory studies on the interactions of predators and puparia and adult G. pallidipes (prey) showed feeding responses that are best described by Holling's Type II and III functional response curves which have density dependent population regulation possibilities.

Predation was assessed by burying known densities of puparia in larviposition sites and scoring them for predation two weeks later. Although predation levels were quite high (about 35%), there was no evidence that mortality was density dependent over the range of densities used (1 - 36 puparia/m^2). Implications of the findings in this study in relation to tsetse control are discussed.

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CHAPTER ONE

1. GENERAL INTRODUCTION

1.1 THE SCOURGE OF TSETSE

All tsetse flies belong to the order Diptera and the genus Glossina. This genus was formerly included in the family Muscidae (Newstead, 1911; Newstead et al., 1924; Patton, 1934; Imms, 1957), but has in recent times been placed in the monogeneric family, Glossinidae (Brues et al, 1954; Haeselbarth et al, 1966; Potts, 1970a). The genus is made up of 30 species and subspecies which are divided into three principal groups, namely, fusca (the forest tsetse), palpalis (the riverine tsetse) and morsitans (the savanna tsetse), (Jordan, 1974).

The scourge of tsetse flies and trypanosomiasis is one of the major factors inhibiting agricultural advancement in over 40% of the African continent (Buxton, 1955; Glasgow, 1963; Ford, 1965; Ford and Katondo, 1977; Langley, 1983). The disease not only constitutes a serious human health hazard, but also imposes a major constraint on general agricultural development, human settlement and livestock production. Breeding of livestock in 7 million km^2 of the affected 13 million km^2 area is impossible due to high incidence of the disease which extends from 14^oN to 29^oS with either continuous or isolated areas of infestation (Ford, 1970; FAO, 1974; Pant et al., 1977).

The most obvious effect of animal trypanosomiasis is enormous losses in livestock which lead to shortage of natural fertilizer for crop production, and shortage of dairy products and animal protein resulting in malnutrition. Human sleeping sickness poses a serious health problem to over 20 million people. This potentially fatal disease affects about

10,000 people each year (FAO, 1974), and it results in poor health and low industrial and agricultural output. It also causes depopulation by death or by migration of people from tsetse-infected areas resulting in large areas being relinquished to tsetse flies and wild animals (Ford, 1971).

The endemicity of the disease is due to the fact that some game animals and also domestic animals, particularly pigs, are reservoirs of the causative organisms called trypanosomes. Four of the six main Trypanosoma species of socio-economic importance infect livestock and have a wild animal reservoir. These are T. vivax Ziemann, T. brucei Plimmer and Bradford, T. simiae Brues et al. and T. congolense Broden. The remaining two species, T. rhodesiense Stephens and Fantham and T. gambiense Dutton are zoonoses with infection in livestock and game and acute clinical infection in man. T. rhodesiense is found in specific foci in East Africa, while T. gambiense is mainly restricted to West and Central Africa (Maclennan, 1975).

Tsetse flies are able to transmit the disease to many animal species and man because of their catholic feeding behaviour. Tsetse, man and animal reservoirs are therefore the three major components in the transmission of the disease. Hence the principle of disease control is the use of ecological, chemical and biological measures to disrupt the transmission between the components.

1.2 PAST AND PRESENT APPROACHES TO CONTROL OF TSETSE AND TRYPANOSOMIASIS

Since the discovery that tsetse flies are vectors of African trypanosomiases, many approaches have been employed in an effort to control the disease. One approach consists of control of the disease

parasites directly by chemotherapy and chemoprophylaxis (Mulligan, 1970; Na'isa, 1971; Finelle, 1975; Challier, 1982). These may be combined with manipulation of the human and cattle populations to break or minimize contacts between man, his domestic animals and the flies (Nash, 1969; Jordan, 1974). These are expensive repetitive procedures which do not prevent transmission of the disease. Apart from that, most of the drugs available for treatment of the disease can have unpleasant side-effects. Trypanocidal drugs have helped to maintain cattle in some areas, but under high challenge the frequency of prophylactic or curative interventions rapidly leads to drug resistance (Finelle, 1975; MacLennan, 1975). There is increasing evidence of development of strains of parasite resistant to many of the drugs currently available (Kupper and Wolters, 1983; Pinder and Authie, 1984).

N'dama and some Baoule cattle breeds in Central and West Africa (Roelants et al., 1987) and the Orma Boran breed in East Africa (Roelants, 1986; Dolan et al., 1986) are known to be naturally resistant to trypanosomiasis. The resistance appears to be inherited and functional against many types of trypanosome. Cross-breeding between known resistant and sensitive animals and/or introduction of trypanotolerant cattle in Cote d'Ivoire, Gambia and Burkina Faso in West Africa, in Gabon, Central Africa and in Kenya, East Africa have met with some degree of success (Dotoum, 1979; Leak et al., 1986; Dolan et al., 1986; Roelants et al., 1987). Because of these successes efforts are being made to promote selective breeding of some of the resistant breeds and introduction of these breeds, without trypanocidal drug protection, into areas of high Glossina density. The development of vaccine and other immunization methods to trypanosomes is still in the research stage (ILCA, 1979).

The alternative approach is to reduce or eliminate contact

between the vectors and the host. Initially, this was achieved through resettling people away from tsetse areas (Cockbill et al., 1963; Smith, 1973), but this was politically unacceptable after African countries gained political independence. Since then the main approach has been to control or eradicate tsetse populations. A full account of tsetse control methodologies used can be found in any review on the subject (Shircore, 1916; Glover and Langridge, 1963; Mulligan, 1970; Finelle, 1974; Jordan, 1976, 1978a, b, c, 1979, 1985, 1986; Dame and Jordan, 1981; Allsopp, 1984). Because the tsetse flies are dependent on game animals for their survival, it was logically suggested that a period without the hosts should reduce the fly population, so in the mid-40's the tsetse numbers were reduced by selective destruction of the favoured host species, thereby removing their food supply and killing the flies by starvation (Baldry, 1964; Bursell, 1970). G. morsitans was practically exterminated in Nagupande, Zimbabwe, by removal of elephants, buffalos, kudu, bushbuck and suidae (Cockbill, 1960, 1967). Destruction of game animals as method of tsetse control has been widely practised in Uganda, Zimbabwe and Zambia, but shooting of only the most frequently used hosts was not sufficient as tsetse can make use of other sources of food hosts (Cockbill, 1972). Apart from the fact that game elimination deprived part of the human population which hunt the animals for food, the method led to loss of considerable assets in countries where wildlife is a main source of foreign exchange in their tourist industry.

The tsetse habitat destruction strategy (Nash, 1940; Jordan, 1974), which renders the habitat inhospitable for resting and breeding, leads to undesirable destruction of vegetation which is a good source of timber and firewood. Though this destructive method eradicated Glossina in some areas, it is labour-intensive and logistically demanding due to regrowth of the vegetation which necessitated repeated bush clearing.

The method is also expensive and ecologically unacceptable because a large number of forest trees must be destroyed to achieve success thus depriving the continent of valuable economic timber and associated foreign exchange revenue. In addition, the deforestation exposed the land to erosion and desertification. Because of high cost of labour, tsetse habitat destruction by hand clearing has virtually ceased to be a large scale method for tsetse control (Jordan, 1974). Only discriminative bush clearing of about 5% of total vegetation cover is now practised on small scale. This selective bush clearing minimizes drastic alteration of the natural ecosystem as well as minimising effects on wild life (Nash and Page, 1953). Although bush clearing and game elimination achieved control in Zambia and Zimbabwe in the early part of this century, the flies were not eliminated, because the flies changed their breeding habitats and fed on alternative or less preferred hosts (Vale and Cumming, 1976).

Since the eggs and larvae are retained in the adult female flies and the puparia are relatively well protected in the soil, the only stage in the life cycle of tsetse readily available for chemical control is the adult. Application of chemical insecticides, which provides the most reliable method for large scale tsetse control, has been widely used in Africa with some measure of success since the 1960's. Earlier use of insecticides was based on the extensive application of persistent compounds to all vegetation types thought to be harbouring tsetse. This was costly and caused unnecessary damage to the ecosystems. The insecticide used first was DDT (as wettable powder), but dieldrin as an emulsion concentrate has been widely used since the 1960s (Finelle, 1980; Robertson et al.,1972). Initially the chemicals were applied by knapsack sprayer, but in recent years helicopters have also been used to apply a similar single deposit of insecticide in areas with rugged terrain.

Later controls were based on selective application of insecticides to known fly resting sites (Nash and Davey, 1950; Hursey and Allsopp, 1983; Shereni, 1985). A total of 10,664 miles^2 was reclaimed from tsetse in Northern Nigeria using this method, making the area safe for grazing (Davies, 1964, 1971). The selective use of insecticides lessened the large scale threats to environmental pollution but did not prevent the indiscriminate destruction of natural enemies of tsetse and other beneficial insects.

An alternative approach is the low volume sequential aerosol technique using fixed-wing aircraft which has been used in large scale operations for tsetse control in Botswana, Burkina Faso, Tanzania, Nigeria Zambia, and Zimbabwe against both savannah and riverine species (Alsop, 1980). This works on the principle that 100% of adult flies are killed at the time of spraying, and subsequent sprays carried out at about 9 days intervals kill emerging flies before they can larviposit. The most commonly used insecticide for these low volume aerial applications is endosulfan. The advantages of this technique over conventional residual spraying methods using ground spraying machines are three-fold. Firstly, it is the least damaging for the environment; secondly, it is usually cheaper per km^2; and thirdly, it allows large areas to be treated in a relatively short time with minimum staff and supervision.

Insecticide control methods have achieved control successes in Kenya (Glover et al., 1960); in Nigeria (Davies, 1964, 1979; Muhammed, 1978); in Uganda (Wooff, 1965); in Zimbabwe (Robertson et al., 1972); in Botswana (Davies, 1981); and in Cote d'Ivoire (Politzar and Cuisance, 1982). Eradication was however not achieved because of the constant problem of reinvasion or resurgence of the population in the treated areas (Davies, 1975; Cuisance et al., 1984; Allsopp, 1984). This was because of financial constraints and sporadic applications as in Zambia

Tanzania, Cote d'Ivoire, and Nigeria (Alsop, 1980), or as result of political disorder or war as was the case in Zimbabwe (Boyt, 1979; Lawrence, 1980). Different methods have been employed to reduce reinvasions. In Nigeria, natural barriers provided by hills were utilized (Allsopp and Muhammed, 1977), while in Cote d'Ivoire and Zimbabwe insecticidal barriers using dieldrin were employed (Cuisance et al., 1981; Hursey and Allsopp, 1983; Hursey and Whittingham, 1985).

Despite the proven ability of insecticides to reduce tsetse infestations, there is a general reluctance to expand their usage because the cost of maintaining an effective barrier zone to prevent reinvasion is often too high and economically not feasible for many affected countries. Furthermore, pesticides are not only expensive and beyond the means of nomadic and livestock farmers, but are also hazardous and disruptive to the environment and affect other non-target organisms in the ecosystem (Baldry, 1963; Graham, 1964; Riordan, 1966; Langridge and Mugutu, 1968; Koeman et al., 1971, 1980). It is therefore clear that pesticides usage is a temporary solution to a permanent and endemic problem. Although the method is successful in certain locations, it cannot be realistically extended to the whole $7 \times 10^6 km^2$ of infested lands adequate for cattle raising in tropical Africa (Jordan, 1986). Other more rational and integrated methods aimed at reducing cost and environmental pollution are therefore being explored. (IDRC, 1974; Laird, 1977; Busvine, 1978; Ferriote, 1981; Challier, 1982). Non-chemical methods are receiving increased priority (Pant et al, 1977; Laveissiere and Couret, 1980; Offori, 1981).

Some of the biological control measures have been directed against the vectors' reproduction (Vanderplank, 1947, 1948b). The

relatively low rate of reproduction suggests that tsetse are suitable candidates for control by the release of sterile males (Dame and Schmidt, 1970; Jordan and Curtis, 1972). The possibility of controlling tsetse by sterilization of males or both sexes has been intensively studied and has been demonstrated by experimental field releases which resulted in eradication of G. palpalis gambiensis Vanderplank in 300km^2 of pastoral area of Sideradougou, Burkina Faso (Politzar and Cuisance, 1982; Cuisance et al., 1984, 1985); suppression of G. morsitans morsitans Westw. in Tanzania (Williamson et al., 1983), and eradication of G. palpalis on a small scale in selected areas of the Lafia Agricultural Development Project in the Guinea Savannah zone, Central Nigeria and of G. palpalis palpalis from gallery forest of the Southern Guinea zone in Nigeria (Oladunmade et al., 1985b). Its large scale feasibility is being investigated in Nigeria and Ghana. (Itard, 1971; Cuisance et al., 1978, 1980). Results so far obtained indicate that the technique is only possible when the population is relatively isolated or after the initial population has been reduced using non-residual insecticide or trapping (Dame et al., 1980; FAO/IAEA, 1981; Politzar and Cuisance, 1982; Oladunmade et al., 1985a; Vale et al., 1986).

Another direct attack on the fly consists of destruction of the flies by use of trapping devices. The early trap types were designed and used to visually attract and capture the flies. Although mainly used for surveys (Harris, 1930; Swynnerton, 1933; Langridge, 1968; Glasgow, 1956, 1970; Glasgow and Potts, 1970; Challier and Laveissiere, 1973; Challier, 1977; Hargrove, 1977), they have been used to control tsetse confined to isolated areas (Laveissiere et al., 1981; Vale, 1982). In the desire to reduce use of pesticides for tsetse control, simple more effective traps have been developed (Challier and Laveissiere, 1973; Hargrove, 1977; Vale, 1982; Flint, 1985; Brightwell et al., 1987). Some of these traps,

notably the Challier-Laveissiere biconical traps, have been widely used for reducing local populations of tsetse in riverine and forest habitats in West Africa. Insecticide- impregnated blue screens have also been used to control tsetse. When deployed at 250/km^2 they successfully reduced density of G. palpalis s.l. in small areas of forest in Cote d'Ivoire (Laveissiere and Couret, 1982; Laveissiere et al., 1981 Gouteaux et al., 1982). Their low cost, ease of construction and simple application make the use of traps and targets most suitable for use by local inhabitants (Ryan and Molyneux, 1980). Purely visual screens and traps were initially however not viable for savanna species because too many would be needed for the vast areas involved.

However, in recent years host odours have proved highly effective in attracting tsetse to stationary and moving targets (Vale, 1974a, b, c; Hargrove and Vale, 1979), and some of the important attractive components have been identified (Hall et al., 1984; Bursell, 1984; Vale and Hall, 1985a). The addition of these components and other odour attractants to traps has increased their effectiveness in field conditions (Vale, 1980, 1982; Vale and Hall, 1985b; Dransfield et al., 1986). These discoveries have increased the potential of baited traps and insecticide-impregnated screens and targets for economical elimination of widely dispersed tsetse species from large areas of savanna. In Zimbabwe, the use of insecticide -impregnated targets baited with acetone and 1-octen-3-ol, has produced a remarkable population reduction among G. pallidipes and G. morsitans in the Rifa Triangle in the Zambezi Valley (Vale, pers. comm.). Considerable progress has very recently been achieved at Nguruman in Kenya using NG2B traps, without insecticide impregnation, baited with acetone and cow urine to control G. pallidipes (Dransfield et al., pers. comm.).

The use of odour-baited, traps and screens is gaining favour because if insecticides are used at all, they are restricted to specific artificial devices rather than applying them directly into the natural habitats. Though cheap and simple to use, the impregnated screens and traps are highly vulnerable to weathering (Lancien, 1981) and logistics of their large scale use could be a disadvantage. However, they do have considerable potential in providing means of reducing reinvasions by protecting boundaries and suppressing population on local scale (Shereni, 1985; Oladunmade et al., 1985a; Takken, 1984; Takken et al., 1986), or in hilly country where aerial spraying is impractical. In addition, the use of natural and synthetic odours to increase trap attractiveness further is still being investigated in Zimbabwe, Cote d'Ivoire and Kenya.

Rather than killing the flies with traps and targets, Langley and Weidnass (1986) have pointed out that sterilization and subsequent release of both males and females would be even more effective. At present, sterilization of insects is by exposure to ionizing radiations or chemosterilants (House, 1982). However, only the latter are appropriate for incorporation into low technology devices for automatic trapping, sterilization and releases of tsetse flies, but the compounds are highly toxic and cannot be placed indiscriminately in the environment (Bursell, 1977). Nevertheless, their incorporation in target devices can perhaps be considered ecologically acceptable and thus justify further exploration (Langley et al., 1982). Very recently, insect growth hormones, notably juvenile hormone analogue (S31183, manufactured by Sumitomo Chemical Company, Tokyo, Japan) (Chaudhury, pers. comm.) have shown great promise.

The simultaneous use of various control methods has been suggested as a better means of tsetse eradication. In recent years, such integrated methods have been attempted in Nigeria and Burkina Faso. In Nigeria,

eradication of G. palpalis palpalis has been achieved in 1,500km^2 area of the central region with integrated use of biconical traps, insecticide-impregnated targets and the sterile insect technique (Takken et al., 1986; Oladunmade et al., 1985b). In this example, continuous removal trapping using biconical traps reduced the target tsetse population by more than 90%, and the insecticide-impregnated targets controlled the population in the marginal habitat as well as acting as efficient barriers preventing reinvasion of the control area, while the sterile males released weekly at minimum ratio of 10 sterile to 1 wild fly achieved eradication in the control area. In Burkina Faso, elimination of G. p. gambiensis and G. tachinoides along 500km of gallery forest in pastoral area of Sideradougou was achieved by use of deltamethrin-impregnated screens in the dry seasons followed by the release of sterile males of the two species in the rainy seasons (Cuisance et al., 1984; Cuisance et al., 1985).

Another biological method suggested for tsetse control involved the use of their natural enemies because different workers recognised that invertebrate and vertebrate predators may significantly influence populations of tsetse. Early releases of parasitoids and parasites in Malawi (Lamborn, 1925) and in Tanzania (Nash, 1933a; Lloyd et al., 1927) encountered numerous difficulties due mainly to insufficient knowledge of the dynamics of both the tsetse population to be controlled and that of the natural enemy to be used. In recent years, considerable advances have been made to the understanding of the dynamics of tsetse species, but very little work has been done on the natural enemies which may regulate their populations.

1.3 TSETSE AND TRYPANOSOMIASIS IN KENYA

In East Africa, the major vectors of trypanosomiases are G. pallidipes, G. morsitans and to a lesser extent G. fuscipes fuscipes. However, the present study is restricted to G. pallidipes Austen 1903 (Plate 1) which belongs to the morsitans group. This species was chosen for the present study because it is the major vector of both sleeping sickness in man and nagana in domestic animals in Kenya (England and Baldry, 1972), and therefore the selected target tsetse species at the International Centre of Insect Physiology and Ecology (ICIPE) where the study was undertaken.

G. pallidipes is found in several countries in East Africa including Kenya, Tanzania and Uganda. Its distribution extends between 3^{o} N and 20^{o} S in East Africa and 3^{o} N and 9^{o} S in Central Africa (Fig. 1 inset), (Ford, 1970; Smith, 1973, Ford and Katondo, 1977). In Kenya, it is estimated that nearly 138,000 km^2 of the 570,000 km^2 (24.2%) land is tsetse infested (FAO, 1974). G. pallidipes is widespread and has a remarkable range in altitude extending from sea level to more than 2000m, and has been found in a wider range of climatic conditions than other tsetse species (Buxton, 1955). In Kenya, it is patchily distributed in thickets restricted to areas below an altitude of 2000m and where annual rainfall exceeds 500mm (Snow, 1980).

The species is distributed either alone or is associated with other tsetse species in Kenya. At the coast, the belt of G. pallidipes includes plains and hill ranges. This species occurs with G. austeni and G. brevipalpis in thicketed woodland or forest-grassland interface and in large areas of semi-arid Acacia-Commiphora thornbush (Snow, 1980). The species also exists with G. brevipalpis in dense secondary thickets dominated with Lantana camara (Snow, 1980). Under the conditions of

Plate 1 - Dorsal view of Glossina pallidipes Austen, important vector of animal trypanosomiasis in the Nguruman area.

Kilifi in the Coast Province, it is evenly distributed throughout all vegetation types with the exception of cultivations. There is preference for the denser vegetation in the hot and dry seasons (Moggridge, 1936).

In the Lambwe Valley in South Nyanza Province, G. pallidipes is found in continuous hill thickets, thicket clumps in the bottom of the valley, in woodland and open country (Allsopp and Baldry, 1972). Turner (1981) reported that, in addition to the thickets, exotic coniferous plantations bordered by Euphorbia tirucali constitute a suitable habitat for the species in the area.

In Meru National Park in the Central Province, G. pallidipes is confined to areas where Acacia-Commiphora and Acacia-Combretum are the prominent vegetation communities (Lambrecht, 1980). In the Rift Valley Province, the species occurs with G. longipennis as in the Nguruman area (Fig. 1), and occupies all the vegetation habitats but is mostly confined to the riverine thickets and mixed woodland in the dry seasons. It tends to spread into other vegetation habitats including the open plains in the rainy seasons (Van Etten, 1981; Dransfield et al., 1986). In Kibwezi in the southern part of Kenya and situated some 211 km from Nguruman, a low density of G. pallidipes occurs with Glossina brevipalpis in wooded thicket (Owaga, 1985).

Studies at ICIPE on the ecology of G. pallidipes in Kenya started in 1974 and since then various scientists have contributed greatly to improve sampling techniques and a better understanding of the ecology and population dynamics of this species in Kenya. Jaenson (1981) compared samples from Moloo traps and from slow-moving vehicles in the Kiboko forest, while Owaga (1980) compared the effectiveness of Langridge, Moloo and Challier-Laveissiere biconical traps. In all these studies samples were analysed regarding sex ratio, age distribution, nutritional status

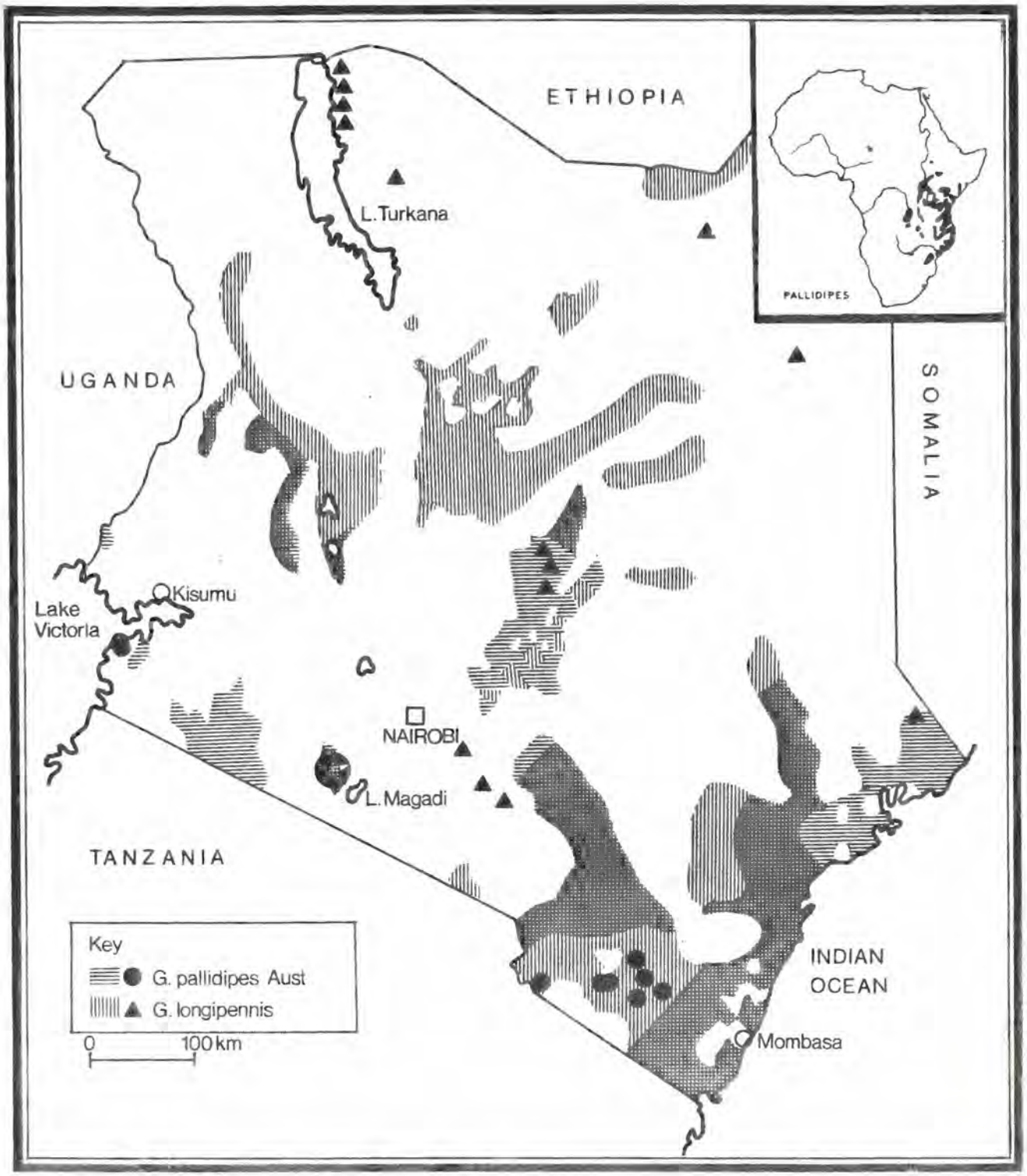

Fig. 1 - Distribution of G. pallidipes Austen and G. longipennis Corti in Kenya. (Inset - Distribution of G. pallidipes in Africa). ✪ Study location.

in different seasons and pregnancy states of the female component of the populations. Observations on seasonal changes in populations in different vegetation habitats have been studied by different tsetse ecologists in different areas in Kenya (Jaenson, 1978a, 1981; Lambrecht, 1980; Snow, 1980, 1982; Turner, 1981, 1984). Turner et al., (1981) investigated mechanisms of population regulation in the Lambwe Valley. The same kind of investigations have been made in the Kenyan Coast (Snow, 1982) and at Nguruman since 1983 (Dransfield, pers. comm.). Mark-release-recapture experiments have been carried out both in Lambwe and Nguruman to estimate the population sizes using various mathematical models (Turner; Dransfield, pers. comm.).

In an isolated forest at Muhaka, Snow (1982) reported that a medium density of G. pallidipes is mainly maintained on cattle and pigs, while in the Shimba Hills a very large population of the same tsetse species is supported by abundant wild hosts including pigs, antelopes, buffaloes and elephants. Allsopp et al., (1972) observed a strong positive correlation between distribution of wild ungulates (especially bushbucks) and G. pallidipes abundance, but the importance of warthogs as a maintenance host was also striking at all localities although their relative importance varied between habitats. The host range and preference of G. pallidipes in the Nguruman area, as obtained from blood meal analysis, are given in Table 1 (Tarimo and Golder, 1984; Tarimo et al., 1985) which shows that suids are the most preferred hosts followed by waterbuck and buffalo in that order. This feeding pattern has confirmed that the species is an opportunist.

In the Lambwe Valley area, G. pallidipes is of both medical and veterinary importance because in addition to animal trypanosomiasis a low grade transmission of Trypanosoma rhodesiense persists in the human

settlements around the periphery of the Ruma Game Reserve (Otieno, pers. comm.). The mean infection rate for all trypanosome species in the flies in 1984-1986 was around 15%.

It is important in the epidemiology of only animal trypanosomiasis at Nguruman. The average infection rates found in G. pallidipes are around 5% for T. vivax, 1% for T. congolense and less than 1% for T. brucei (Tarimo et al., 1985). The overall infection rates in cattle vary from 0 to 50% and the isolated parasites are T. congolense and T. vivax with only two occasions of T. brucei. Low incidence of brucei infection may be attributable to the fact that the sampling technique is less efficient for brucei.

Control of tsetse in Kenya started in the 1940's (Moggridge, 1949). The selective application of residual insecticide like DDT to tree trunks, lower branches and other resting sites using knapsack sprayers has been the main method of tsetse control in Kenya. This method resulted in successful elimination of G. pallidipes in some areas in South Nyanza Province and of G. fuscipes in some areas along the Lake Victoria shore. (Glover et al., 1960; Baldry, 1971). Attempts have been made since 1981 to eliminate the disease by eradicating G. pallidipes in the Lambwe Valley because Rhodesian human sleeping sickness is endemic in the area. The major chemical control method employed has been sequential aerial application of low dosage endosulfan aerosol sprays supplemented by ground spraying of residual dieldrin and cypermethrin (Turner, 1984). Limited bush clearing has also been carried out in areas of difficult terrain (Turner and Brightwell, 1986).

While some temporary control has been achieved through the sequential spraying method, total elimination of the flies has remained a major problem because of apparent reinvasion and/or resurgence of the

Table 1 - Host Preference of *Glossina pallidipes* Austen at Nguruman, Kenya.

	Number of flies		
Host	Males	Females	Flies %
Suid	75	29	34.9
Waterbuck	21	17	12.8
Buffalo	21	12	11.1
Cow	13	9	7.4
Wildebeest	11	6	5.7
Kongoni	8	7	5.0
Human	5	8	4.4
Goat	5	6	3.7
Bushbuck	4	6	3.3
Giraffe	6	4	3.3
Elephant	6	2	2.7
Gazelle	1	3	1.3
Sheep	2	1	1.0
Impala	2	1	1.0
Eland	1	2	1.0
Felidae	2	-	0.7
Rabbitidae	1	1	0.7
Total	184	114	100

population in the treated area. There has been no insecticide spraying at Nguruman.

1.4 REASONS FOR CHOICE AND OBJECTIVES OF PRESENT STUDY

For decades, laboriously planned tsetse control operations have encountered numerous difficulties. This has been due partly to operational problems and partly to insufficient knowledge of the dynamics of the tsetse populations in their natural habitat (Randolph et al., 1984). A long term study of tsetse population dynamics and epidemiology of animal trypanosomiasis in the Nguruman area was started in 1983 by ICIPE scientists. A multidisciplinary team approach was adopted with each scientist concentrating on a different aspect of the problem. The principal aim of the study was to develop new approaches to tsetse and trypanosomiasis control through a better understanding of vector and disease dynamics and more appropriate control strategies. For the latter, the main aim was to develop a trapping technology which would allow local Maasai to control tsetse using odour-baited traps, and concomitantly improve the awareness and community participation in the control programmes until they became as natural as other agricultural treatments.

In order to get a better understanding of vector and disease dynamics, the modelling approach was adopted with the objective of developing a tsetse population model. In 1984 several gaps remained, of which the most important were pupal ecology and quantification of the role of predators and parasitoids in population regulation, both at the pupal and adult stages. This study was therefore instigated in October 1984 to provide data on pupal mortality rates and mechanisms of population regula-tion through the action of predators and parasitoids. Since little was known of the breeding sites, work was initially concentrated on pupal

ecology. Research was then expanded to also cover predators of the adults. The specific objectives are: -

(1) to study the characteristics of the larviposition sites of Glossina pallidipes Austen with respect to vegetation types, degree of shading, soil types, and soil depths;

(2) to study seasonal changes in puparial densities and distribution in relation to the adult population;

(3) to determine the major climatic factors causing changes in puparial density and distribution;

(4) to determine the role of pathogens, predators and parasitoids in the natural regulation of the G. pallidipes population at Nguruman, and

(5) to provide quantitative data on these components in the population dynamics of this species for the later construction of tsetse population models in collaboration with other ICIPE tsetse ecologists working in the same study location.

CHAPTER TWO

2. LITERATURE REVIEW

2.1 BREEDING SITES OF GLOSSINA PALLIDIPES

The ecology of puparia of tsetse involves the relationship between puparia population and the edaphic, abiotic and biotic components of the breeding habitats. Breeding sites of tsetse were studied in the past by Swynnerton (1936); Harley (1954); Buxton (1955); Ford (1963); and Atkinson (1971a), and recently by Challier (1982) and Laveissiere et al., (1984b). Glossina species do not larviposit at random within their geographical ranges, but typically breed in specific habitats, although the degree of specificity varies. Forest or riverine species appear to larviposit in areas with narrowly defined characteristics, whereas the savannah species which are exposed to great seasonal changes in climate and vegetation, use many types of breeding places. (Nash, 1939; Vanderplank, 1948a; Buxton, 1955; Jewell, 1958; Glasgow, 1961; Nash and Trewern, 1972; Challier, 1973; Gouteaux and Kienou, 1982).

Work of the early tsetse ecologists helped to define the general characteristics of breeding sites of Glossina which are known to be shaded protected spots with dry loose soils. However, only a little is known about the characteristics of G. pallidipes larviposition sites. The puparia of G. pallidipes have been found in a wide variety of habitats in the geographical range of the species. In Mozambique, Swynnerton (1936) recorded puparia of this species from the same fallen logs from which puparia of G. morsitans were recovered. He also studied the breeding places of G. pallidipes in Zimbabwe and regarded thicket, game and water pools as ecological requirements for satisfactory breeding of this species in that country. In East Africa the puparia were found in

thickets and under carpets of dry leaves and leaning trees. In Zimbabwe, Phelps et al. (1966) and Phelps and Vale (1978) demonstrated that G. pallidipes uses sand in river beds in dense thicket in the cool dry season and animal burrows in the hot dry season in the same way as G. morsitans. Wet season puparia collections have rarely been successful (Parsons, 1930; Swynnerton, 1936; Nash, 1937, 1942; Vanderplank, 1944).

Several authors have reported on plant species associated with breeding sites of different tsetse species (Langridge et al., 1963; Gruvel 1974b; Turner, 1981). G. pallidipes is found in forest fringing permanent surface water as well as vegetation of banks of seasonal pools, rivers and streams that are dry for most of the year, as the species is not dependent on the proximity of permanent water (Smith, 1973). It is also associated with thicket patches, some evergreen trees and secondary shrubs on banks of seasonally dry streams and rivers. The flies appear to be attracted more to woody vegetation than to herbaceous plants (Buxton, 1955; Smith, 1973).

In any habitat the choice of specific site in which larvae are extruded is determined by the behaviour of the pregnant females (Nash, 1930). Responses involved in the selection of larviposition sites have been investigated by many workers (Lamborn, 1915; Swynnerton, 1936; Lewis, 1934; Burtt, 1952 ; Parker, 1956a; Page, 1959; Phelps and Jackson, 1971; Atkinson, 1971a; Davies, 1977; Rowcliffe and Finlayson, 1981). Investigations into the responses involved in the selection of breeding sites by gravid G. palpalis carried out in Nigeria by Parker (1956a, b) showed that a variety of black objects were strongly attractive, and there was a strong preference for rough surfaced soil, while soils with moisture content of 25% or more were avoided in favour of those in equilibrium with the atmosphere. In Northern Botswana, G. morsitans

submorsitans was found to prefer holes as breeding sites during the dry season due to reduced temperatures and higher relative humidity (Finlayson, 1967; Atkinson 1971b).

2.2 MORTALITY FACTORS AFFECTING TSETSE PUPARIA

Pupal mortality is one of the factors that may affect the distribution and abundance of tsetse puparia. Mortality of puparia may occur due to adverse climatic factors which are density independent (Rogers and Randolph, 1985). The obvious effects of weather on tsetse survival shown in West and East Africa (Nash, 1939; Buxton, 1955) demonstrated the importance of abiotic mortalities. Mortality in puparia may also be due to effects of potentially density dependent factors such as parasites, predators and pathogens (Nash, 1970). Density independent mortality determines population change, whilst density dependent mortalities tend to regulate the population density around an equilibrium level by preventing indefinite increase or decrease (Rogers & Hubbard, 1974; Rogers and Randolph, 1984).

Numerous instances of predation and parasitism on tsetse have been reported by different tsetse field workers and literature on parasites and predators of Glossina is reviewed by Buxton (1955) and Mulligan (1970). Lists and bibliography of all records of natural enemies are provided by Saunders (1960), Jenkins (1964), IDRC (1974) and Laird (1977). Little attempt is made to separate their contributions since they now resemble a cake in which most of the ingredients are too well-blended to distinguish. However, all these accounts indicate that Glossina species are attacked by numerous and varied natural enemies, which presumably contribute more or less to the natural regulation of the tsetse population. However, most of the parasites and predators are not very specific so little detailed work has been done on them.

2.2.1 PATHOGENS OF TSETSE

Many pathogens have been reported in tsetse. These include micro-organisms namely bacteria, fungi, viruses, protozoa, rickettsiae and nematodes. The infrequent observations, detection and isolation of these organisms are due to individual scientists who recorded their association with tsetse but could not do further investigations because of technical inadequacy of investigations or practical failure of the organisms as effective biotic agents or failure to breed them for further studies.

Bacillus species have been reported from puparia of G. tachinoides in Chad (Gruvel, 1970). Another bacteria-like organism is described in spermathecae of inseminated females of G. pallidipes from field population in Uganda (Rogers, 1973).

Several species of fungi have been reported in association with different tsetse species, but most of the reports are consistent in not providing identifications of the fungi or evidence of their pathogenicity. This is because mycoses were thought to be less important as a population regulating factor and were considered mere contaminants. Nash (1933b, 1937) recorded a great decline in population of G. morsitans in Tanzania following spells of very heavy rains and floods. The probable causes of death were drowning of the puparia, with considerable mortality among the adult flies attributed to fungus, Phycomycete. After the flood the population in the study area recovered rapidly and this was attributed to repopulation by immigration. Vey (1971) showed that two mycoses affecting puparia of G. fusca congolensis in the Central African Republic are due to Absidia repens and Penicillium lilacinum. Though both fungi are commonly isolated from soils, several infectivity studies confirmed that the fungi are primarily pathogens and not contaminants.

Unidentified Phycomycetes have been reported in adults of G.

palpalis from Ghana (Macfie, 1916) and from Tanzania (Swynnerton, 1936), and in G. morsitans in Tanzania (Nash, 1933a). In Nigeria, Lester (1934) also observed mycoses in 10% of field-collected G. tachinoides females. The mycoses found in abdomen of adult G. brevipalpis captured in Somalia were found to resemble those found in Tanzania (Moggridge, 1936).

Virus-like particles have been found in salivary glands of G. pallidipes (Jaenson, 1978b), and these have been proved to cause sterility in flies (Odindo et al., 1981)

Intracellular rickettsiae have been described in midgut epithelial cells associated with fat body, developing oocyte and in association with muscles in adult G. brevipalpis, G. fuscipes, G. morsitans and G. pallidi -pes (Reinhardt et al., 1972).

The first nematode ever recorded as parasitising a tsetse fly was found in the body cavity of adult G. palpalis in Uganda and described by Leiper (1910). Since then mermithid nematodes have been found in G. morsitans in Uganda (Carpenter, 1912; Rogers, 1973); in Zambia (Lloyd, 1912) and in Tanzania (Thomson, 1947). They have also been reported in G. pallidipes and G. brevipalpis in Uganda (Moloo, 1972). In West Africa, mermithids have been recorded in G. palpalis in Liberia; in G. tachinoides in Burkina Faso and in G. palpalis, G. m. morsitans and G. longipalpis collected from four areas in Nigeria (Foster, 1963).

2.2.2 PARASITOIDS OF TSETSE PUPARIA

Twenty-three species of Hymenoptera and over twelve species of Diptera of family Bombyliidae are listed by Jenkins (1964) as important parasites of tsetse puparia, but most rarely parasitised tsetse exclusively. Ten species of Exhyalanthrax are the only Diptera which are parasitic on tsetse (Mulligan, 1970). All the ten species are widely

distributed in East and Central Africa, but reports on Exhyalanthrax from West Africa are scarce. However, E. argentifrons has been found in G. m. submorsitans in Nigeria (Lester, 1931; Taylor, 1932), while E. beckerianus was found in G. tachinoides in Chad (Gruvel, 1974a).

Analysis of incidence of Exhyalanthrax species (formerly called Thyridanthrax) in field-collected puparia have indicated important variations between localities, habitats and seasons (Nash 1942, 1970; Hursey, 1970; Gruvel, 1970). Nash found variation in parasitism by Exhyalanthrax in relation to habitat. Whereas incidence in 726 puparia from Berlinia globiflora and Acacia usambarensis woodland was 15.7%, the incidence for 783 puparia collected in hilly Brachystegia microphylla woodland was 7.8%. Field observations on puparia of G. morsitans suggested no emergence of Exhyalanthrax in the cold dry season, but a greater emergence in hottest weather just before the rain (Chorley, 1929). In Gadau, Northern Nigeria, Taylor (1932) recorded that parasitization rate of G. tachinoides by E. beckerianus is highest in warm dry months and lowest after the rain. Hursey (1970) recorded a high parasitization rate of 46.6% with E. abruptus (E. lineus) Lw. in puparia of G. pallidipes near Lesser Kiboko River in Machakos, Kenya. Other species of the same genus which have been reported in puparia of G. pallidipes are E. lugens (Lw), E. alliopterus Hesse, E. beckerianus Bezzi (E. argentifrons Austen), and E. brevifacies Hesse. Species reported in other tsetse species are E. curtis Hesse and E. transciens Bezzi (Potts, 1955, 1970b; Hursey, 1970; Mulligan, 1970). In his search for parasitoids for control of tsetse, Markham (1982, 1986) carried out an extensive collection of tsetse puparia from Zimbabwe, Zambia and Malawi, and obtained information on the seasonal occurrence, distribution, mating, oviposition and feeding habits of E. lugens, E. transiens and E. alliopterus. The puparia he collected

from Zimbabwe failed to yield any mutillid parasites though pupal cases from Malawi showed 18% mutillid parasitism. He also recorded that the mutillid, Chrestomutilla ?glossinae develop from Sarcophaga argyrostoma and G. morsitans pupae in 45-50 days.

In Uganda, Kangwagye (1971) found puparia of G. pallidipes to be parasitised by Trichopria capensis robustior Silv. (Hymenoptera :Diapriidae). Among the Hymenopterans, Syntomosphyrum (Eulophidae) and Mutilla (Mutillidae) species are the most important (Nash 1947). In Zimbabwe, Chorley (1929) observed that Mutilla glossinae Turner were rare in cold dry seasons, forming only 0.5% of total emergences of tsetse and parasites. However, in the hot dry season the weekly rates were often over 20%, but dropped to 6-12% at the start of the rains. Heaversedge (1969b) confirmed that peak parasitization by M. glossinae is associated with hot dry weather. M. glossinae and M. auxilliaris Turner have been found to be important parasites of G. morsitans and G. pallidipes respectively in Zambia, Malawi and Zimbabwe (Heaversedge, 1969a, b; Nash 1970). Rates of parasitization ranged from 0 to 10% (Lamborn, 1925).

Syntomosphyrum albiclavus Waterston and S. glossinae Wtstn were first reported in puparia of G. fuscipes by Waterston, and their distributions were reported by Saunders (1960, 1961), Potts (1970b) and Baldry (1979). S. glossinae is found in Kenya, Uganda, Tanzania, Malawi, Senegal, Liberia, Nigeria and Zimbabwe from G. palpalis, G. fuscipes, G.m. orientalis, G.m. submorsitans and G. pallidipes. The natural incidence in G. morsitans in Malawi is 0.22% to 6.8% (Lamborn, 1925). Both species have been found abundant in nature, but S. glossinae has received considerable attention since Lamborn reported favourably on its short life cycle, great fecundity, longevity and ease with which it could be bred in pupae of Glossina, Sarcophaga and Musca species. However,

attempts to control G. morsitans by releasing this parasite on a peninsula of Lake Malawi resulted in 6.8% infestation in the first month, but eight months later the percentage parasitism dropped to an ineffective 0.2% (Lamborn, 1925). At present no one has related percentage parasitism due to these parasitoids to pupal densities.

2.2.3 PREDATORS OF TSETSE PUPARIA

Many vertebrate and invertebrate predators have been reported or suspected of preying on tsetse because they are observed burrowing, feeding, scratching or wandering in tsetse breeding areas (Swynnerton 1936; Nash, 1970; Laird, 1977; Challier, 1982). In Uganda, Fiske (1920) made reference to adult and larvae of Coleopteran families of Carabidae, Elateridae and Cicindelidae preying upon and destroying greater numbers (7% of 9000) of puparia of G. palpalis. Larvae of Merylis palliventris (Coleoptera: Merylidae) were also observed devouring tsetse puparia (Nash, 1939, 1970). In Tanzania, Ford (1940) observed ants of the genus Pheidole (Hymenoptera : Formicidae) carrying pupae of G. swynnertoni into their nests and considered them efficient predators of puparia. Predation experiments carried out on puparia of G. f. fuscipes Newstead in South Busoga Forest in Uganda showed that most puparial mortality was mainly caused by Pheidole (Rogers, 1974). Larvae of G. palpalis and G. morsitans are devoured by the ant species, Euponera senaarensis and Paltothyreus tarsalis (Carpenter, 1912).

Large crickets found in larviposition sites of G. palpalis gambiensis Vanderplank in Burkina Faso by Challier (1982) were considered occasional predators of puparia.

Guinea fowls (Numida spp.), bush fowls (Francolinus spp.), Dicrunus and Bradornis species of birds are often found wandering and scratching

the soil in tsetse breeding areas for food and hence are suspected of uncovering and swallowing significant numbers of puparia.

Swynnerton (1936) observed traces of scraping, foot prints and excreta of mongoose and African elephant shrews, Petrodromys tetradactylus in larviposition sites of G. morsitans and G. austeni. He thus concluded that these mammals may destroy important quantities of puparia and other shallowly-buried insects.

2.2.4 PREDATORS OF ADULT TSETSE

Various insects and spiders are suspected of predating on adult tsetse. Members of Coleoptera, Diptera, Hymenoptera, Orthoptera and Odonata are believed to play a predatory role in tsetse population regulation. Several species of dragonflies, Cacergates spp., Orthetrum chrysostigma and O. branchiale have been identified as enemies of G. palpalis and G. morsitans (Carpenter, 1913; Campion, 1921; Southon, 1959b). These dragonflies, hunting wasps (Bembex spp.) and robberflies (Diptera : Asilidae) are recorded catching tsetse either in the air or when about to alight on vegetation. Simpson (1918) described Bembex species as voracious enemies of G. morsitans. This observation was confirmed by Fiske (1920) and Nash (1970). In Zaire, G. palpalis was found in nests of Sphex, Synargris and Bembex species (Bouvier, 1936). Ford (1940) recorded the capture of G. tachinoides by a hymenopteran Sphecidae, Oxylelus lamellatus.

There are numerous reports of captures of Glossina adults by spiders. Simpson (1918) observed that jumping spiders of the family Attidae, Plexippus paykulli catch large numbers of G. palpalis in the Gambia, while ignoring other flies. The predatory role of Nephilid and Hersiliid spiders was demonstrated by Fiske (1920) on some islands of Lake

Victoria. This was confirmed by Glasgow (1963) who recorded that invasion of Sumba Island by Nephilia spiders led to the disappearance of G. palpalis. Southon (1959a) studied the effect of Hersilia setifrons Lawrence (Araneae : Hersiliidae) on G. swynnertoni and suggested that daily mortality due to this spider might be about 650 adults per square mile. In Kenya, Minter (1971) reported that resting and moribund G. pallidipes caught in webs at higher levels and those on the ground are eaten by scorpions and spiders. Spiders of Theriidae and Clubionidae are reported catching G. palpalis gambiensis at night (Challier, 1973). Gruvel (1975b) observed that concentration of Hersiliid spiders on Morelia senegalensis trees coincided with G. tachinoides concentration in the woodland during the hot and cold seasons, and ascribed part of the mortality to the numerical response of the spider population to the high tsetse density.

Robberflies (Diptera:Asilidae) are also suspected of preying on tsetse adults. However, studies in forest galleries of Lower Chari River, Chad showed that G. tachinoides are not captured by asilids living in the same habitat. Here the asilids are most often observed to prey on Hemiptera, small Orthoptera or Coleoptera (Gruvel, 1974b). Nevertheless, under similar ecological conditions in Nigeria, asilids were observed capturing Glossina. Similar observation has been made in Ethiopia by Tikubet (1984). Out of 330 asilids caught in Eastern Africa, 15% of their prey were found to be made up of G. swynnertoni (Southon, 1959a).

Since Simpson (1918) was unable to identify remains of tsetse in his dissections of amphibians and lizards little is known of the influence of these creatures on tsetse. However, the disappearance of large numbers of adult flies introduced into large experimental cages in natural habitat of G. tachinoides is attributed to predation by lizards (Gruvel, 1975b).

Swynnerton (1936) reported having observed tsetse fragments in crops of Dicrunus and Bradornis species of birds which were seen feeding on Glossina resting on branches and bark of trees. Simpson (1918) examined the meals in crops and contents of stomachs of 379 birds and found no traces of Glossina remains.

Some mammals are also suspected of actively catching both resting and flying tsetse flies. Gruvel (1975b) suspects that bats moving in the semi-darkness of forest use tsetse as part of their food source. It is asserted that baboons (Papio spp.) and monkeys, shrews, small rodents and mongoose can catch tsetse which land on their bodies, because they are quick in their reactions to biting insects (Lloyd, 1914). Like bats, however, they are yet to be confirmed as tsetse predators. The only large mammal, other than man, which has eradicated tsetse by discriminative bush clearing is the elephant. Ford (1969) reported that the debarking of hundreds of square miles of Terminalia woodlands in Murchinson Falls National Park in Uganda by elephants resulted in the disappearance of G. morsitans.

2.3 LEVEL AND MODE OF MORTALITY FROM PREDATORS

The lack of critical experiments to investigate biotic mortalities, coupled with general reluctance to believe in them, led to the view that climate both controlled and regulated population size. However, tsetse population resurgence to changes brought about by insecticides (Tarimo et al., 1970; Rogers et al., 1984; Turner, 1984; Turner and Brightwell, 1986) indicates interference with some density related process. The few experiments previously carried out to assess the level and mode of mortality from predators will now be described. In Kakoma, Tanzania, Jackson (1937) replaced puparia collected in spots in breeding places and left them in

the field over a period. Out of the 180 puparia buried, 49 were lost or taken by predators, but all the others emerged so there was no mortality due to disease or failure to develop or emerge. He, however, dissected another group of puparia as they were found and noted high natural mortality. Ford (1940) attempted a quantitative estimation of predation of ants upon G. swynnertoni puparia in Tanzania by comparing the decrease in numbers of puparia that were artificially distributed, according to a definite plan, in a natural forest and savannah habitats. He found the estimated predation rates to be 11-18% in the forest habitat and 25-44% in the savannah habitat, and observed members of the genus Pheidole carrying puparia into their nests and considered them very efficient puparia predators. Ford's experiments were repeated by Kemp (1951) who buried some tsetse puparia individually at marked spots and dug for them 14 days later. The results showed that the intensity of predation by Pheidole ants was high in the absence of other sources of food.

Using similar field experimentation, Rogers (1975) quantified puparial losses from predation experiments on puparia of G. fuscipes fuscipes Newstead in South Busoga Forest in Uganda. He showed that most pupal mortality was caused by the same ant species, which took a constant number of puparia at lower densities of tsetse, but an increasing percentage at higher densities indicating a density dependent process.

Southon (1959a) estimated the predation of Hersilia setifrons Lawrence on adult G. swynnertoni by counting the number of silken envelopes containing prey which the spider makes and attaches to tree trunks. He dissected the envelopes and found that the tsetse species constituted up to 3% of the prey of the spider. He could not determine the density relationship between spider numbers and predation levels because he did not estimate the density of the spiders. The predatory

role of nersiliid spiders on resting G. tachinoides was also studied in the forest galleries of Lower Chari River, Chad and the nigh concentrations of spiders on tree trunks during the not seasons were found to correspond to periods of aggregations of resting tsetse (Gruvel, 1974b). This spatial and temporal coincidence ensured efficient predation and it was thought that the spiders exerted a decided limiting effect on the tsetse population, though Glossina was not the only prey of these spiders.

Predation on tethered adult G. fuscipes fuscipes by unidentified birds were found to be strongly density dependent (Rogers, 1974), while that by invertebrates was not dependent on density of the flies.

Little is known about the density relationship between predator density and functional responses of the predators to changes in tsetse numbers due to difficulty in witnessing actual contact between Glossina and their natural enemies. Furthermore, there is no evidence to show any specificity of action of any of the predators upon tsetse. There is therefore a great need for quantitative evaluation of specific action of the reported natural enemies in order to firstly, understand natural regulatory processes, and secondly, to identify those that can be manipulated or possibly incorporated into an ecologically safe and rational strategy for the control of tsetse in tropical Africa.

CHAPTER THREE

3. STUDY LOCATION

3.1 REASONS FOR CHOICE OF STUDY AREA

The Nguruman area, which is located in the Kajiado District of the Rift Valley Province in southwestern Kenya, was chosen as the study area because it is a very fertile semi-arid area with potential for livestock and agricultural development. The area supports an indigenous Maasai population with their cattle, goats, donkeys and sheep. In addition, there are a few irrigated farm schemes producing fruits and vegetables, and small rural industries producing charcoal. The area is rich in game animals, a resource which when developed will boost the tourist industry in Kenya. In spite of such potential, the presence of large numbers of Glossina pallidipes, G. longipennis and other biting insects has rendered the greater part of the area inhospitable for high grade cattle ranching, and hence the potential of the area has not been realised.

Another reason for selecting the area for study is that the tsetse population there has never been exposed to insecticide application and thus provides an undisturbed and isolated tsetse ecosystem.

3.2 GEOGRAPHY AND GEOMORPHOLOGY

The study area (Fig. 2), which lies within latitude $1^{o}48'N$ and longitude $35^{o}66'E$ and 720m above sea level, is part of the alluvial plains of the Rift Valley of East Africa. The dense forested area extends 35 km north to south and 10 km east to west, with a total area of 330 km^2 (Sayad and Sayad, 1980). It lies between Ewaso-Ngiro River ("Mighty water" in Maasai language) to the east, the Nguruman escarpment to the

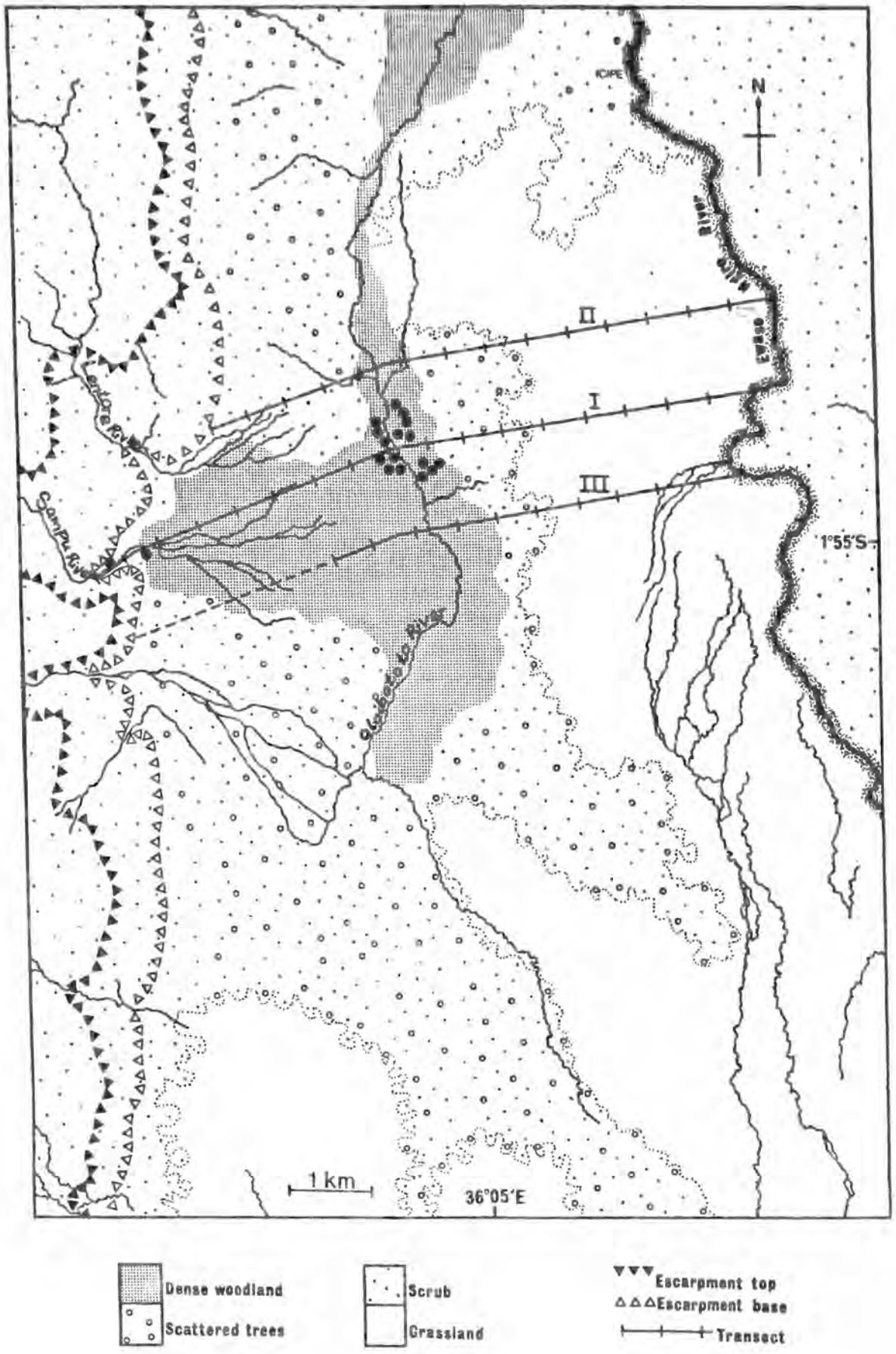

Fig. 2 - Map of study area at Nguruman showing main vegetation types, sampling transects I - III with biconical trap positions (-+--+-) and pupal sampling sites (●) marked. (Redrawn from survey of Kenya map 1974).

west, Mt. Shompole to the south and Olkeriamatian plains to the north.

All the field observations, sampling and experiments were carried out in the riverine thickets and the deciduous/evergreen woodlands near the Sampu and Oloibototo rivers which lie within the area extending from the Ewaso-Ngiro River to the Nguruman Escarpment (Fig. 2). The altitude ranges from 700m at the level of Magadi to 2800m at the crest of the escarpment. The soil is volcanic in nature and is made of red-brown, friable clay and grey loamy sands overlying a rugged terrain.

3.3 CLIMATE

The general climate at Nguruman may be divided into two wet and two dry seasons characterised as short rainy, hot dry, long rainy and long cold dry seasons. The short rainy season occurs during October to December with grasses generally resuming growth and providing good short-lived pasture for the cattle in December.

The hot dry season generally starts in January and is characterised by extreme heat and increasing temperatures towards the end of March. The grasses dry up and ground vegetation becomes sparse before the onset of the long rains which start between February and March and lasts until May.

The long and cold dry season occurs between June and September, and is characterised by clear skies. The ground flora is tinder dry from mid-July and the deciduous vegetation becomes leafless.

The meteorological records for Nguruman taken over the study period from October 1984 to August 1986 are plotted in Fig. 3 and summarised in Appendix 1. The mean monthly maximum and minimum temperatures varied between 32-41^{o}C and 18-22^{o}C respectively. The mean monthly minimum relative humidity ranged from 29% in January 1984 to 43% in April - May 1985. The mean maximum saturation deficit was 49.5 mb. and the minimum

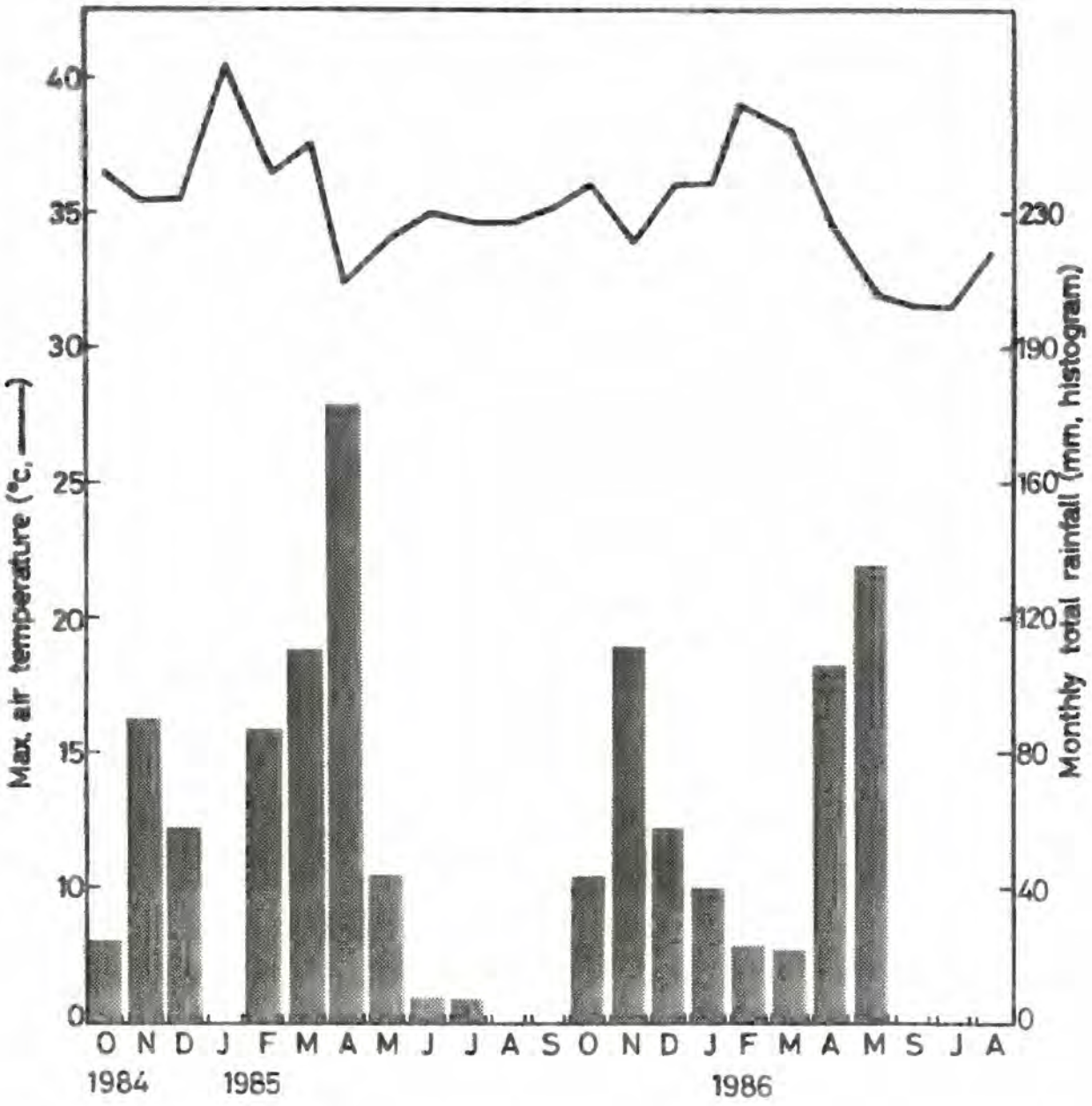

Fig. 3 - Mean monthly maximum temperature and rainfall at Nguruman during the study period.

was 27.5mb. The annual rainfall followed a typical bimodal seasonal pattern with maximum precipitation in April-May, and mean annual rainfall of about 500-700mm. Both 1983 and 1984 were abnormally dry years due to the long drought.

3.4 DRAINAGE

The area is drained by the permanent Ewaso-Ngiro River and the semi-permanent Oloibototo, Sampu and Lentore River systems. The Ewaso-Ngiro River drains the area between the Sampu Hills and the Nguruman Escarpment. The river courses in the escarpment are often marked by water-falls which carry storm torrents after heavy rains into the valley and the plains with impervious soils, thus resulting in extensive flooding during the long rainy season.

3.5 VEGETATION

The vegetation of the area is described in detail by Sayad and Sayad (1980) and Van Etten (1981). Five fairly distinct types of vegetation communities are encountered from the Ewaso-Ngiro River to the escarpment. They are :-

(a) Open floodplains which occur adjacent to riverine vegetation bordering the river. It is in a poorly drained clay soil subjected to seasonal flooding and is characterised by isolated stands of Acacia seyel fistula and A. sieberiana in grassland. The plain is quite bare in the dry season except for scattered acacia and trees of special types, but covered with a vegetation of scrub and tall grasses in the rainy season;

(b) Acacia woodland is a savanna woodland community dominated by fairly dense stands of Acacia species notably Acacia albida, A. seyel

fistula and Acacia tortillis;

(c) Riverine thicketed low-land woodland is found besides rivers and streams which form a belt between the Sampu plains and the drier deciduous woodland. The thickets have a mosaic of vegetation types dominated by tall trees such as Eupnorbia candelabrum which often attain a height of more than 10m, Acacia pennata, and Cassine aethiopica with undergrowths of shrubs comprising of Sautia myrtina and Scolopia and Aloe spp., lianes and thorny bushes;

(d) The wooded bushland consists of acacias and rather scattered trees of many types growing in grasses which are tall in the rainy seasons and short in the dry seasons. During severe dry seasons the cattle enter this area in order to get grass; and

(e) The dense valley woodland have a mosaic of vegetation type dominated by tall trees and shrubs. Dominant tree in the area is Ficus capensis; the dominant shrubs are Salvadora persica and Cordia sinensis; while the dominant grasses are Sporobilis consimulis, Setaria spacelata, Themeda triandra and Cynodon dactyolon.

Out of the five distinct vegetation types encountered, the thicket and the mixed dense woodlands are heavily infested with the two species of tsetse responsible for transmission of animal trypanosomiasis in the area.

3.6 MACROVERTEBRATES

Wild animals and Maasai cattle are abundant and there is no shortage of potential tsetse hosts throughout the area. Plains game include impala (Aepyceros melampus Lichtenstein), eland (Taurotragus oryx (Pallas)), Grant's gazelle (Gazella granti Brooke), spotted hyaena (Crocuta crocuta Erxleben) wildebeest (Connochaetes sp.), hartebeest

(Alcelaphus buselaphus Thomas), warthog (Phacochoerus aethiopicus), zebra (Equus zebra L.), and striped hyaena (Hyaena hyaena (L)). These are largely restricted to the grassland of the Sampu plains and the grassland -woodland interfaces. The bush-dwelling game, including buffaloes (Syncerus caffers Sparrman), bushbuck (Tragelaphus scriptus Pallas), monkeys (Cercopithecus sp. and Colobus sp.), baboons (Papio anubis), lions (Panthera leo (L)) etc., are found in the thicketed areas and woodland. Giraffe (Giraffa camelopardalis (L)), dikdik (Madoqua (Rhynchotragus) guentheri Thomas), side-striped jackal (Canis adustus Sundevall) and black -backed jackal (Canis mesomelas, Schreber), are usually found in the acacia woodland. Buffaloes, zebras, impalas, warthogs, baboons, giraffe and Grant's gazelle appeared to be particularly numerous.

Several species of birds like ostriches (Struthio camelus), Kori bustards (Ardeotis kori), Francolins (Francolinus spp.), Guinea-fowls (Numida spp.), etc. are also abundant in the acacia woodland and the open plains.

3.7 HUMAN AND DOMESTIC ANIMAL POPULATION

The area is sparsely populated and divided into group ranches. Like most of the Rift Valley Province in Kenya, the area is populated by peoples of the Maasai tribal group who are Nilotic pastoralists. The indigenous Maasai live in small dispersed family settlements called manyattas located in the plains along the Ewaso-Ngiro River. Other tribes found mostly in the irrigation scheme area include Luhya, Kikuyu, Kamba and a group of Tanzanian origin.

Livestock throughout the area include zebu cattle, sheep, donkeys and goats. The cattle are seldom slaughtered for meat because they are kept for milk and as convertible assets used mainly for 'purchase' of

brides. Goats provide the major source of meat for general consumption.

3.8 TSETSE AND TRYPANOSOMA SPECIES IN THE AREA

The two species of tsetse flies which occur in the area are G. pallidipes Austen and G. longipennis Corti.

The trypanosome species transmitted by the tsetse flies are T. vivax Ziemann and T. congolense Broden. A few instances of occurence of T. brucei brucei have been recorded (Golder and Tarimo, pers. comm.) but there is no human sleeping sickness in the area. Livestock losses from nagana coupled with drought seriously affect the local economy. Unlike other tsetse-infested areas in Kenya, no control measures have been carried out in the area to control or eliminate the tsetse flies. However, the disease is contained by trypanocidal drugs, notably Novidium and Berenil.

CHAPTER FOUR

4. CHARACTERISTICS OF LARVIPOSITION SITES OF GLOSSINA PALLIDIPES AT NGURUMAN.

4.1 INTRODUCTION

Regardless of whether the species appears to be habitat generalist or specialist, the choice of a breeding site may be based on well defined and specific cues (Klopfer and Hailman, 1965). The problem then is to identify the environmental criteria that induce the pregnant females to larviposit at some sites and not others in the same vicinity. Thus one of the objectives of this part of the study was to define the characteristics and seasonal distribution of larviposition sites of G. pallidipes in an attempt to identify factors influencing site selection in this species.

Evidence employed to determine the cues used by this species in choosing larviposition sites was based on quantitative data on the environmental characteristics of sites where puparia were found. Other ecological aspects investigated included :-

(a) effect of additional artificial shading on puparia abundance;

(b) vertical and horizontal distributions of the puparia in the larviposition sites; and

(c) variations in puparia depths in three simulated ground cover situations in the laboratory.

4.2 MATERIALS AND METHODS

4.2.1 PUPARIA SAMPLING

It is of critical importance to devise methods of estimating the population of the insect stage being studied. Since the principal objective of the present study is on the fluctuations in puparia numbers rather than on development of a trapping technique, the existing methods for sampling puparia were considered and one selected for the routine monitoring of the puparia population at Nguruman, Kenya.

The three methods which can be used in sampling Glossina puparia are flotation (Abedi and Miller, 1963), sieving (Phelps et al., 1966) and hand-searching (Glasgow and Phelps, 1970). The flotation method could not be used because of the risk of damaging the puparia. The sieving method, on the other hand, is time-consuming and was found to be ineffective because of the nature of soil at Nguruman. Phelps (1968) has shown that the sieving method is only effective in areas with very fine soils as in animal burrows, a condition not found in 'productive' larviposition sites in the study area. Moreover, it has been shown that more puparia can be found by hand-searching than by sieving for the same period of time. The monthly puparia sampling was done using hand-searching of soils for 2-man hours per site per month.

For the initial selection of larviposition sites, the author, one technician and two Maasai field assistants went through the different vegetation habitats along the three transects passing through the study area, and stopped at regular intervals to examine probable sites for puparia by searching the soil for 20 minutes. All empty and live puparia found at each site were collected and counted. Presence of only empty puparia was used as indicator of former breeding sites, while live puparia

signified sites being used at the time of the survey. Sites for regular monitoring of the population were then randomly selected based on availability of both empty and live puparia.

The searching efficiency of pupae collectors was evaluated. The insides of empty puparial cases were carefully marked with bright orange paint and the cases were buried at different natural depths (1 to 5cm) in plots measuring 2 x 1 meters in natural breeding sites. The numbers of puparia buried were not disclosed to the searchers who searched three different plots in different sites for 30 minutes per plot, two plots were searched on the same day and the third plot was searched the following day. At the end of the searching period, the numbers of marked cases recovered by each searcher were scored and the searching efficiency of each searcher, expressed as percent recovery of marked puparia, was determined.

4.2.2 MEASUREMENT OF CHARACTERISTICS OF LARVIPOSITION SITES OF *G. PALLIDIPES* AT NGURUMAN.

During the course of the field work on puparia distribution and abundance, data was also collected on the features of the larviposition sites in an attempt to define specific characteristics which probably influence their site selection. The measurements were taken at forty seven different sites in three different vegetations types, namely open plains, riverine thicket and valley woodland. Aspects investigated included location of the sites in relation to water courses and game paths; topography; soil colour; soil types; degree of shading; size of the sites; leaf litter depth in relation to season and amount of ground herbaceous vegetation cover. Topography was based on the local slope or inclination of the site and the land around it, and whether or not the rising

or setting sun fell on the larviposition area. The appearance of the surface of the soil; the presence and amount of herbs and grass stands present and the area of the site covered by such vegetation types were noted. Leaf debris depths were measured in centimeters. The depth was taken as the distance from the surface of the litter to the surface of the underlying soil.

For logistics reasons, only six sites were selected for studying the distribution of relative amounts of different particle sizes, the soil pH and soil moisture. Three of the sites corresponded to spots where puparia densities were high and the remaining three had low densities of puparia. Soil samples were analysed for colour by comparing the colours of the dried samples. They were then divided into different types, based on the relative amounts and size distribution of sand, loam and clay particles, as determined by their capacity to pass through a set of 20cm diameter sieves of mesh sizes of 250 um; 50 um; 1.0mm and 2.0mm. About 400gm of oven-dried soil samples per replicate were sieved for 10 minutes. Soil moisture was measured of soils collected at a depth of 2-4 cm. Three soil samples from six sites were collected every month in tied polythene bags and weighed in the field, and then dried to constant weight in the laboratory. The moisture content was then determined by difference in weights before and after complete drying, and expressed as percentage of water content by weight. Soil pH was determined using a standard pH meter.

4.2.3. SIZE OF LARVIPOSITION SITES

The boundaries of a site were determined by the extent of deep shading, and marked with rocks. The size of the site (assuming an elliptical shape) was then determined using the following formula:-

$$S = 1/2\ L \times 1/2\ B \times Pi$$

where, L is the length, B is the breadth and Pi is a constant with the value of 3.14.

4.2.4 DETERMINING THE EFFECT OF ADDITIONAL ARTIFICIAL SHADING ON PUPARIA ABUNDANCE.

To determine the effect of additional shading on puparia abundance and on the concentrating of puparia in confined area, the relative puparia densities from under two artificial shelters were compared with those found in two natural unsheltered sites. Puparia numbers were transformed to log. (N + 1) and two-way analysis of variance (ANOVA) carried out.

The artificial shelters consisted of sloping thatched roofs constructed over an area of approximately 2 x 1 meters. The roofs were put at an angle of 45^{o} to the ground to prevent flies from flying through, and to encourage them to rest on the underside of the roof. Such shelters provided very deep shade considered to increase the suitability of the sites for larviposition. They were, therefore, expected to attract and induce gravid females to concentrate puparia under the roofs. The unsheltered sites were of the same dimensions but had no thatched roofs. The study sites were located in recognised natural larviposition sites.

4.2.5 FIELD STUDIES ON SPATIAL DISTRIBUTION OF PUPARIA WITHIN THE SOIL IN LARVIPOSITION SITES

Little attention has been given to the spatial distribution of puparia within larviposition sites. Yet this is an important element of pupal ecology which could throw light on the resting sites of larviposi-

ting females.

The horizontal distribution of G. pallidipes puparia within the natural larviposition sites was determined. The shading regime in the site was noted and the leaf debris was methodically scraped and the soil searched to expose puparia. 30cm long white-painted wooden sticks were pushed into the spots where puparia were found. When the whole area had been searched, a number of photographs were taken across the site to show the relationships of one puparium to another. Distances between nearest puparia neighbours were then measured within the twelve study sites in the riverine thicket using a 100m measuring tape.

The vertical distribution of puparia in the soil was determined by the measurement of depths at which puparia were found in the soil in natural larviposition sites in different seasons.

4.2.6 LABORATORY STUDIES ON DEPTH PREFERENCE OF PUPARIA IN THE SOIL

The preliminary experiments were conducted in relatively damp soil covered with leaf debris. The depth preference of puparia was then studied under six simulated situations commonly found in the field: wet or dry, light or shade and with or without leaf debris. The floors of perspex cages measuring 20.5 x 15 x 15cm were covered with 7 cm depth of loam soil obtained from natural breeding sites at Nguruman. These cages were used as receptors of puparia extruded by adult female G. pallidipes. The soil-containing cages were divided into two groups. One group had no leaf debris on top of the soil, while the other group had 2 cm deep leaf debris also collected from the natural sites. A pair of cages, one with leaf debris and the other without debris, were kept moist by regularly sprinkling with water (Plate 2a). A pair of cages with dry soils, one with leaf debris and the other without debris, were also kept under 12L:

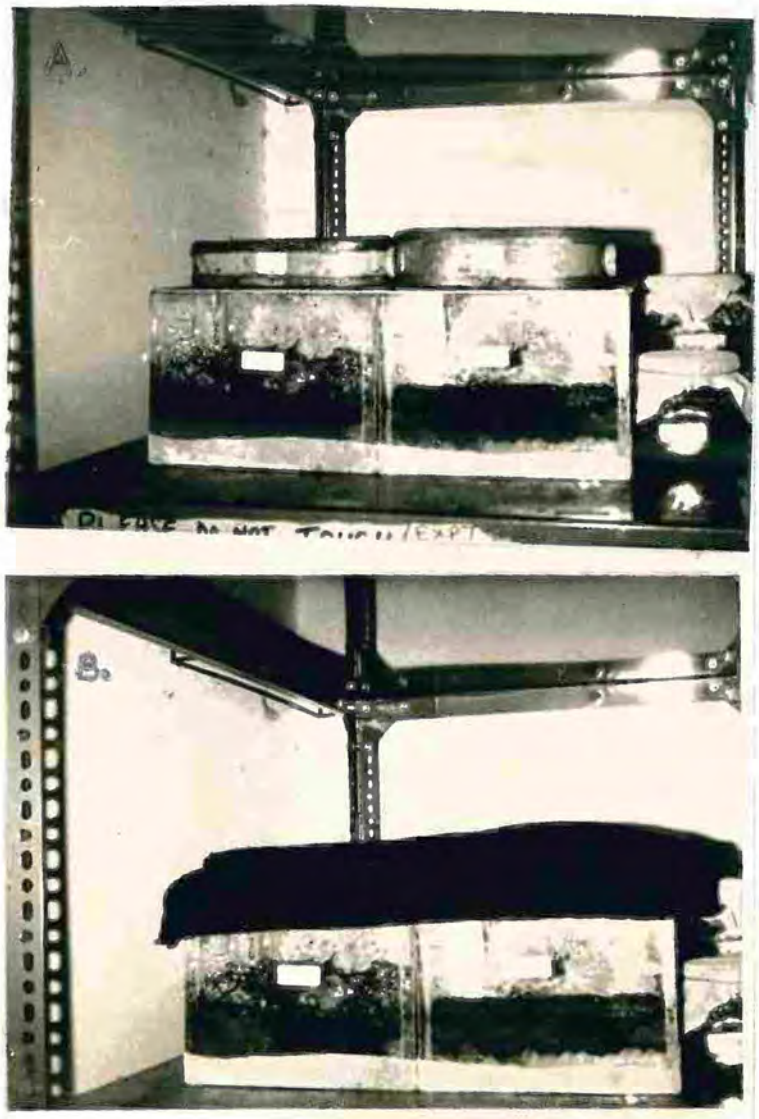

Plate 2 - Laboratory set up for studying depth preference of puparia in the soil.

12D photoperiod. Another pair of cages with dry soil, one with debris and the other one without debris, were kept under a black cloth throughout the duration of the experiment (Plate 2b). The black cloth provided additional shading and the effect of it on puparia resting depth was determined.

The open tops of the perspex cages were covered with a metal netting rack with a mesh of size 5 mm which allowed larvae to pass through and fall into the soil below. The flies were kept in oblong PVC cages which were placed on the metal rack. Each perspex cage had two PVC cages, each containing 30 mated and fed adult females and two to five males to inseminate the females that were not previously inseminated when exposed to males in a 1:1 ratio for 48 hours. The flies were fed every other day on rabbits. The experiments were conducted in an insectary at an average temperature of 25°C (range 22 - 27°C), 60-70% RH and 12L:12D photoperiod (conditions which approximated natural conditions in larviposition sites at Nguruman.

The soils were searched weekly, layer by layer, and puparia found at different depths were scored. The depth preference of puparia in the soil was determined and differences in mean numbers were compared using Duncan's Multiple Range Test.

4.3 OBSERVATIONS AND RESULTS

4.3.1 EFFICIENCY OF PUPARIAL SAMPLING

The mean searching efficiency of pupal collectors per 2 m^2 plots ranged between 56.7 and 63.3% and averaged 60 ± 7.3% (Table 2). The efficiency was 80-100% (replicate 3) when searchers were aware that a test was being conducted, but was 50-60% (replicate 1) if they had not been informed beforehand. The first two replicates were done one after the other; there was some indication that the efficiency of the collectors decreased by 10% as they became tired (replicate 2). Based on these results, the regular monthly sampling for puparia was scheduled with resting intervals between searches so that any decline in searching efficiency due to tiredness was minimised.

Table 2 - Searching Efficiency of puparia collectors in the field.

Searcher's identity	Replicate	No. of marked puparia buried in the soil	No. of marked puparia recovered	% Recovery	Mean % Recovery
DMK	1	10	5	50	
	2	10	4	40	63.3
	3	10	10	100	
JK	1	10	6	60	
	2	10	4	40	60.0
	3	10	8	80	
JM	1	10	5	50	
	2	10	4	40	56.7
	3	10	8	80	

If the efficiency of a half hour search over an area of 2 m^2 was 60%, then the recovery rate from a two hours search over an area of 42 m^2 (mean size of larviposition site at Nguruman) will be ca 12%.

4.3.2 CHARACTERISTICS OF LARVIPOSITION SITES OF G. PALLIDIPES AT NGURUMAN, KENYA.

The larviposition sites of G. pallidipes at Nguruman (Plate 3 A-D) were found in riverine thickets and dense patches of woodland savannah, which contained evergreen and deciduous trees with the crowns united by creepers and lianes to form a dense canopy. The edges of the canopy were sometimes bounded by thorny creepers. The sites in the evergreen thickets and woodland were used throughout the year, but sites with shade provided by deciduous trees were only used seasonally. Larviposition sites of G. pallidipes at Nguruman may be divided into two categories: sites in low lying areas which are subject to seasonal flooding and sites on hilly slopes which are never flooded. The relative importance of these two classes of sites varies throughout the year. Puparia were found mainly in the low-lying areas in the riverine thickets and under rock outcrops on hilly slopes in the valley woodland. Although most flies larviposited in the riverine woodland there was some movement away from this area during the rainy season. Individual flies marked and released by Dransfield and co-workers in the riverine thickets were later found in other areas in the study location indicating how widely the flies dispersed within the area. Characteristics of the larviposition sites are summarised in Table 3.

Out of the 14 sites sampled on transect I, 92% of the sites were located on flat ground within a distance of 30m from banks of Sampu River or its tributaries, though most of them were dry for about nine months of the year. Further confirmation of sites being located close to water-

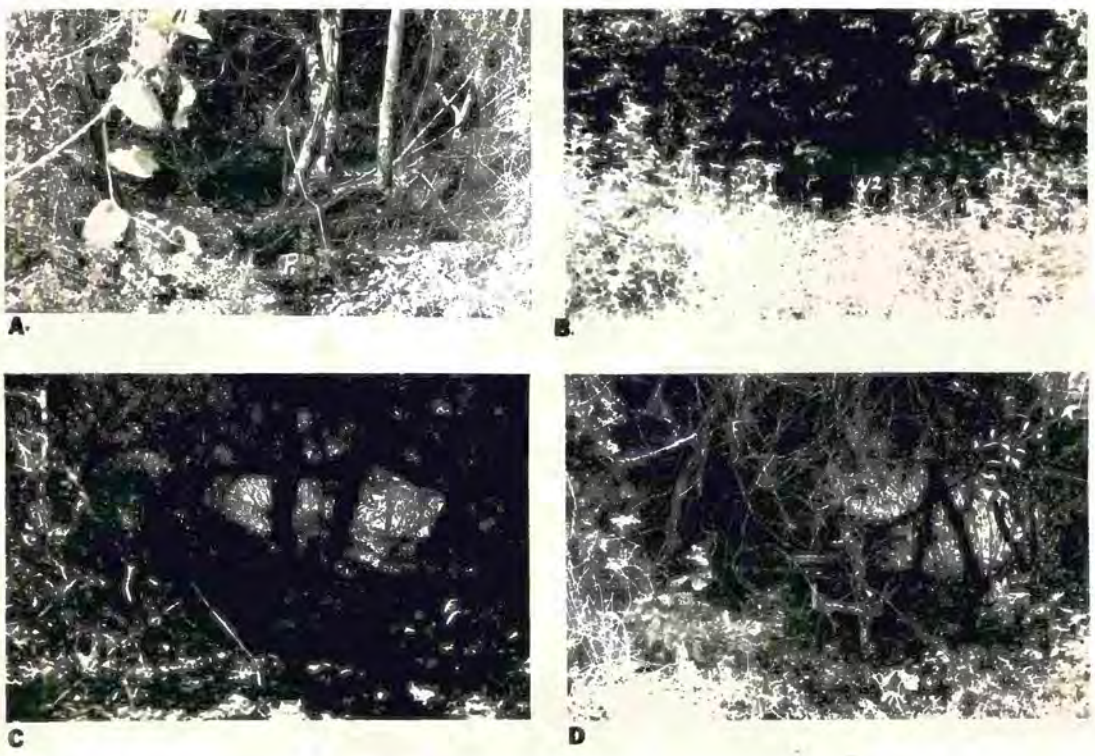

Plate 3 - Haunts of G. pallidipes at Nguruman, Kenya.

Table 3 - Characteristics of Larviposition Sites of G. pallidipes at Nguruman, Kenya.

Feature in order of importance	No. of sites recorded at	% of total
A. Topography (inclination)		
Flat surface	43	91.5
Hilly slope	4	8.5
Total	47	100.0
B. Soil Colour		
Greyish brown	28	59.6
Black	15	31.9
Grey	3	6.4
Light brown	1	2.1
Total	47	100.0
C. Soil types		
Loamy sand	30	63.8
Sandy loam	10	21.3
Loam	5	10.6
Clay	2	4.3
Total	47	100.0
D. Herbaceous Vegetation cover		
None (only leaf litter)	34	72.3
Few (less than 5% cover)	13	27.7
Total	47	100.0

courses, came from the other two transects in the study area (Fig.2). In all, 90% of the 36 sites surveyed on these transects were within 20 meters of a river or stream bed. Because of the proximity of the sites to water-courses some of the sites were flooded in the rainy seasons.

In all 43 of the 47 sites studied were found in the low-lying areas in the riverine thickets (Table 3). These sites were subjected to seasonal flooding and waterlogging. The remaining 4 sites were found in hilly slopes under overhang rocks in the valley woodland.

G. pallidipes larviposited in soils with colours ranging from black through very dark brown and greyish-brown to light brown (Table 3). However, the greyish-brown soils were the most preferred colour (59.6%), followed by black soils (31.9%) and the least preferred soils had light brown colour (2.1%).

Most soils in the breeding sites showed a predominance of sand mixed with loam and clay and were therefore described as sandy-loam, loamy-sand, loam or clay depending on the relative amounts of the different soil particles in the samples (Table 3). Though puparia of G pallidipes were found in a wide range of soil types, they occurred more frequently in loamy -sand soils (63.8%) and less in clayey soils (4.3%).

Table 4 shows the particle size distribution of soil samples from six different sites. The soil particle sizes did not vary appreciably from one good site to another suggesting the uniformity of soil types selected for larviposition by G. pallidipes.

The edaphic factors of the soil at larviposition sites are physical and chemical. The pH of soils in the sites (Table 4) varied from mildly acidic with pH 6.5 to mildly alkaline with pH 7.9 (N = 54), with a mean of 7.3 $\pm$ 0.05. The monthly mean soil moisture at the sites varied between 5.1 and 49.8% and averaged 28.6 $\pm$ 2.5% (N = 432). Soil temperature in the

Table 4 - Percent soil particle size by volume of soil samples, soil pH and % soil moisture of six larviposition sites of G. pallidipes.

Site No.	Percent soil particles of different sizes (Mean ± S.E.)					Soil pH	% Soil Moisture
	> 2.0mm	2.0mm	1.0mm	0.5um	0.25um		
1	31.9±0.6	23.7±1.1	20.4±1.1	13.7±0.5	10.4±0.7	7.5± 0.1	29.9±3.2
5	28.2±0.0	15.0±0.5	26.0±0.4	15.2±0.1	15.5±0.8	7.6± 0.1	25.8±2.5
7	27.5±3.9	30.9±2.0	21.5±2.5	11.6±0.6	8.9±1.0	7.2± 0.1	33.1±3.8
9	47.4±1.6	28.7±4.6	18.8±2.2	10.6±2.1	5.4±1.2	7.0± 0.2	33.8±2.7
10	36.4±1.1	27.0±0.9	18.6±0.9	11.8±1.0	6.2±0.2	7.3± 0.1	26.9±3.0
11	34.7±0.4	26.9±0.4	14.7±0.1	9.8±0.1	13.9±0.2	6.9± 0.1	28.0±2.9

Sites 1, 5, and 7 had high puparia densities, while sites 9, 10 and 11 had low densities.

larvipositions sites (see Appendix 2) was always 1 to 5°C lower than the ambient temperature indicating that puparia in the soil never experienced nigh temperatures known to be fatal to Glossina.

G. pallidipes larviposited under clumps of vegetation providing good snade (Plate 3 A-D), hence soils in most sites did not receive direct sun because of the dense overnead vegetation canopy. However, where there are breaks in the canopy, the soil surface received dappled sunlight. On some occasions puparia were found in the unshaded spots within the site. In all, 72.3% of the 47 sites nad no vegetation cover in the form of grass or nerbs except for the leaf debris from the overhead vegetation canopy, while 27.7% nad less than 5% nerbaceous or grass cover (Table 3).

For practical purposes, snade plants and herbaceous vegetation cover at larviposition sites can be classified into two categories: (1) the tall trees and shrubs which exceed 2 metres in height; and (2) the ground cover which is generally less than 1 metre and is composed of graminae and dicotyledonous species and dead leaf litter cover. The dominant shrubs found at the larviposition sites were Opilia amentacea Roxb. (syn. O. celtidifolia) (Opiliaceae); Boscia coriacea Pax and Capparis fascicularis DC. var. elaeagnoides (Gilg) De Wolf (Capparaceae). The nerbaceous plants found included Sida alba L., Hibiscus pariduriformis Burm. f., Wissadula rostrata (Schumach.) Hook.f (Malvaceae); Justicia caerulea Forssk., Commelina sp. (Commelinaceae) and Justicia flava Vahl. (Canthaceae). The grasses species included Echinochloa haploclada (Stapf), Setaria sagittiflora (A. Rich) Walp., Brachiaria deflexa (Schumach.) C.E. Hubb. (Gramineae).

Soils of some sites were covered with a thick carpet of dead leaves, while others nad a much thinner layer of the leaf debris. The depth of the debris varied monthly in relation to the phenology of the vegetation

forming the shade under which G. pallidipes larviposited. The depth of the litter ranged from 1.0 to 6.0 cm with a mean of 2.8 ± 0.2 cm (N = 100).

4.3.3 SIZES OF LARVIPOSITION SITES

Table 5 shows considerable variations in the sizes of larviposition sites (range 7.1 and 66.5 m^2). The mean area of site was 41.6 ± 6.2 m^2, while the mean number of puparia per site was 32.8 ± 5.1 (range 1 - 64). The question is "Is pupal number per site proportional to the size of the site?. The demographic data showed that 64 puparia were collected from site 7 which measured 12.3 m^2, while only one puparium was obtained from site 11 with an area of 60.5 m^2. Again, site 10, the largest site measuring 66.5m^2 yielded only 6 puparia in contrast to 48 puparia collected from the smallest site with an area of 7.1m^2 (site 1). There was thus no relationship between size of site and the number of puparia found there ($r = 0.31$, $P > 0.05$) over the 22 months.

4.3.4 EFFECT OF ADDITIONAL SHADING ON PUPARIA ABUNDANCE

Table 6a gives data on the seasonal changes in abundance of puparia in the natural and artificially sheltered sites. The means (± S.E.) per site per month for the sheltered and unsheltered natural sites were 2.7 ± 1.9 and 0.4 ± 0.4 respectively, a ratio of 6.8 : 1. Thus the artificially sheltered sites were approximately 7x better than the natural sites. The relative efficiency of sheltered sites was greatest in January 1985 and least in October 1985. In all, 86.6% of a total of 119 puparia were collected from the sheltered sites as against 13.4% from natural sites.

The differences in puparia densities between the two shading regimes

Table 5 - Distribution and abundance of puparia of G. pallidipes in relation to size of larviposition sites at Nguruman, Kenya.

Site Number	Area of site (m2)	Total No. of puparia collected (Oct. 1984 to April 1986)
1	7.1	47
2	36.5	24
3	62.7	48
4	60.5	46
5	21.5	29
6	61.7	41
7	12.3	64
8	33.7	32
9	26.3	25
10	66.5	6
11	60.5	1
12	50.2	30

Table 6a - Distribution and abundance of puparia of G. pallidipes in natural unsheltered (without additional shade) and in sheltered sites (with additional shade provided by thatched roof).

Year	Month	Number of puparia collected			
		Natural sites		Artificial shelters	
		E	L	E	L
1984	November	32	3	103	12
	December	16	1	4	1
1985	January	8	5	15	28
	February	10	5	45	15
	March	10	0	40	9
	April	14	1	Areas flooded	
	May	0	0	0	0
	June	15	0	1	0
	July	4	0	1	0
	August	0	0	21	4
	September	0	0	51	5
	October	0	0	5	1
	November	0	1	20	1
	December	0	0	10	0
1986	January	1	0	0	0
	February	0	0	30	0
	March	0	0	52	4
	April	1	0	8	0
	May	0	0	Areas flooded	
	June	Areas waterlogged		0	0
	July	1	0	42	1
	August	0	0	0	0
	Total	112	16	448	81

E = Empty puparial cases L = live puparia.

was found to be statistically significant ($F = 9.36$, $P < 0.001$). The differences between months were also significant ($F = 2.42$, $P < 0.05$, see Table 6b). The interaction between treament and month was also significant ($F = 2.35$, $P < 0.05$), indicating that the relative attractiveness of the artificial shelters varied significantly from month to month. Thus, many more puparia were found in the artificial shelters during the dry seasons (October-November 1984 and January-Feburary 1985) than in the unsheltered sites. During the rains however, very few puparia were found in either shaded or natural sites.

Table 6b - ANOVA TABLE - Effect of additional shading of sites on larviposition by G. pallidipes at Nguruman, Kenya. (October, 1984 - March, 1986).

Source of Variation	SS	df	MS	F ratio
Factor A (shading)	79.54	1	79.54	9.36***
Factor B (month)	384.93	17	20.53	2.42*
A x B interaction	339.62	17	19.98	2.35*
Residual	204.09	24	8.50	
Total	972.18	59		

*** $P < 0.001$ * $P < 0.05$.

4.3.5 SPATIAL DISTRIBUTION OF PUPARIA IN LARVIPOSITION SITES

a) Horizontal distribution of puparia within larviposition sites.

Plate 4 shows the spatial distribution of puparia as indicated by white wooden pegs in one site in March 1985. The puparia in all sites showed a marked tendency to be aggregated in shade underneath big horizontal branches. This is supported by results with the artificial

Plate 4 - Horizontal distribution of puparia within a larviposition site at Nguruman, Kenya.

shelters.

The distances (in metres) measured between 87 nearest live puparia neighbours in different larviposition sites (Table 7) ranged from 0.07 to 8.3m, with a mean of 0.8 ± 0.1m. There was no relationship between these distances and size of sites.

b) Vertical distribution of puparia in the soil.

Field and laboratory observations on depth at which puparia occur in the soil are given in Table 8. In the field (Fig. 4a), puparia were found to a depth of 5cm or more from the surface of the soil (excluding the depth of the litter), but the majority were found between 1 and 3 cm with a mean depth (X ± S.E) of 2.3 ± 0.1cm (N = 131). The mean depth for 40 puparia found in the wet season was 2.49 ± 0.1cm, while that for 71 puparia in the dry season was 2.45 ± 0.3cm.

In the preliminary laboratory experiments (Table 8), the majority of the puparia were at depths of between 0 and 2 cm with a mean of 1.8 ± 0.1 cm (N = 267), though the distribution stretched to 5cm (Fig. 4b). It appeared that certain unnatural experimental conditions affected the burrowing behaviour and hence the puparial depths. For instance, the use of relatively moist soils resulted in most puparia being near the surface of the soil. Further experiments were therefore carried out in the laboratory.

4.3.6 LABORATORY STUDIES ON DEPTH PREFERENCE OF PUPARIA.

Fig. 5 and Table 9 give the results of varying conditions of light, leaf litter cover and soil moisture on pupal depths and a summary of ANOVA. In general, puparia depths were shallower in wet soils than in dry soils, depths shallower in soil with debris than in soils without debris. Analysis of variance (Table 9) showed that the treatments effect

Table 7 - Distances in meters between nearest puparia of G. pallidipes in different larviposition sites at Nguruman, Kenya.

Site No.	area of site (m^2)	Number of pairs measured	Distances (m) between nearest puparia. Range	Mean (± S.E.)
1	7.1	6	0.12 - 0.90	0.43 ± 0.1
2	36.5	10	0.07 - 2.41	0.38 ± 0.2
3	62.7	16	0.23 - 1.50	0.78 ± 0.1
4	60.5	12	0.22 - 1.84	0.81 ± 0.1
5	21.5	3	0.15 - 2.46	1.68 ± 0.8
6	61.7	6	0.27 - 2.67	1.05 ± 0.4
7	12.3	13	0.10 - 0.65	0.32 ± 0.1
8	33.7	1		2.18
9	26.3	3	0.45 - 2.00	1.34 ± 0.5
10	66.5	4	0.16 - 1.10	0.57 ± 0.2
11	60.5	1		1.00
12	50.2	12	0.10 - 8.26	1.48 ± 0.6

Table 8 - Vertical distribution of puparia in the soil.

Depth intervals at which puparia were found (cm)	No. of puparia found at different depths: Field observation	Laboratory observation
0.0 - 1	9	117
1.1 - 2	43	116
2.1 - 3	54	22
3.1 - 4	21	11
4.1 - 5	3	1
5.1+	1	0
Total	131	267

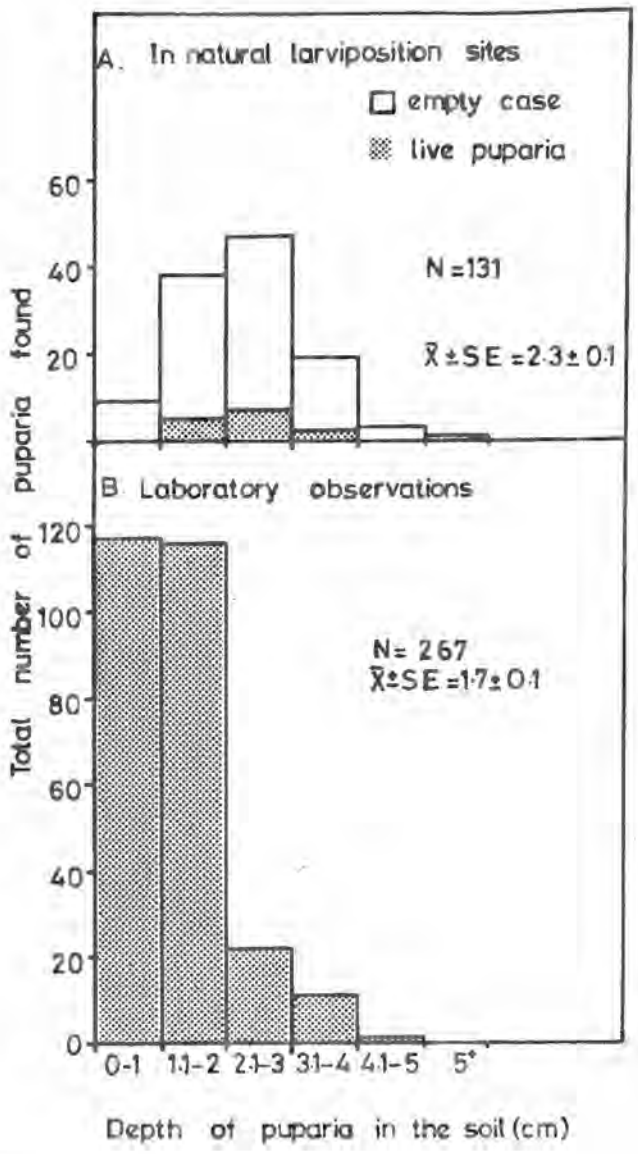

Fig. 4 - Vertical distribution of puparia of G. pallidipes in the soil in the field.

was significant ($F = 9.35$, $P < 0.001$). The mean depths in the different treatments were then compared by Duncan's Multiple Range Test (Table 10). It is clear that lack of moisture in the soil increases depth of burrowing so the puparia rested near the surface of moist soils. In the dry soil the larvae burrowed deeper probably to avoid dessication. Lack of leaf litter also increases depth of burrowing. Results of the effect of light were not clear, but in dry soil with no debris, mean depth of puparia was significantly greater in the dark than in the light. In dry soil with leaf debris puparia were found nearer the surface of the soil in darkness than in the light, although this difference was not significant.

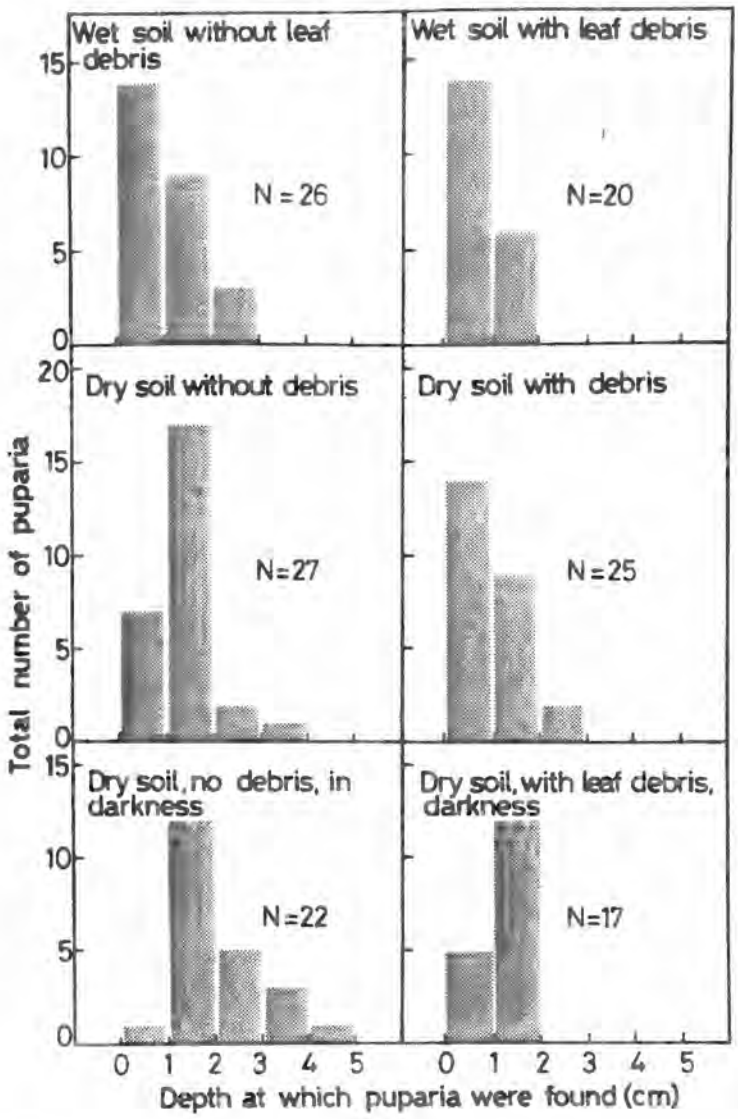

Fig. 5 - Vertical distribution of puparia of G. pallidipes in different soil conditions in the laboratory.

Table 9 - Depths occupied by puparia of G. pallidipes exposed to different soil conditions in the laboratory.

Depth of pupa (cm)	SOIL CONDITIONS (Treatments)						Total
	Wet soil with no leaf debris (T 1)	Wet soil with leaf debris (T 2)	Dry soil with no leaf debris (T 3)	Dry soil with leaf debris (T 4)	Dry soil with no leaf debris, in dark (T 5)	Dry soil with leaf debris, in dark (T 6)	
1	14	14	7	14	1	5	55
2	9	6	17	9	12	12	65
3	3	0	2	2	5	0	12
4	0	0	1	0	3	0	4
5	0	0	0	0	1	0	1
6	0	0	0	0	0	0	0
Total	26	20	27	25	22	17	137
Mean	1.58	1.30	1.89	1.52	2.59	1.71	

SUMMARY OF ANOVA TABLE

Source	D.F.	SS	MS	F ratio
Between groups	5	22.225	4.445	9.346***
Within groups	131	62.300	0.475	
Total	136	84.525		

*** $P < 0.001$

Table 10 - Mean puparial depth in different soil conditions compared by Duncan's Multiple Range Test.

Treatment	Moisture	Litter	Light	Mean depth (cm)
T 5	-	-	-	2.59 a
T 3	-	-	+	1.89 b
T 6	-	+	-	1.71 b c
T 1	+	-	+	1.58 b c
T 4	-	+	+	1.52 b c
T 2	+	+	+	1.30 c

(Means followed by same letters are not significantly different).

4.4 DISCUSSION AND CONCLUSIONS

Though one might suppose that the immobile puparia would readily lend themselves to sampling, a thorough half hour search in $2m^2$ plots of what was regarded as good breeding sites in the dry season yielded only about 60% of puparia present. Efficiency may even be lower in the rainy seasons when soil is wet, and searching is more difficult due to water-logging and adhesive nature of clayey soils. Lloyd (1935) also had difficulty in recovering puparia from wet soil. He found puparia of G. swynnertoni more difficult to locate in terms of puparia per man hour than those of G. morsitans. Since yields per site were not proportional to size, the latter could not offer a useful index for comparing relative densities of puparia from different sites, or for predicting the expected yields of sites.

Data on the field surveys suggest a marked tendency for the sites to be close to water courses where sufficient shade is available. This confirms the observation made by Swynnerton (1936) in southern Africa, who regarded thicket, game and water pools as ecological requirements for the satisfactory breeding of G. pallidipes in that region. The present study indicated that G. pallidipes preferred sites which are shady and well-protected by good overhead vegetation canopy. This finding agrees with those obtained for G. brevipalpis in Malawi (Lamborn, 1915; Swynnerton, 1936), G. fuscipes fuscipes in Uganda (Okoth, 1985), G. palpalis palpalis in Nigeria (Nash, 1948), G. palpalis gambiensis in Senegal (Toure, 1980), G. tachinoides in Cameroons (Gruvel, 1975a) and G. pallidipes in southern Africa (du Toit, 1954). Nash (1939, 1940), studying the ecology of puparia of Glossina in Northern Nigeria noted that shade removal leads to decrease in the population of G. tachinoides. There are several

advantages to have the larviposition sites situated in shady areas. Such areas afford good resting sites for wild animals on which the flies feed so that the pregnant female flies will get readily available blood meals, and thus ensure the production of healthy and viable puparia with high rate of survival. In addition, the repeated passages of the animals make the soil loose, a condition which will facilitate the burrowing of the larvae into the soil.

It has been shown that sites for larviposition at Nguruman were mostly in the riverine thickets and mixed woodland, and puparia were especially deposited in sandy-loam soils under dense vegetation. In Zimbabwe, the puparia were also found under leaf litter in thickets (Swynnerton, 1936; Du Toit, 1954). In East Africa, puparia of this species were found in the same sort of breeding sites as G. swynnertoni in the dry season, but in Mozambique, the puparia were collected from the same fallen logs from which G. morsitans were recovered (Swynnerton, 1921). Fallen logs did not appear to be used by G. pallidipes at Nguruman. Phelps et al. (1966) and Phelps and Vale (1978) observed that G. pallidipes use sand in river beds in dense thickets in the same way as G. morsitans. Though G. longipennis at most times uses sites under fallen logs in open areas (Lewis, 1942; Buxton, 1955), a few were recorded in haunts of G. pallidipes at Nguruman, indicating that their breeding requirements may overlap in some areas.

There seemed to be no selection of particular species of plants so long as they provided good permanent shade and favourable habitat microclimate. In all, only 5% of the 47 sites studied had herbaceous vegetation cover in the form of grass or herbs except for the leaf debris from the overhead vegetation canopy, indicating that shade provided by tall trees, shrubs and canopy vegetation was more important in site selection

than the herbaceous vegetation covering the soil surface. It appeared that the most important factor in the choice of larviposition site is good permanent shade which reduces the temperature experienced within the larvi-position sites and thus minimize mortality caused by high temperatures. This conclusion is supported by results from the artificial shelters which were most effective during the hottest times of the year.

However, since many shady sites were not used it appeared that other factors are also influencing choice of site. Most sites were covered with dry leaf litter, but in the rainy seasons most of the debris was washed away leaving some of the sites bare for a month or two. Such conditions may expose puparia to predation in the following dry periods.

Topographical features of the area could play an important role in the survival of the species by providing alternative sites when the primary sites were made unsuitable by catastrophic density independent factors like heavy rainfall and flooding. Soil colour may also be important. In loamy soils the colour is at least a qualitative measure of the amount of organic matter present. Its presence probably has an effect on soil porosity and moisture retention capacity. Preference for the greyish-brown or black soils may also have a survival value for the dark-brown puparia, because the puparia scraped up by predators would be less visible against a dark soil.

No puparia were found in sites with large particles or very fine clayey soils. Larvae of G. palpalis and G. swynnertoni were found to burrow more easily in coarse soils than in fine soils (Lewis, 1939), and the former took 5 minutes to burrow to a depth of 3-5 cm in riverine sand and 15 minutes to enter garden soil to a depth of 1.2 cm (Hoffman, 1954), this difference was attributed to difference in mechanical stimulations of the soils. By choosing breeding site with dry, loose loamy-sand soils,

the pregnant females ensure that their offspring develop in the best drained soils available.

In all the larviposition sites, the puparia were found mostly in shade underneath horizontal branches, which probably indicate that the pregnant females larviposited from their resting sites underneath such branches, as has been observed in G. morsitans (Simpson, 1918). It is less likely that they extruded their larvae directly onto the the leaf litter overlying soil surface as seen in G. fuscipes (Carpenter, 1912; Symes and Southby, 1938). A similar concentration of puparia underneath horizontal branches and lianes within larviposition sites has also been observed in G. tachinoides (Nash, 1936, 1939) and in G. morsitans (Shircore, 1916). On their work on factors affecting choice of larviposition sites in the laboratory, Rowcliffe and Finlayson (1981) also observed that shade provided by horizontal models was attractive to G. morsitans though the flies also larviposit while resting in a vertical position.

Puparia were found in soil down to a depth of 5cms but the majority were found between 1 and 3cms. Similar ranges in puparia depths have also been observed under natural conditions for G. tachinoides (Laviessiere, 1978) and G. palpalis (Hoffman, 1954). On the contrary, Carpenter (1920) observed puparia of G. palpalis on the shores of Lake Victoria to be almost always at the ground level, whilst puparia of G. swynnertoni were found between 0.6 and 7.6 cm (Burtt, 1952). The depth difference observed between puparia in different seasons was not significant, indicating that the seasons do not have a significant effect on the depth at which puparia occur in the soil.

This was surprising given the evidence from the puparia depth preference studies that the amount of leaf debris covering the soil,

amount of light entering the site and particularly the soil moisture significantly affect the depth to which larvae burrow. These observations agree with those made by other authors which indicate that the depths at which puparia are found depend on variety of conditions including temperature (Buxton & Lewis, 1934; Bursell, 1960b), soil texture (Lewis, 1934; Hoffman, 1954) and soil moisture (Burtt, 1952). Bursell (1960b) showed that deeper burrowing was induced by high temperatures, so the higher the temperature, the deeper they burrowed. Presumably, the female flies avoid larvipositing in wet soil in the field, or puparia near the surface are eliminated by predators. In general there was no difference between pupal depths of live and empty puparia suggesting that the adults emerged without pulling the cases behind them to the soil surface as they left the soil.

From the sampling point of view, knowing depths at which puparia rest in the field will help in future studies on puparia sampling using hand-searching. Searchers will know how deep into the soil they should search for puparia in different seasons so that time is not wasted searching to depths where there are no puparia. There has long been a need to develop a cheap and effective trap for concentrating pregnant females, and inducing them to larviposit in defined sites from where puparia could be collected (Carpenter, 1923). In the dry season, when most trees were leafless, the additional shading provided by the artificial shelters was effective in providing good shaded conditions for inducing gravid females to larviposit their larvae resulting in the concentration of puparia under the shade. These shelters, could possibly be further improved for sampling puparia.

CHAPTER FIVE

5. SEASONAL FLUCTUATIONS IN DISTRIBUTION AND ABUNDANCE OF PUPARIA OF *GLOSSINA PALLIDIPES* AT NGURUMAN, KENYA.

5.1 INTRODUCTION

The overall distribution and abundance of puparia of tsetse in any area are directly related to the overall distribution and abundance of the adult reproductive females. Earlier tsetse workers observed that under adverse weather conditions, suitable sites tend to be localised, but are more scattered in a stable and favourable environment, and that the hot season sites differ from the rainy season sites (Nash, 1933b; Moggridge, 1936). This seasonal spread and retraction of breeding ranges in tsetse were first described in *G. morsitans* in Malawi by Shircore (1914). Since then such a phenomenon has been observed in *G. palpalis* in Ghana (Simpson, 1918); in *G. tachinoides* in Nigeria (Nash, 1936); and in *G morsitans* in Tanzania (Jackson, 1937). Nash (1936), working on *G. tachinoides* in Nigeria, could not identify the breeding sites in the rainy season and attributed absence of puparia in that season to cessation in breeding. Jordan (1974), on the other hand, attributed it to the difficulty in recovering puparia from wet soils. The objectives of the present section on distribution and abundance of puparia of *G. pallidipes* at Nguruman were :-

(1) to study the seasonal changes in puparia densities and distribution in two vegetational habitats; and

(2) to relate changes in puparial density and distribution to adult population density and climatic factors.

5.2 MATERIALS AND METHODS

5.2.1 DETERMINATION OF SEASONAL FLUCTUATIONS IN DISTRIBUTION AND RELATIVE ABUNDANCE OF PUPARIA AT NGURUMAN, KENYA

The principal indices recorded were apparent densities of the puparia and reproductive female flies and meteorological conditions during the sampling periods. Fluctuations in relative abundance and distribution of puparia in (a) different months; (b) in the same seasons in different years; (c) different sites and (d) in two vegetation types were monitored. The puparia were sampled from fourteen natural sites using the time-constant search method for 2 man-hours. Twelve of these sites were in the riverine thicket and two in the mixed valley woodland on transect I (Fig. 2). Sampling was done between 9 a.m. and 6 p.m. on each sampling occasion. As much as possible the same pupal searchers were used to minimize variation in numbers due to skills of searchers, and all sites were searched in the same order on each sampling occasion. Puparia were also collected from Transect II and III (see Fig. 2) at bimonthly intervals. On Transect II, sites were mainly in the open lowland woodland and near seasonal streams, while sites on Transect III were widely scattered in the dense more wooded areas.

The adult sampling method has been described elsewhere (Dransfield et al.,1982, 1985). The flies were sampled over five days at monthly intervals using 41 biconical traps. Pairs of traps 50m apart were set at 500m intervals along Transect I. At ends of the transect six traps were set at 50m intervals along the Ewaso-Ngiro river and three traps were set near the edge of the escarpment. Over the first two days, the traps were emptied at 3h intervals, this was followed by a 24h sample on the third

day. Over the remaining two days, traps in acacia and lowland woodland were sampled at one and half hours intervals, while the remaining traps were emptied at 24h intervals. 16 pairs of traps were used per transect in order to cover the whole length of the transect and to sample flies from all the five vegetation types found in the area. The traps at ends of the transect were for sampling immigrant flies entering the study area. The differences in the time intervals for fly collection were fixed to provide flies for different studies. Flies collected within short time intervals were used for ageing and bloodmeal analysis, while those collected within long time intervals were examined for trypanosome infection rates. Ageing of flies was done using Saunder's method (1962).

5.2.2 DETERMINING ENVIRONMENTAL FACTORS ASSOCIATED WITH CHANGES IN PUPARIA ABUNDANCE.

The climatic conditions were recorded at two sites, T1S4 and T1S7, in the riverine thicket for three days in each month. Air temperatures and humidity in the larviposition sites and in the general breeding area were recorded with maximum-minimum thermometers and thermohygrographs. Soil temperatures at 2 cm and 4 cm depths were also recorded using maximum -minimum thermometers placed horizontally in the soil. Rainfall was recorded using a rain gauge. All climatic indices were derived by summing or averaging measures of the various factors recorded. Logarithm transformations of puparia numbers were used in the analyses. The association between the changes in log puparia density and the corresponding climatic indices of the same month or previous month was investigated by multiple regression analyses.

5.3. RESULTS

5.3.1 SEASONAL FLUCTUATIONS IN RELATIVE PUPARIA DENSITIES OF GLOSSINA PALLIDIPES AT NGURUMAN, KENYA.

Monthly fluctuations in relative densities of puparia from all three transects at Nguruman are given in Table 11. On transect I, low numbers of puparia were collected during or immediately after the wet seasons. Thus low numbers of puparia were collected in December 1984 (after the short rain in October that year), in April-May and October- December 1985 (these were the long and short rainy seasons respectively in 1985), and in May-June in 1986 (another long rainy season) when most of the sites in the riverine thicket were flooded by the Sampu river. The highest numbers of puparia were obtained in the dry seasons, especially in October-November in 1984, January-March in 1985 and in July-August 1986. The population trend on transect II was similar to that on transect I, while puparia numbers collected from transect III showed little variation.

In the wet season further surveys were conducted in vegetation patches scattered between the three parallel transects (see Fig. 2) to discover what could be regarded as rainy season sites. Bushes in the acacia woodland, in the open plains and in patches of grassland in the lowland woodland were searched. Pupae of other insects were found but there were no tsetse puparia, not even empty cases, indicating that such sites had never been used by the flies. Breeding of this species in scattered sites during the rains could not be demonstrated in spite of an intensive search.

Puparia numbers in the same seasons in the two successive years of study are shown in Fig. 6 to compare the annual puparia population patterns observed in the area. Table 12 shows that puparia populations

Table 11 - Monthly fluctuations in relative puparial numbers of *Glossina pallidipes* from natural breeding sites over three transects at Nguruman, Kenya. Numbers of *G. longipennis* puparia in brackets.

Year	Month	Number of puparia collected					
		Transect I		Transect II		Transect III	
		E	L	E	L	E	L
1984	October	201	21	-	-	-	-
	November	603	61	300	1	-	-
	December	169	8	-	-	38	3
1985	January	237	55	193	31	-	-
	February	206	111 (2)	-	-	63	3
	March	247 (1)	31	80	12	-	-
	April	151	9	-	-	59	2
	May	92 (1)	2	61	0	-	-
	June	145 (2)	10	-	-	70	1
	July	151	9	-	-	-	-
	August	157	5	-	-	-	-
	September	200	9	-	-	-	-
	October	81 (1)	2	-	-	-	-
	November	117 (1)	7	-	-	-	-
	December	95 (2)	0	-	-	-	-
1986	January	73 (5)	1	-	-	-	-
	February	105 (2)	13	-	-	-	-
	March	79	9	-	-	-	-
	April	101 (4)	13	-	-	-	-
	May	25	2	-	-	-	-
	June	28	0	-	-	-	-
	July	72	21	-	-	-	-
	August	98	50	-	-	-	-
	Total	3,443 (19)	450 (2)	734	54	230	9

E = Empty puparia cases. L = live puparia. Puparial collections on Transects II and III were discontinued from July 1985 because sites were inaccessible due to flooding.

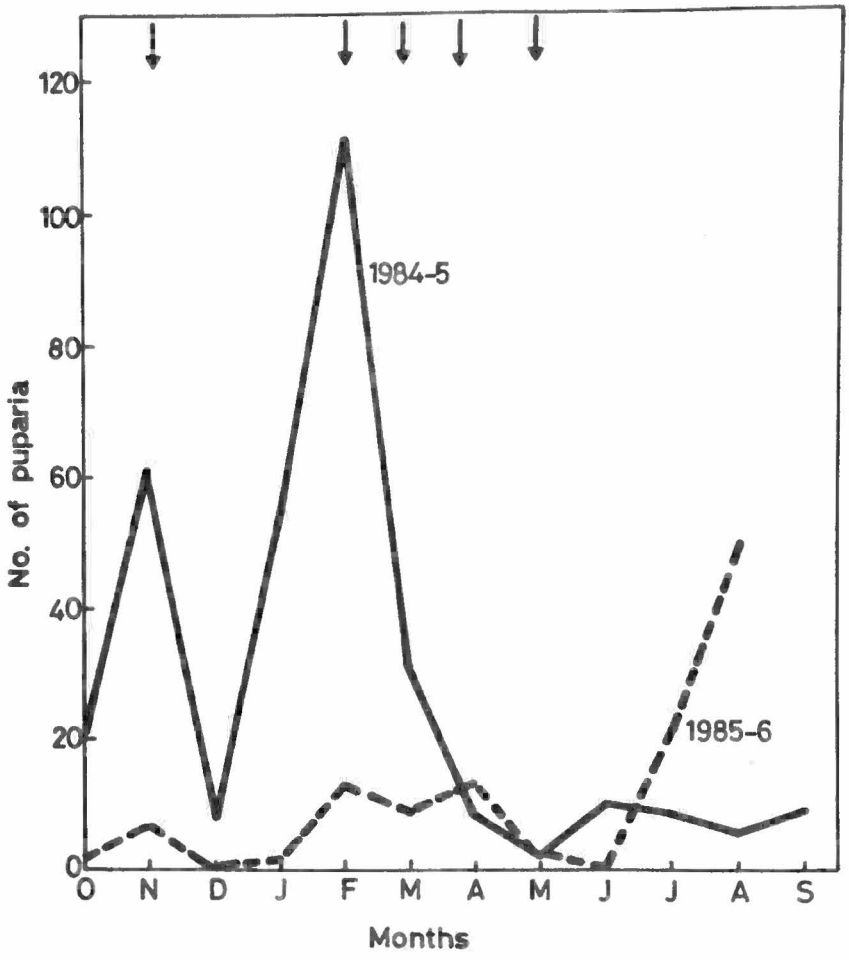

Fig. 6 - Comparing relative densities of live puparia of G. pallidipes in the same months of successive years on transect I. Arrows indicate months with rainfall over 80 mm.

Table 12 - Seasonal fluctuations in relative densities of puparia over transect I in the two successive years of study.

Season	Months	1984-85		1985-86	
		E	L	E	L
Short rains	Oct.-Dec.	973	90	293	9
Hot dry	Jan.-Mar.	690	197	257	23
Long rains	Apr.-June	383	21	154	15
Cold dry	Jul.-Sept.	513	24	170*	71*

* - values based on only July and August data.

were higher in the first year than the second year, though there was a good degree of consistency between the two years in terms of increases in the dry seasons and decreases in the wet seasons. The population decline from March -June was more during the operations of a long period of rain than from October to December. There was a rapid recovery in July and January respectively as the rain subsided (Fig. 5).

5.3.2 SEASONAL ABUNDANCE AND DISTRIBUTION OF PUPARIA IN DIFFERENT SITES WITHIN THE SAME HABITAT

Census data in Table 13 from the various sites showed that mean puparial density within sites may be as low as 0.04 in one site and as high as 2.78 in another, which gives 70-fold difference in average puparia density. Even in sites only 10 meters apart there can be 2-3 fold differences in density. The monthly mean puparia for between sites ranged from 0 to 7.9. Breeding intensity in sites varied monthly and the favoured sites were recognised by the large numbers of puparia larviposited and

Table 13 - Monthly variations in relative puparia density in different sites along transect I at Nguruman, Kenya.

Year	Month	Number of puparia collected at each site														Total	Mean
		Riverine thicket												Valley			
		1	2	3	4	5	6	7	8	9	10	11	12	1	2		
1984	Oct.	8	3	1	1	3	0	1	2	1	0	1	0	-	-	21	1.8
	Nov.	3	8	10	9	4	1	6	13	3	4	0	0	-	-	61	5.1
	Dec.	1	0	0	0	0	0	0	0	1	0	0	0	3	3	8	0.6
1985	Jan.	2	1	7	4	0	3	12	2	1	0	0	6	11	6	55	3.9
	Feb.	11	4	4	7	6	11	36	2	13	0	0	12	4	1	111	7.9
	Mar.	3	1	3	1	3	1	2	9	3	0	0	0	3	2	31	2.2
	Apr.	1	0	0	1	0	3	2	0	0	0	0	0	1	1	9	0.6
	May	0	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0.14
	June	0	0	0	0	0	0	0	0	0	0	0	0	2	8	10	0.7
	July	0	0	2	0	0	1	0	0	0	0	0	0	4	2	9	0.6
	Aug.	0	0	1	0	1	0	0	0	0	0	0	0	4	0	6	0.4
	Sept.	1	0	5	1	0	1	0	0	0	1	0	0	0	0	9	0.6
	Oct.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.14
	Nov.	0	0	2	1	0	1	2	0	1	0	0	0	0	0	7	0.5
	Dec.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
1986	Jan.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.07
	Feb.	5	0	1	1	2	0	2	0	0	0	0	1	1	0	13	0.93
	Mar.	3	0	1	1	1	0	0	0	2	0	0	1	0	0	9	0.6
	Apr.	0	1	2	2	4	3	1	0	0	0	0	0	0	0	13	0.93
	May	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0.14
	June	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
	July	2	1	3	7	3	4	0	1	0	0	0	0	0	0	21	1.5
	Aug.	7	5	3	3	2	11	0	3	0	1	0	10	0	0	50	3.6
Total		47	24	48	45	29	41	64	32	25	6	1	30	34	23	450	

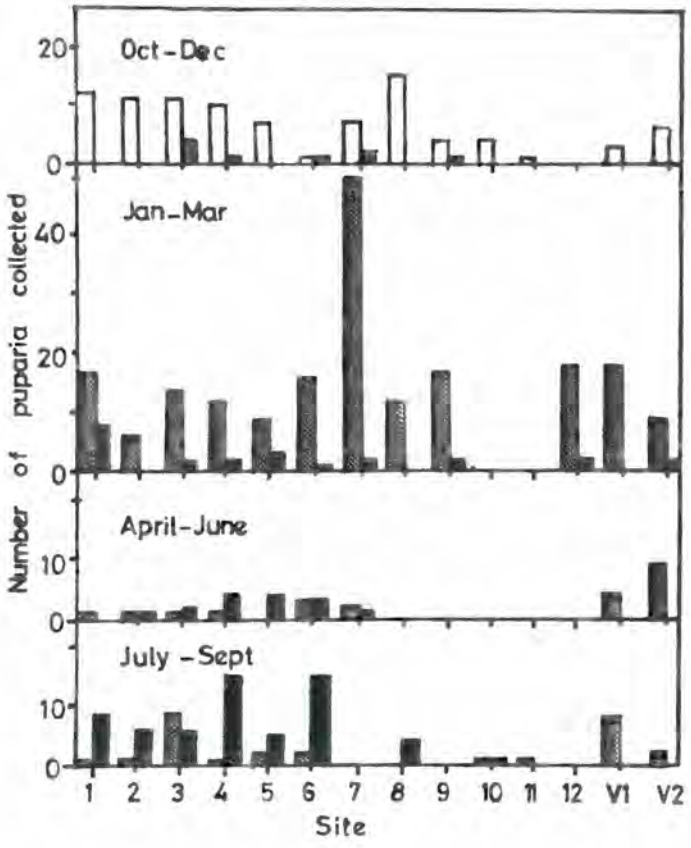

Fig. 7 - Site variations in relative puparial density illustrating seasonality of larviposition sites of G. pallidipes at Nguruman. ☐ for 1984, ▨ for 1985; ■ for 1986.

(collected) during the study period (Fig. 7). Two-way analysis of variance of square-root transformed data showed significant differences in puparia numbers between different sites ($F = 2.2$, $P < 0.05$).

5.3.3 SEASONALITY OF DIFFERENT VEGETATION HABITATS FOR LARVIPOSITION

Under the semi-arid climate prevailing in Nguruman, G. pallidipes appeared to prefer the dense riverine thicket with tall trees and an undergrowth of shrubs, herbs and grass. Out of the 14 selected sites on Transect 1, 12 were found in the riverine thicket the remaining 2 sites were found in the mixed woodland in the valley of the Sampu River.

Table 14 gives the monthly fluctuations in the relative density of puparia in the riverine thicket (12 sites) and valley woodland (2 sites). There were two major peaks in both vegetation types (Fig. 8), but peaks in the thickets coincided with low densities in the valley woodland and vice versa. Numbers of puparia collected from the hilly slopes in the valley woodland were few during the dry seasons in 1984, but increased greatly when most low-lying sites in the riverine thickets got flooded in the heavy rainy season in 1985. Thus, while densities in the thicket declined following heavy rains, those in the woodland increased. There is therefore clear evidence of a shift in breeding sites within the locality in relation to the seasons.

Breeding in all sites in the riverine thicket fell to low levels from April 1985 onwards, but at no time was there a complete withdrawal, suggesting that these sites were the primary breeding sites used throughout the year except when they were adversely affected by the floods. The mean puparia density per vegetation habitat per month was 17.09 ± 5.3 for the thicket and 2.71 ± 0.9 for the valley woodland, a ratio of 6.3 : 1.

Table 14 - Relative puparia abundance and distribution in relation to two vegetation types along transect I at Nguruman, Kenya.

Year	Month	Number of puparia categories collected			
		Riverine Thicket		Valley woodland	
		Empty cases	Live puparia	Empty cases	live puparia
1984	October	201	21	-	-
	November	603	61	-	-
	December	131	2	38	6
1985	January	134	38	103	17
	February	189	106	17	5
	March	183	26	64	6
	April	124	7	27	2
	May	45	1	47	1
	June	67	0	78	10
	July	66	3	95	5
	August	99	2	68	4
	September	147	9	63	0
	October	45	2	36	0
	November	62	7	55	0
	December	39	0	50	0
1986	January	50	1	23	0
	February	76	12	29	1
	March	50	9	29	0
	April	88	13	13	0
	May	17	2	8	0
	June	23	0	6	0
	July	48	21	24	0
	August	86	50	13	0
	Total	2,572	393	865	57

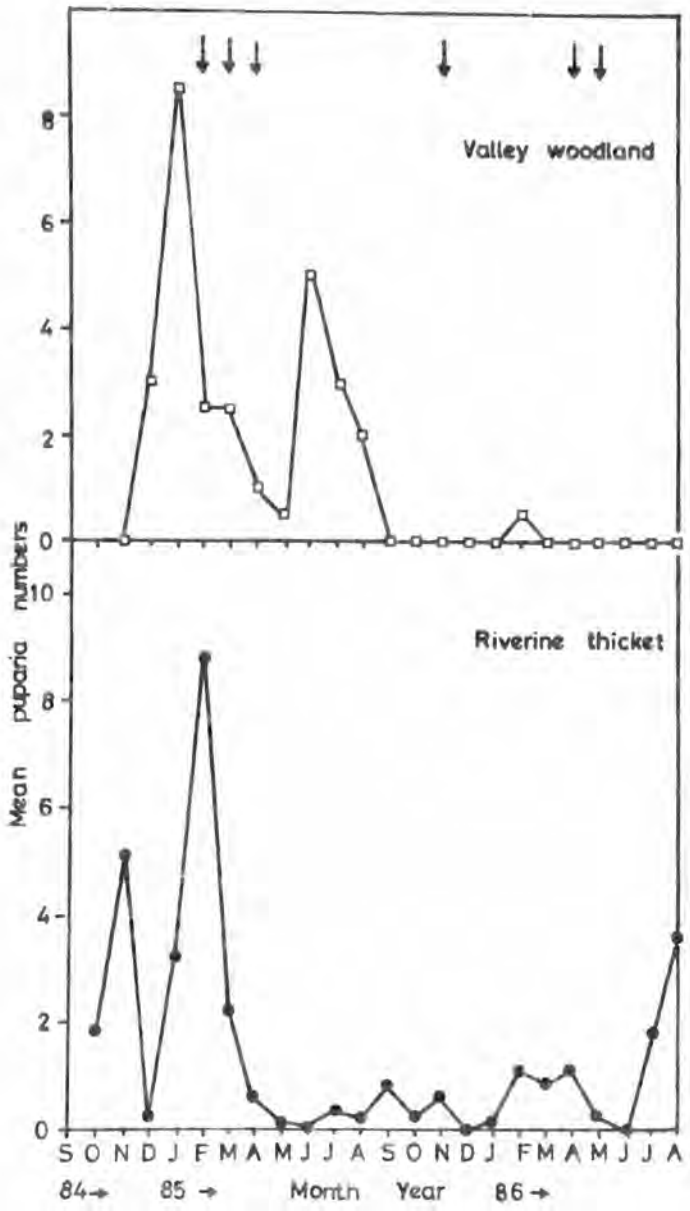

Fig. 6 — Seasonal fluctuations in pupal abundance and distribution in two vegetation types at Ngurdman, showing shift in breeding sites. Arrows indicate months with rainfall over 80 mm.

5.3.4 RELATIONSHIP BETWEEN PUPAL AND NON-TENERAL FEMALE APPARENT DENSITIES.

A significant positive correlation ($r = 0.66$, $P < 0.01$) was found between density of puparia within a particular month and apparent density of non-teneral (reproducing) female flies (having mating scars and different stages of egg and larval developments in their uterus) in previous month (Fig. 9). Thus distribution and abundance of puparia are, to a large extent, dependent on the density of the female flies.

The monthly changes in distribution of female flies in different vegetation types along transect I are shown in Fig. 10. The female flies were found in great numbers in the lowland riverine thicket throughout the year, while numbers in other vegetation habitats varied monthly. During the months of November 1984 to January 1985, and April to June 1985, the population showed a slight shift from the lowland riverine thicket to the Upper and Valley woodlands, whilst during the months of February-March and July-September, the population showed a reversed shift from the Upper and Valley woodlands into the lowland riverine thicket, acacia woodland and the open plains. A close inspection of Fig. 8 and Fig 10 shows that these apparent seasonal movements of the female flies are closely related to seasonal distribution and abundance of the puparia in the different vegetation types. The increases in puparia numbers in the valley woodland during the rainy seasons, and in the riverine thicket in the dry seasons coincided with higher numbers of the female flies in these vegetation types.

5.3.5 RELATIONSHIP BETWEEN PUPAL DENSITY AND CLIMATIC FACTORS

Climatic data for the general tsetse area and larviposition sites are given in Appendices 1 and 2 respectively and shown in Fig. 11. The highest monthly maximum temperature recorded in the general area was

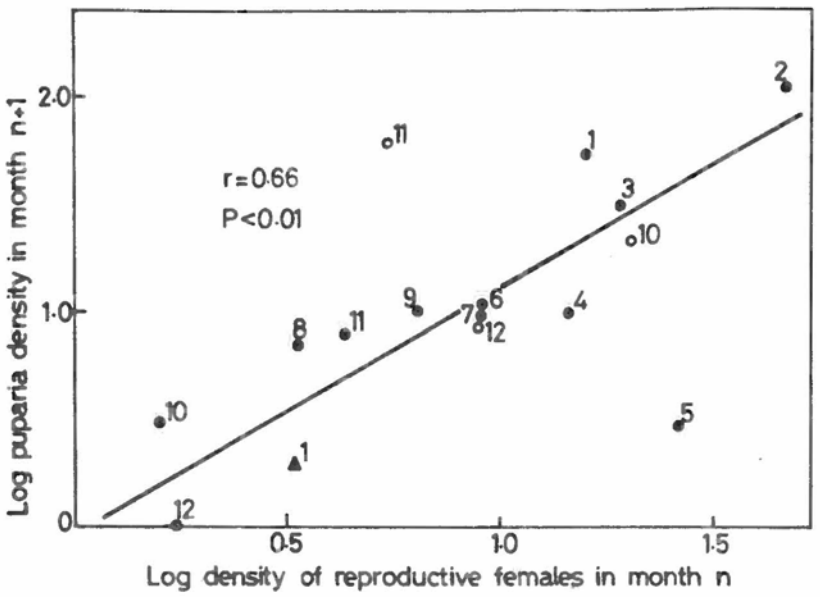

Fig. 9 - Relationship between puparia density and apparent density of reproductive females. Numbers refer to months. O for 1984; ● for 1985; ▲ for 1986. Sampling period: October 1984 to January 1986. n and n+1 refer to successive time periods.

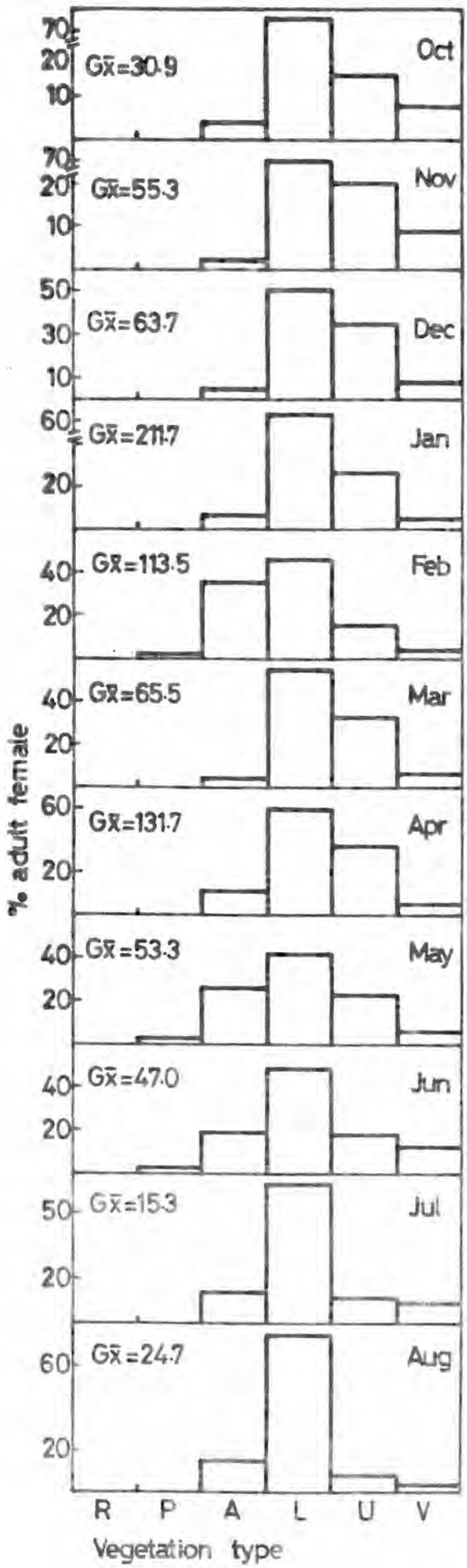

Fig. 10 - Monthly fluctuation in distribution of female G. pallidipes in different vegetation types along transect 1, showing shift in site in relation to months. Sampling - Oct. 1985 - Aug. 1986.

R - River vegetation.
P - Open plains.
A - Acacia woodland.
L - Riverine thicket.
U - Upper woodland.
V - Valley woodland.

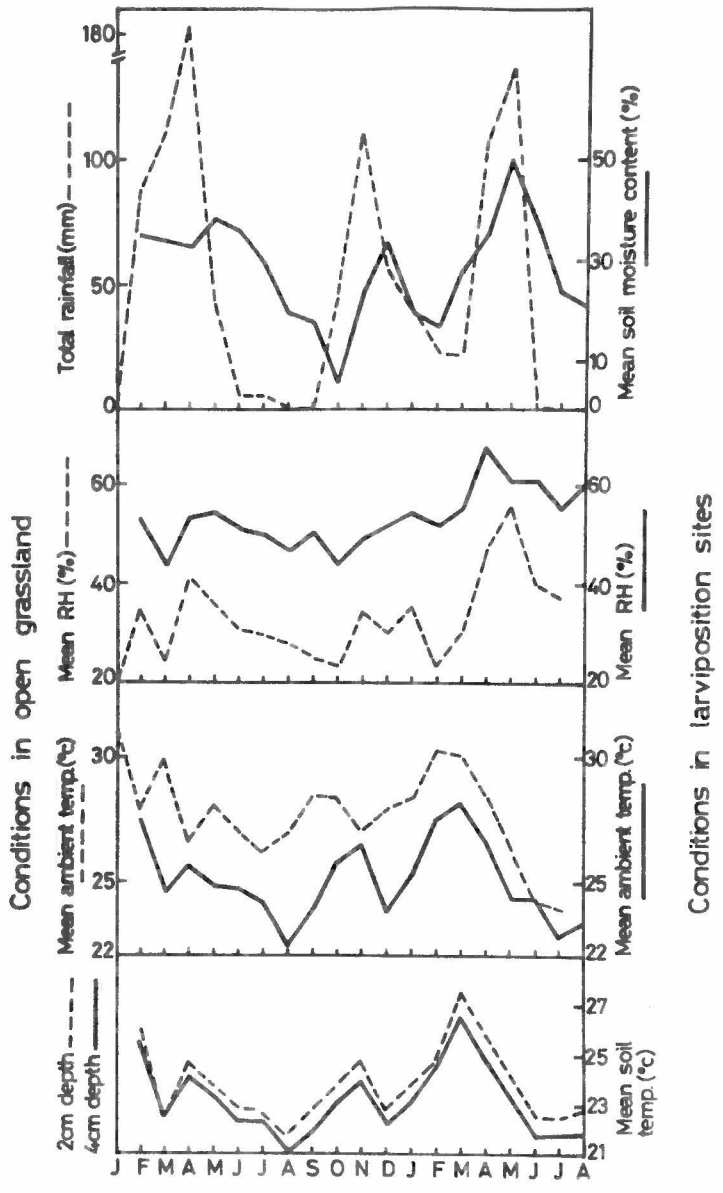

Fig. 11 - Changes in climatic factors in breeding area of G. pallidipes (January, 1985 - August, 1986).

40.6°C (January 1985) which could be lethal, but that for the larviposition site was 36.3°C (February 1986). Thus the mean maximum temperature in the sites never reached 40°C which is regarded lethal to Glossina (Nash, 1933b). The lowest monthly minimum temperature for the general area and larviposition site were 15.1°C and 14.2°C respectively (both recorded in July 1986). The monthly mean air relative humidity in the site was always higher than 40% as compared to 25% in the open area within the vicinity of the sites. Although the soil at most times appeared completely dry it contained enough moisture to maintain suitable soil conditions for successful pupal development. The monthly mean soil moisture at Nguruman was 28.6 ± 2.5% (N = 432, see Table 4). The highest rainfalls of 182.9 mm and 136.3 mm were recorded in April 1985 and May 1986 respectively, while the highest soil moisture content of between 30% and 50% were recorded during the months of May and June respectively (both are months following months of heavy rains). It is evident from Fig. 11 that climatic conditions within the larviposition sites were more equable than in the general area.

Regressions of log. puparia against climatic factors were carried out. Of all climatic factors in the same month investigated, only soil moisture was significantly correlated to puparia numbers ($r = 0.59$, $P < 0.05$, $t = 6.64$). The climatic factors found to be most closely related to seasonal variations in overall pupal numbers were those recorded for previous month, which were the factors experienced by the parent female flies. There were significant positive correlations of puparia numbers with maximum temperature ($r = 0.74$, $P < 0.001$, $t = 3.76$) and mean temperature ($r = 0.60$, $P < 0.05$, $t = 2.95$) of the previous month, while the negative relationship with saturation deficit was statistically significant ($r = -0.65$, $P < 0.05$, $t = -2.09$).

5.4 DISCUSSIONS AND CONCLUSIONS

Fluctuations of apparent densities of puparia in different seasons, different sites, different shading regimes and different vegetation habitats have been established using the time-constant hand-searching method. The method is considered a very useful one for sampling puparia. It would however be valuable to develop a simple, cheap and efficient method for puparia sampling because the hand-searching method is laborious, time-consuming and the efficiency is dependent on nature of the soil and the skill of the puparia collectors (a source of serious sampling bias). The presence of puparia in most of the sites month after month indicated that the monthly hand-searching involving apparent soil disturbance did not prevent flies from larvipositing in the sites. This supports the idea that G. pallidipes uses the same sites year after year.

In general, fewer puparia were found in the larviposition sites after the rains, and rainfall over 30 mm was always followed by a reduction in apparent puparia density. Considerable decline in pupal numbers which occured in 1985 was attributed to the exceptional heavy rains and waterlogging of many sites in the lowland riverine thicket. Such low yields in wet seasons have also been reported for other Glossina species. Parson (1930) and Nash (1937, 1942) found puparia collection in the wet seasons unsuccessful, while Harley (1954), in an area of unspecified size, obtained only 10% recovery rate of G. morsitans puparia in the same season. At Nguruman, some of the sites were too waterlogged to be searched, while other sites yielded only few puparia. Burtt (1952) attributed the low recovery of puparia in wet seasons to the adhesive nature of the soil. Whilst this may be true to some extent there is

considerable evidence from this study that the flies are switching their larviposition sites to areas less liable to flood. Firstly, there was sudden drop in puparia numbers in the lowland riverine thicket at the same time as a sharp increase in the upper and valley woodlands. Secondly, there was corresponding change in adult distribution. Seasonal shift in sites by Glossina has been reported by other tsetse workers. Nash (1937), for instance, observed that adult G. tachinoides concentrated in sites along water courses and in dense vegetation habitats in hot dry seasons, but shifted to other areas at the onset of the rains. At Nguruman, the shift in site usage from the lowland riverine thicket to the sloping sites with good drainage in the upper and valley woodlands coincided with the onset of the long and heavy rains. This is an indication that the reproducing females probably changed sites to avoid flooding and consequent mortality in the puparia.

There was a prolonged decline of puparia numbers from April 1985 to June 1986, and the recovery of the pre-rainy seasons population density expected in October 1985 was not achieved seven months after cessation of the rains. What could be the reason for the relatively low levels in the early part of 1985-86 as compared to the same period in 1984-85?. Intensive trapping of adult flies within the area began in June 1985 by ICIPE scientists. This reduced the adult fly population thereafter until adult catches were maintained at low levels suggesting that a new lower equilibrium had been established. The prolonged decline in puparia density in this period was thus attributed to a real change in population due to lower equilibrium caused by the trapping of the adults.

Though G. longipennis occurs in the study area, only 2 live puparia and 19 empty cases of this species were found in haunts used by G. pallidipes. This probably indicates that there are differences in their

requirements for larviposition.

There is evidence that within any particular vegetation habitat, sites showed considerable unsynchronised variations in numbers of puparia found in different seasons, suggesting that some sites were perhaps abandoned in favour of more suitable sites. Site attachment may involve the pregnant females concentrating in the same locality month after month, or year after year because of their common attraction to particular local environmental micro-conditions. Secondly, pregnant females may be concentrated in the same locality because of the availability of their preferred hosts in such areas (Vale, 1971).

Increases in puparia numbers in dry seasons and decreases in the rainy seasons suggests that puparia population fluctuations are probably related to rainfall and temperature. However, no strong relationship could be established between puparia density and most of the climatic factors within the same month. Significant correlations were however found with some climatic factors in the previous month, which is to be expected since distribution of the puparia is largely determined by distribution of adults in previous month. The positive relationship with temperature suggest a concentration effect with the high temperatures in the dry seasons inducing the adults to concentrate in the relatively cool and dense vegetation. The negative relationship with rainfall suggests that the flies perhaps detect the increase in relative humidity associated with the early showers and probably avoided larvipositing in sites that are likely to be flooded before the advent of the heavy rains.

C H A P T E R S I X

6. ASSESSMENT OF MORTALITY RATES IN PUPARIA OF G. PALLIDIPES AT NGURUMAN

6.1 INTRODUCTION

One method of assessing pupal mortality is to keep field-collected puparia under laboratory conditions to determine percentage emergence. This also enables a determination of percentage parasitism and identification of the parasites involved. The technique cannot however provide data on loss rates of puparia through predation and other causes. One way in which this can be done is by estimating mortality rates from relative abundance of different age groups of the population.

Various methods which have been suggested for the determination of age of insects are reviewed by Southwood (1966, 1978). Different ages of insects may be determined by dissections where various categories of physiological processes or developmental features can be recognised. This was done by Bursell (1959, 1960a) who showed that the age of puparia of G. tachinoides could be determined by some developmental characteristics of the developing pupa-imago inside the puparium. An alternative is to keep the puparia alive until emergence and record the time from collection to emergence. The age of the puparia at time of collection can then be estimated by subtracting time to emergence from estimated pupal duration. Once the age distribution is known, the decline in progressively older age groups will reflect the mortality rate in a stable population. Although estimates from a single month's data could give misleading results, pooling over several months data should give a reasonable estimate of average mortality rate (Challier & Turner, 1985).

As well as estimating the mortality rate from the frequencies of different age categories of puparia, an index of mortality was also obtained from the difference between the apparent density of puparia and apparent density of teneral adults the following month. Since different sampling methods were used, this method cannot give an absolute estimate but can give a useful index.

Another approach was suggested by Rogers (1979) and is adopted here. He suggested using the Moran curve for determining monthly changes in density independent mortality acting on tsetse populations under natural conditions. Although he applied it to adult tsetse numbers, there is no basic reason why it should not be used with puparia as well with the proviso that generation mortalities (i.e. combined pupal and adult mortality rates) will be estimated.

The last technique utilised was the experimental approach in which known numbers of live puparia were buried, and checked two weeks later to determine numbers of puparia missing or killed. Results of these experiments are deferred till Chapter 9, since they relate most directly to work on predation. To summarise, three approaches are reported in this chapter for assessing pupal mortality at Nguruman.

(a) Puparia were kept in the laboratory to determine emergence rate.

(b) The age distribution technique was used to estimate a survivorship curve from which the mortality rate was calculated; similarly the difference between relative numbers of puparia and tenerals each month gave an index of mortality;

(c) Seasonal changes in generation mortality due to abiotic mortalities were estimated from Moran curve.

6.2 MATERIALS AND METHODS

6.2.1 DETERMINATION OF RATE AND PATTERN OF ADULT EMERGENCE

The live puparia collected monthly from the field were kept individually in 6.3 x 2.3 cm ventilated plastic containers which were in turn placed in a large metal tray of wet sand. The tray was kept in the pupal room at Nguruman at average temperature of ca. 25°C until eclosion (Higher temperatures were experienced by puparia for the first 2-3 months of the project until the arrangement above could be set up). Dates of collections and emergences were noted and the frequency of emergences at different time periods (06, 09, 12, 15, 18 and 21 hours) within each day was also noted and used to determine the diurnal rhythm in the emergence pattern of adult G. pallidipes and parasites or parasitoids which emerged. The emergence rate in different months from October 1984 to August 1985 was estimated using the following formula :-

$$\text{Emergence rate (E)} = \frac{\text{No. of puparia which emerged (NE)}}{\text{Total No. of puparia collected (N)}}$$

It should be noted that calculated changes in E may arise through real changes in emergence rates or through sampling biases. The percent emergence was found by multiplying this index by 100.

6.2.2 DETERMINATION OF PUPARIAL DURATION OF FIELD-COLLECTED PUPARIA

The expected pupal period duration (EPD) in each month was estimated using Jackson's formula (1937) : -

$$EPD = \frac{1}{0.0323 + 0.0028\ (t - 24)}$$

Where t is the mean temperature (°C) experienced by the puparia. Mean

soil temperatures recorded in the field were used to estimate expected pupal duration in the field (A). For the duration of collected puparia kept in the pupal room, the average of mean temperatures in the field and in the room (B) were used, because it was assumed that on the average the puparia spent one half of their life in the field and the other half in the room.

6.2.3 DETERMINING AGE DISTRIBUTION OF PUPARIA COLLECTED FROM THE FIELD.

The ageing of live puparia was by back-calculation. This method was based on the estimated pupal developmental period. The age of each normal tsetse puparium was estimated by subtracting the number of days from collection to emergence from corrected expected pupal duration calculated using mean of temperatures in the field and in the room. The age distribution thus tabulated provided information on seasonal changes in age distribution. Combined data on the age distribution for the whole study period was used to construct an age-specific survivorship curve of puparia of G. pallidipes. It was drawn by plotting logarithms of frequencies of puparia against four puparia age categories.

6.2.4 ESTIMATING PUPARIAL LOSS RATES FROM RELATIVE DENSITIES OF PUPARIA AND TENERAL FEMALE FLIES

Indirect evidence of puparial losses was derived from analysis of densities of puparia from hand searches and apparent densities of 0A teneral female flies. These are newly emerged (0-2 days old) females which have not fed. The dissections were carried out by J. Kiilu using the technique of Challier (1963). Pupal loss rate was determined by subtracting the log density of 0A flies in a particular month from log.

puparia density of previous month.

6.2.5 ESTIMATING LOSS RATES FROM MORAN CURVE

An analytical approach suggested by Rogers (1979) is appropriate in investigating the seasonal levels of abiotic mortalities. This method, which estimates the generation mortality rates from changes in total sample sizes, is based on the logarithmic version of Ricker's plot and is called the Moran curve. In this curve, the density at a point in time is plotted against the density of the same life stage at some previous point in time. The Moran curve which represents maximum population growth in the absence of density independent mortality is then added. The maximum rate of increase of puparia numbers per month (x 1.9) was obtained from runs of a G. pallidipes simulation model (Dransfield, pers. comm.). Distances between the curve and any point below the line is a measure of density independent mortality acting on the population during the interval from t to t + 1.

6.3 OBSERVATIONS AND RESULTS

6.3.1 RATE AND PATTERN OF EMERGENCE OF G. PALLIDIPES AT NGURUMAN.

Based on variable numbers of field-collected puparia, the percent emergences in different months ranged from 21.4 to 100% and averaged 45.90 ± 0.61 (Table 15 and Fig. 12) with higher emergence rates occurring in October 1984, January-February, April-May and July 1985; and January and March 1986, while fewer adults emerged in November 1984, March and September 1985 and February 1986. These lower emergences mostly coincided with seasonal transitions of climatic conditions from hot and dry to cold and wet. This suggests that conditions in these periods are probably not favourable to the tsetse. The highest temperature at which development and hatching occur in nature at Nguruman was not precisely known, however, satisfactory emergences occurred in January 1985 when maximum shade air temperature was above 40°C.

Table 15 gives the seasonal fluctuations in mean percent emergence of puparia just over transect I. On the average, 45.0 ± 0.1% (range 15 - 100%) of puparia collected yielded adult tsetse. Generally, pupal to adult survival increased in the dry seasons, but was low in the rainy season, indicating that conditions in the seasons affect survival of the puparia.

Fig. 13 shows the diurnal rhythm of emergences of 305 flies from field collected puparia (combined males and females). It shows a bimodal pattern with the first and minor peak occurring between 0600h and 0900h, and the major peak of the day occurring in the late afternoon between 1500 and 1800h. There were no emergences around midday.

Table 15 - Monthly percent emergence and estimated duration of puparia of *Glossina pallidipes* at Nguruman.

Year	Month	Puparia collected	Percent Emergence	Estimated pupal duration in days. Field	room
1984	Oct.	43	62.8	30.4	23.6
	Nov.	74	36.5	35.2	24.8
	Dec.	9	44.4	32.4	23.8
1985	Jan.	88	77.3	29.7	25.6
	Feb.	130	79.2	25.3	26.8
	Mar.	40	32.5	24.7	27.6
	April	9	66.7	31.8	30.6
	May	2	100.0	33.9	32.1
	June	10	40.0	34.6	35.2
	July	14	50.0	37.5	36.0
	Aug.	10	30.0	36.3	36.7
	Sept.	14	21.4	33.0	31.5
	Oct.	3	33.3	30.4	30.0
	Nov.	9	33.3	35.2	32.3
	Dec.	0	0	32.4	31.4
1986	Jan.	1	100.0	29.7	29.3
	Feb.	13	38.5	25.3	26.9
	March	13	69.2	28.0	29.6
	April	13	46.2	31.2	29.1
	May	2	0	36.7	33.4
	June	0	0	36.7	36.1
	July	21	47.6	36.3	36.3

Note: Numbers of puparia include all those collected from regular sampling sites, artificial shelters and sites used for other studies.

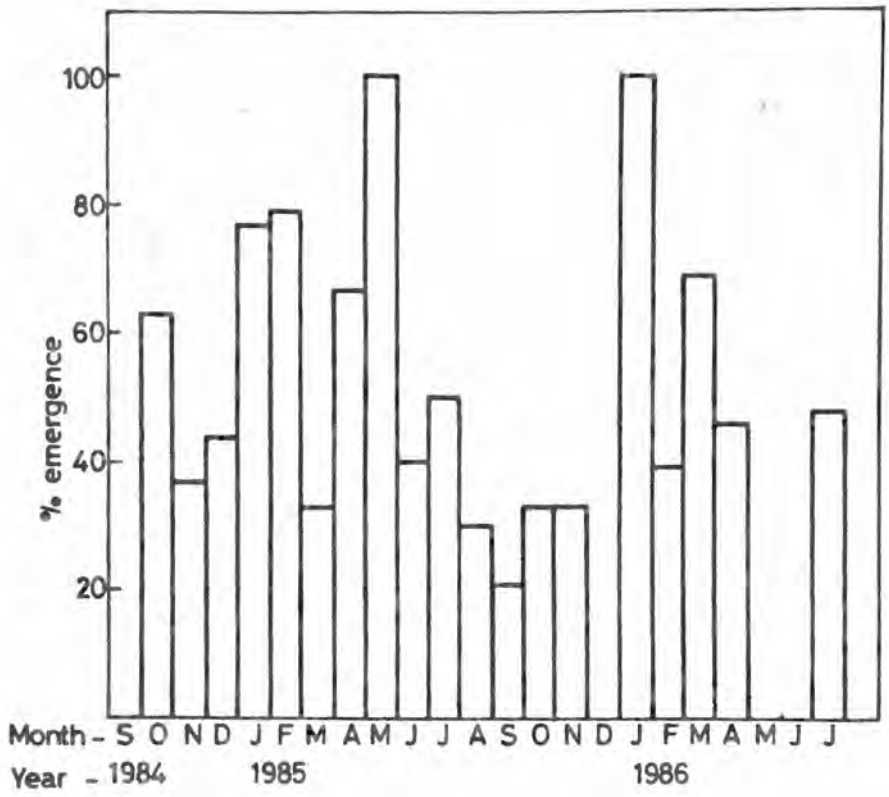

Fig. 12 - Monthly adult emergence from field-collected puparia at mean temperature of 29.4°C.

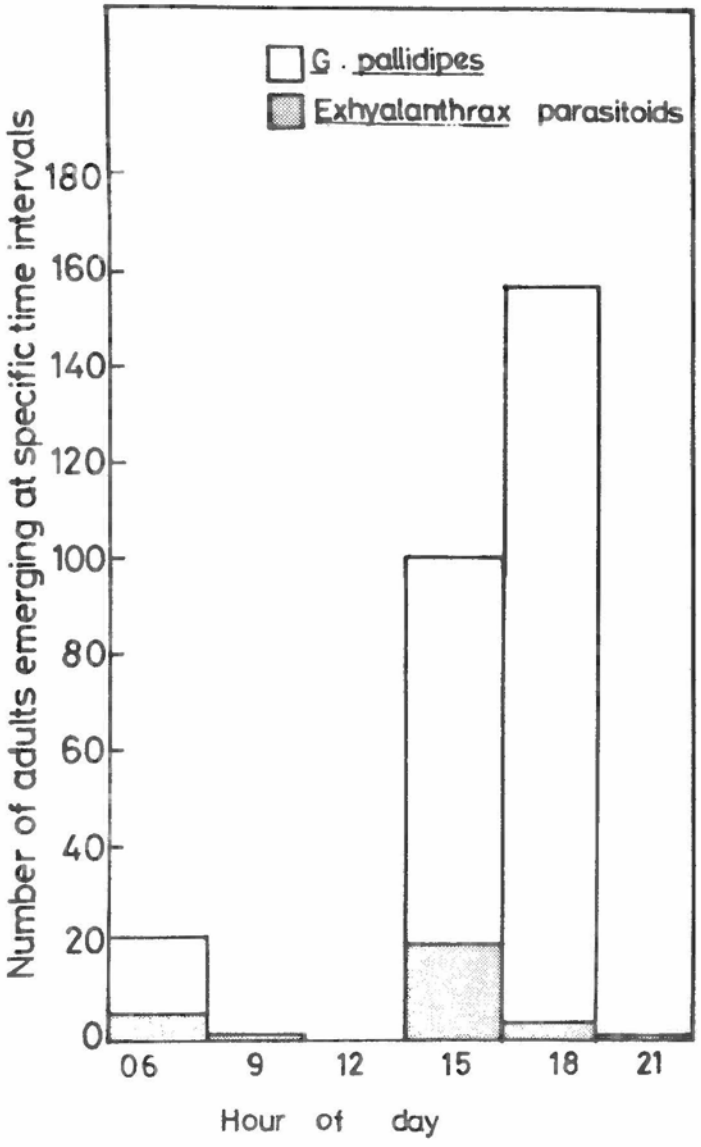

Fig. 13 - Diurnal pattern of adult emergence.

Table 16 - Seasonal fluctuations in emergence rates of G. pallidipes over transect I. No. = Number of puparia.

Season	Months	1984 - 1985		1985 - 1986	
		No.	% emergence	No.	% emergence
Short rains	Oct.-Dec.	90	33.30	9	44.4
Hot dry	Jan.-Mar.	197	62.98	23	65.2
Long rains	April-June	21	33.30	15	40.0
Cold dry	July-Sept.	24	45.80	21	47.60*

* Value based on only July data.

6.3.2 PUPAL DURATION IN DIFFERENT SEASONS AND SITES.

The estimated durations of field-collected puparia at Nguruman are also given in Table 15. The fluctuations in estimated mean duration of puparia in the field is shown in Fig. 14. Duration ranged from 24.7 in March to 37.5 days in July and averaged 32.2 $\pm$ 0.8 days. In general, duration of pupae in the field was relatively longer than in the room, with the longest (36 days) in July-August.

6.3.3. AGE DISTRIBUTION OF FIELD-COLLECTED PUPARIA OF G. PALLIDIPES AT NGURUMAN.

The age distribution of the puparia population at Nguruman is given in Table 17. Puparia of all ages occured at all times reflecting the overlapping nature of tsetse populations. Fig. 15 shows the monthly fluctuations in the age distribution of puparia from October 1984 to March 1985. When individual months are considered, the age distributions probably reflect more whether larviposition is increasing or decreasing

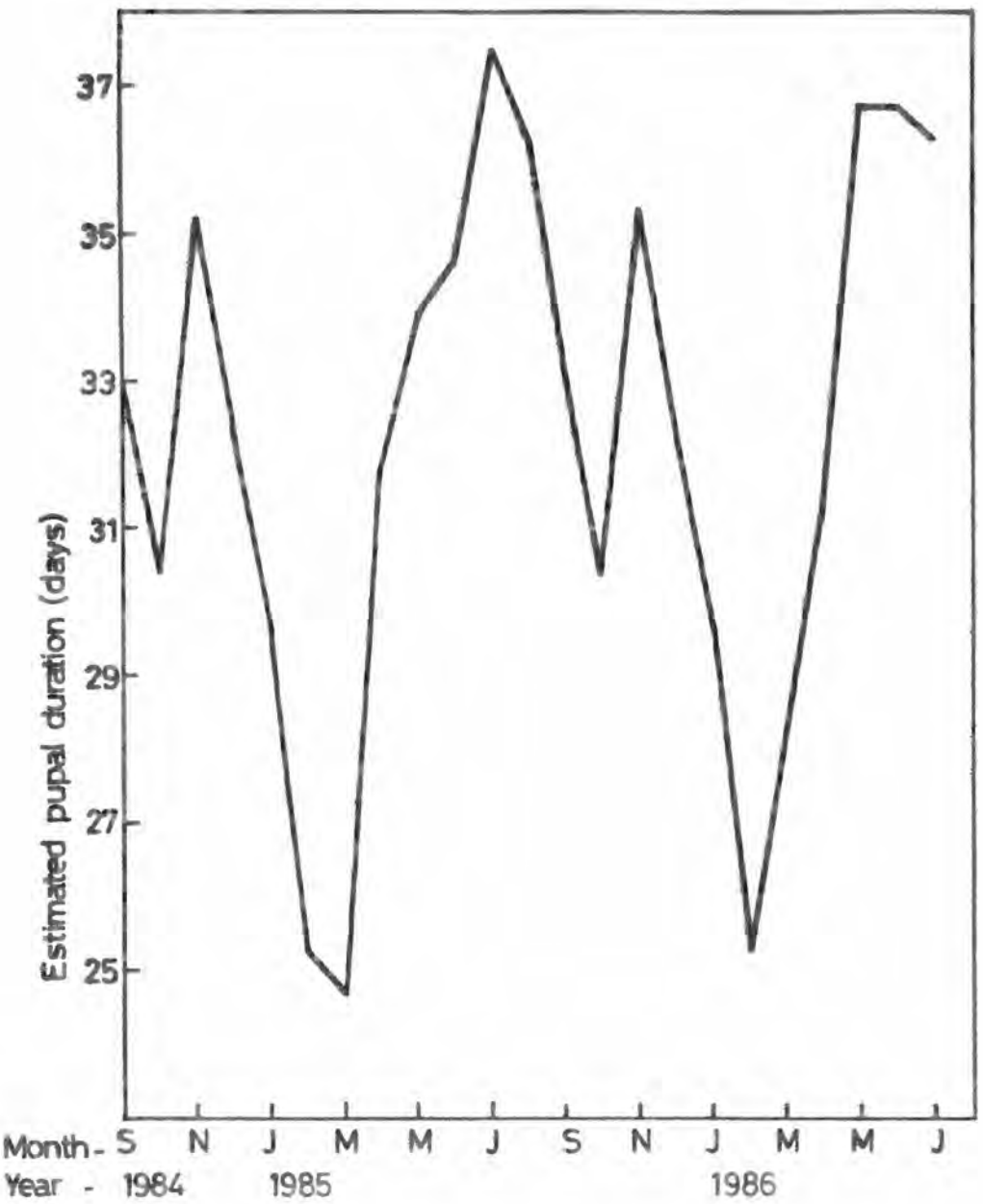

Fig. 14 - Fluctuations in estimated mean duration of puparia of G. pallidipes from transect I at Nguruman.

Table 17 - Monthly age distribution of Puparia of G. pallidipes at Nguruman, Kenya.

Year	Month	Corrected pupal duration	Number of Puparia in each age group 1	2	3	4	Total
1984	Oct.	24	4	7	7	9	27
	Nov.	24	5	8	8	6	27
	Dec.	24	3	0	0	1	4
1985	Jan.	28	47	19	1	1	68
	Feb.	28	42	16	30	15	103
	Mar.	28	6	4	3	0	13
	April	32	0	2	4	0	6
	May	32	0	0	0	2	2
	June	36	4	0	0	0	4
	July	36	1	5	1	0	7
	Aug.	36	0	1	1	1	3
	Sept.	32	0	0	3	0	3
	Oct.	32	1	2	3	0	6
	Nov.	32	0	0	1	2	3
	Dec.	32	0	0	0	0	0
1986	Jan.	28	0	1	0	0	1
	Feb.	28	3	0	2	0	5
	Mar.	32	5	1	1	2	9
	April	28	0	3	3	0	6
	May	32	0	0	0	0	0
	June	36	0	0	0	0	0
	July	36	6	4	0	0	10
	Total		127	73	68	39	307
	Log. Tot.		2.10	1.86	1.83	1.59	

Note: - Estimated pupal duration is rounded to the nearest multiple of four days. Age groups: 1 = 0 - 7 days old; 2 = 8 - 15 days old; 3 = 16 - 23 days old; 4 = over 24 days old.

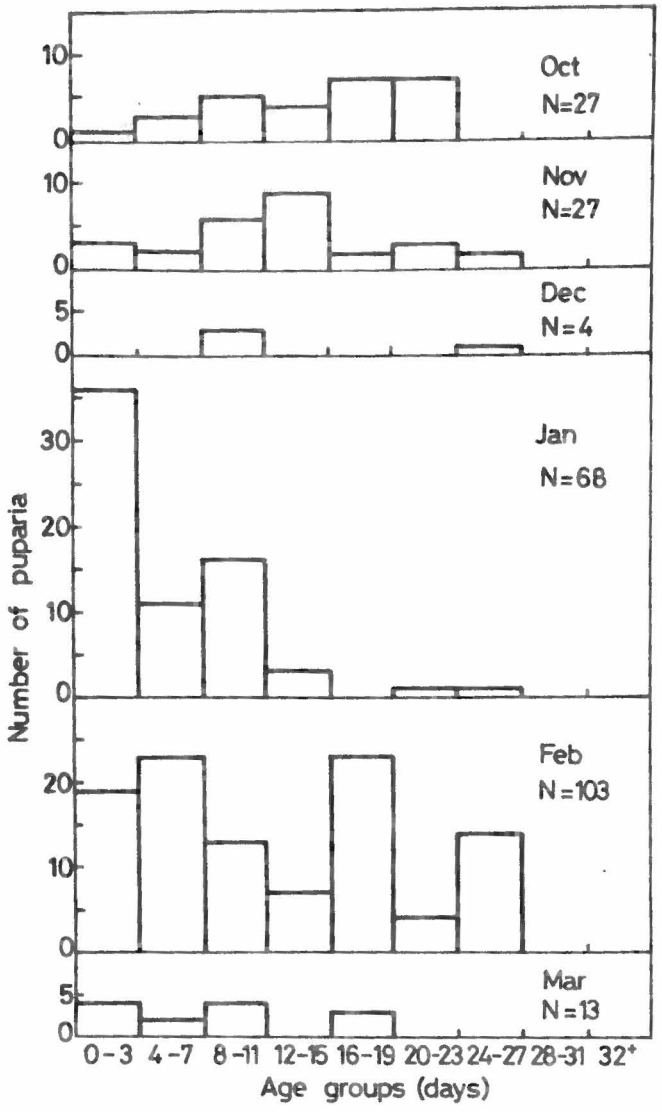

Fig. 15 - Monthly age distribution of puparia of G. pallidipes. Sampling period: October, 1984 - March, 1985.

in the site, than the mortality rate. Thus, the population was apparently decreasing in the short rainy season (October-November 1984), but increasing from January to March 1985 (hot dry season). It decreased again in April-June (long rainy season).

Fig. 16 shows the overall survivorship curve. The correlation between the log numbers of puparia and the four age groups (solid line) was found to be significant ($r = 0.81$, $P < 0.01$), suggesting that if each developmental cycle lasts approximately 8 days then very few puparia at Nguruman will survive to emergence. The estimated mortality rate (k-value) from the slope of the survivorship curve was 0.16, indicating a mortality rate of 4.5% ($k = 0.02$) per day. The mean mortality rate was however lower (slope = 0.14 with mortality rate of 4.0% per day) when only the first three age groups (dotted line) were considered.

6.3.4 PUPAL LOSS RATES FROM RELATIVE DENSITIES OF PUPARIA AND TENERAL FEMALE FLIES.

Seasonal changes in the index of pupal loss rates operating between puparia of a particular month and the teneral female flies of the following month given in Table 18 are shown in Fig. 17. In general, the pupal loss rates were higher in 1984-85 than in 1985-86. Losses were higher during the short rains and the dry season immediately following the short rains, but were much lower in the long rains.

6.3.5 GENERATION MORTALITY RATES FROM MORAN CURVE

Fig. 18 shows the Moran curve for puparia of G. pallidipes at Nguruman from which seasonal levels of density independent mortalities were estimated. Since the mortalities are differences between two log densities, the estimates are logarithmic (i.e. k-values). Density

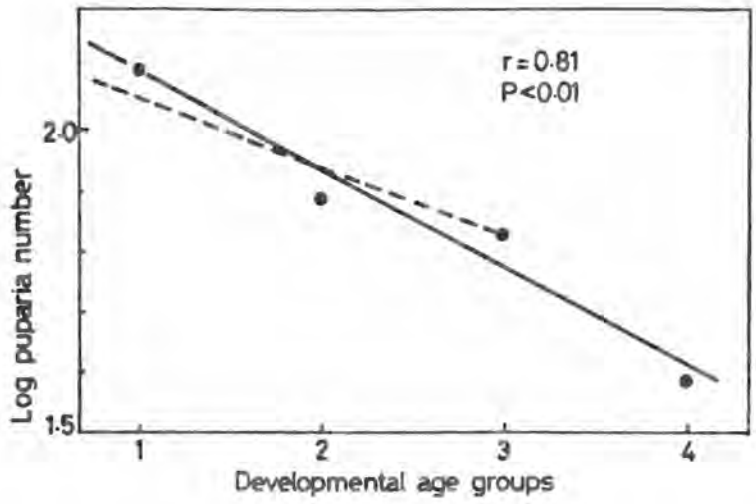

Fig. 16 - Survivorship curve for puparia population of G. pallidipes at Nguruman. Sampling period: October, 1984 - July, 1986.

Table 18 - Monthly fluctuations in index of pupal loss rates estimated from relative densities of puparia and teneral female flies

Year	Month	Puparia collected in month n		Mean No. of OA flies in month n + 1		Index of pupal loss
		P	ln P (a)	OA	ln OA (b)	(a-b)
1984	Oct.	21	3.0	0.5	-0.7	2.3
	Nov.	61	4.1	0.4	-0.9	3.2
	Dec.	8	2.1	0.6	-0.5	1.6
1985	Jan.	55	4.0	2.9	1.1	2.9
	Feb.	111	4.7	1.1	0.1	4.6
	Mar.	31	3.4	1.5	0.4	3.0
	April	9	2.2	1.0	0.0	2.2
	May	2	0.7	0.6	-0.5	0.2
	June	10	2.3	0.4	-0.9	1.4
	July	9	2.2	0.4	-0.9	1.3
	Aug.	6	1.8	0.2	-1.6	0.2
	Sept.	9	2.2	0.1	-2.3	-0.1
	Oct.	2	0.7	0.1	-2.3	-1.6
	Nov.	7	1.9	0.2	-1.6	0.3
	Dec.	0	0	1.4	0.3	-0.3
1986	Jan.	1	0	1.7	0.5	-0.5
	Feb.	12	2.6	3.1	1.1	1.5
	Mar.	9	2.2	0.2	-1.6	0.6
	April	13	2.6	1.3	0.3	2.3
	May	2	0.7	4.1	1.4	-0.7
	June	0	0	3.1	1.1	-1.1
	July	21	3.0	2.4	0.9	2.1
	August	50	3.9	2.1	0.7	3.2

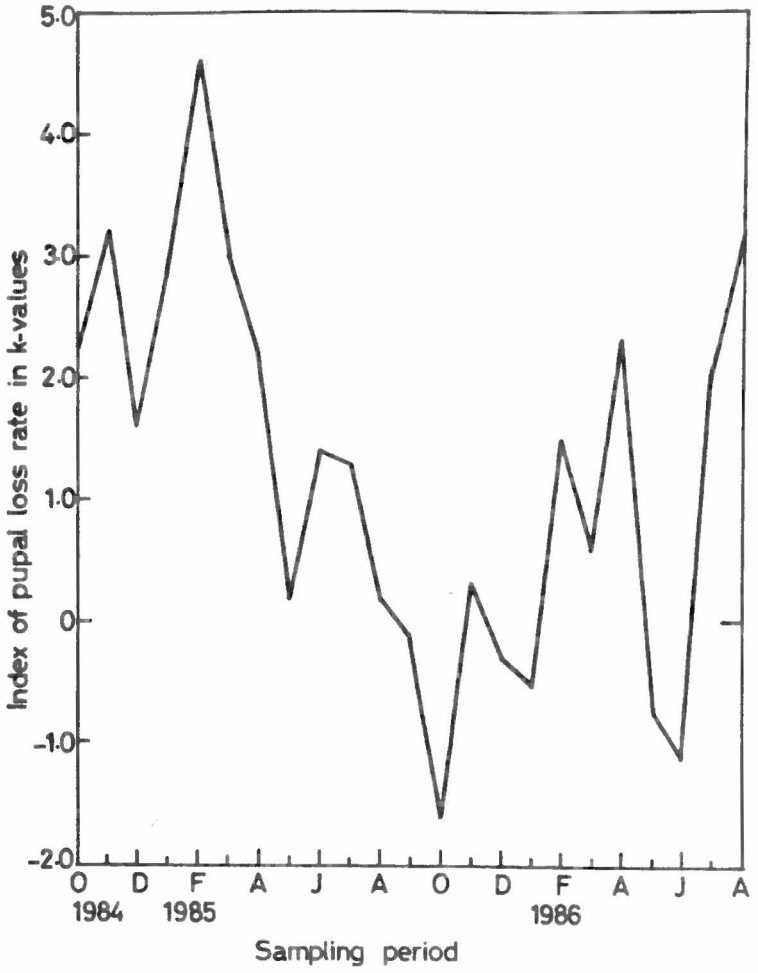

Fig. 17 - Monthly changes in index of pupal loss rates estimated from relative densities of puparia and teneral female flies (OA) of the following month.

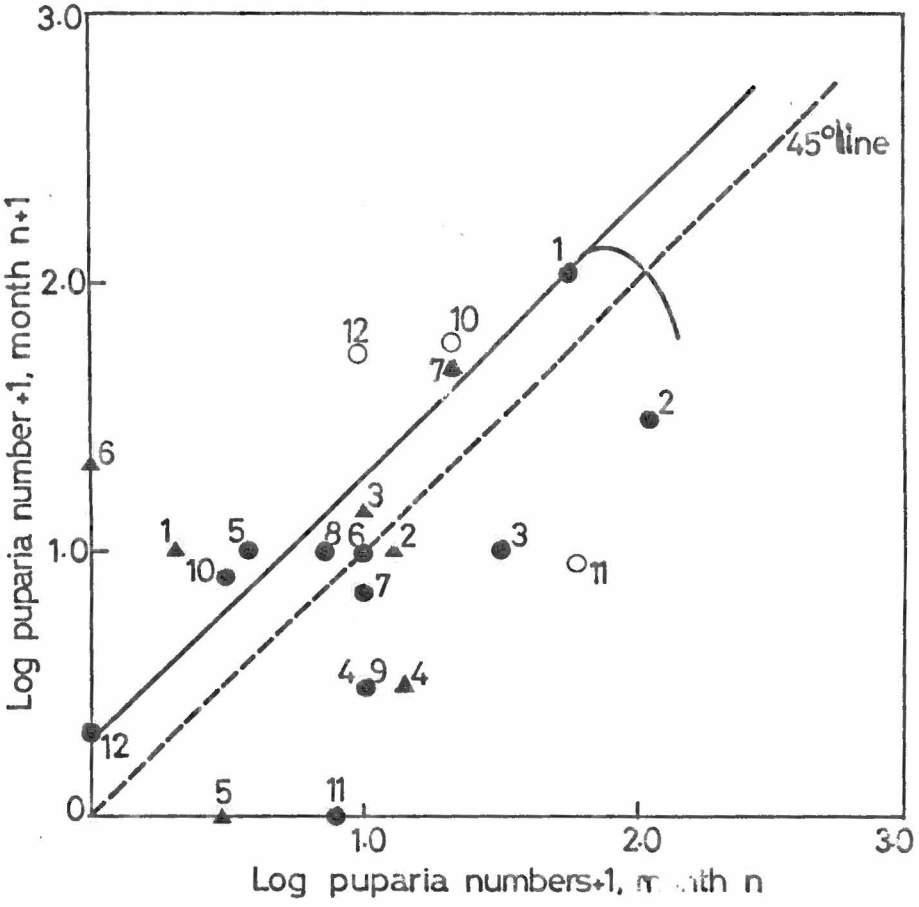

Fig. 18 - Moran plot for 22 months hand-searching data for puparia G. pallidipes at Nguruman. Thick line represents maximum monthly pupal increase in the absence of density independent mortality, where it crosses the 45° line is point of equilibrium. Numbers refer to month, O for 1984; ● for 1985; ▲ for 1986. n and n + 1 refer to successive time intervals.

independent mortality rates varied from -1.14 to 1.18. Most of the points fell below the solid line which is the population maximum rate of increase (1.9x per month). However, some points fell above the solid line, which probably reflect concentration of the adults, resulting in increases in numbers of puparia found in particular sites above that which could be explained by the population increase. The population is said to follow a fairly regular annual change in abundance if points for the same months in successive years tend to fall in the same part of the Moran curve. In the present study, changes in October-November and January-April are regular annual changes.

The monthly changes in density independent mortality is shown in Fig. 19. Generation mortality appear to be low in October, increase in November when the short rains come, and then decline in December. It increased from January-February to March-May.

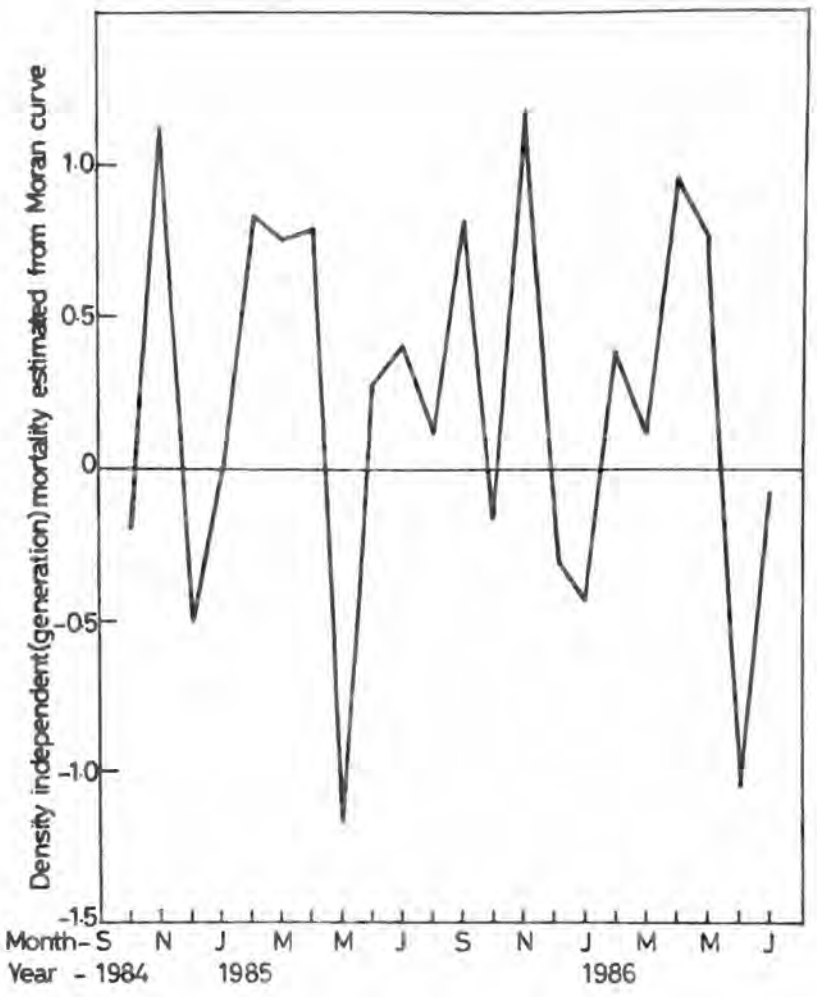

Fig. 19 - Monthly changes in density independent (generation) mortality rate estimated from the Moran plot.

6.4 DISCUSSIONS AND CONCLUSIONS

The emergence rate of G. pallidipes in the pupal room at Nguruman was between 30-70%. This is within the range of 30-93% reported from the same species reared in a grass-thatched hut at ICIPE Mbita Point Research Station, South Nyanza, Kenya (Otieno, L.H., pers. comm.). The emergence at Nguruman showed a bimodal pattern with peaks between 0600-0900h and 1500-1800h. Similar bimodal emergence pattern has been reported in adult G. pallidipes population studied by Jaenson (1978a, 1981) and Van Etten (1981), and in other species (Pilson & Leggate, 1962; Challier, 1973; Okiwelu, 1977, 1982). In Burkina Faso, Challier (1973) observed the emergence rate of laboratory bred G. palpalis gambiensis to be low in the morning (1000- 1100h), with most of the adult flies emerging after 1700h. He also observed that in the wild, most emergences occurred in the morning and late afternoons. In Zambia, G. morsitans morsitans mostly emerged between 0600-0900h and 1200-1500h (Okiwelu, 1977). G. morsitans submorsitans in Mali were also found emerging at the same time periods (Okiwelu, 1982). Laveissiere et al., (1984a) reported that emergence of G. tachinoides in humid savanna in West Africa was irregular, but occured mainly in the early mornings around 0900 and 1000h and late in the afternoon.

Pupal duration of G. pallidipes in the present study was 25-38 days. This agrees with data presented by Hursey (1970), who reported that the time taken for emergence of G. pallidipes in Kiboko area in the Machakos District varied between 29 and 35 days. The results also compare very well with data obtained on other species. In Ghana, Simpson (1918) observed an interval of 22-29 days in G. tachinoides, while data obtained on the same species by Nash (1937) at Gadau, Nigeria were between 19 and 41 days. The only detailed study on this subject carried out in the

natural conditions and starting with puparia of known age was done by Challier (1973) in Burkina Faso on G. palpalis gambiensis. The pupal duration was found between 26 and 50 days. This falls within the 22-58 days observed by Laveissiere et al., (1984a) for G. tachinoides in humid savanna of West Africa.

In general the pupal duration was relatively shorter in the dry seasons (between September-October and February-March), while that in the wet seasons (between April-July) was longer. This could result in accumulation of puparia during the middle part of the cold season. These accumulated populations of puparia will then produce numerically important cohorts of tenerals which could be manifested in adult catches by a sudden increase in proportions of young flies. Such an event was suspected to have occurred at Nguruman when the populations of the puparia and tenerals in January 1985 grew numerically after the short cold spell in November-December 1984. Such contraction in time of emergences and accumulation of puparia and subsequent increase in numbers of teneral flies have also been observed in G. tachinoides in West Africa (Laveissiere et al., 1984a, b).

Though the longest duration of tsetse puparia at Nguruman was 38 days, puparia which have been parasitised by Exhyalanthrax parasitoids have much longer duration, sometimes extending to 80 days. This observation is comparable to those made by Chorley (1929) who observed the duration of E. abruptus recovered from puparia of G. morsitans to be 80 days in November and December and 30 days in other months. He also observed long periods of dormancy of about 197 days and this led to the suggestion that there is diapause in these parasitoids. The duration of the pupal stage of the parasitoid has been found to last for only 11 - 14 days, while the larval stage lasts for several weeks (Chorley, 1929;

Nash, 1930; Friedler and Kluge, 1954; Hursey, 1970; Gruvel, 1974a). This situation makes the determination of the age of parasitised puparia more complex, because the duration of such puparia will vary considerably and will be dependent on the age of the parasitoid at time of parasitization of the host.

One interesting finding revealed in this study is the age-specific survivorship curve for the puparia population. Although mortality rate estimates varied slightly, the linear inverse correlation obtained for the puparia population agreed with Slobodkin's Type II survivorship curve (Slobodkin, 1962), which indicated that mortality was constant in all age groups. This could be attributed to increasing pupal losses through predation which is directly related to how long the puparia are exposed to mortality factors (Wohlschlag, 1954; Clements and Paterson, 1981). If all age groups were equally susceptible to predation then the regression reflected the rate at which puparia succumbed to predation. However, 4.5% per day seems an exceptionally high mortality rate since it would give an overall pupal mortality of 77%. Even if it is assumed that the last developmental category has lower frequency than it should because of early emergence, the overall mortality rate/month still comes out at 70%. Whether this is a realistic estimate will be reconsidered in Chapter 9, after examination of the data on the pupal burying experiments. This figure is certainly much higher than the 10% pupal/teneral mortality assumed by Nash and Page (1953).

The method of analysis based on the Moran curve provides direct estimates of generation mortality. Some of the points which fell outside the realistic range of reproductive rates gave rise to negative k-values and could represent months of population migration into the area, or could result from sampling errors. Since it is an attempt to define the best

possible performance of the population in absence of any density independent mortality, it is therefore desirable to have a long series of population counts before applying the Moran curve fitting technique.

CHAPTER SEVEN

7. IDENTIFICATION OF CAUSES OF MORTALITY OF G. PALLIDIPES PUPARIA AT NGURUMAN.

7.1 INTRODUCTION

In devising technique for managing insect pests and vectors, it is important to identify the key mortality factors that influence population trends (Varley and Gradwell, 1960; Varley et al, 1973), so that we can either avoid removing their effects or deliberately enhance their effectiveness. It is generally accepted that seasonal fluctuations in living creatures are caused by adverse climatic and environmental factors which are density independent, while the regulation of the population around an equilibrium level is attributed to density dependent processes. Density dependent mortalities are due to interactions with other members of their kind (through intraspecific competition) or with other living creatures (interspecific competition, pathogens, parasites and predators).

In the previous chapter, there was clear evidence for a substantial mortality rate affecting tsetse at the pupal stage, both in terms of non-emergence and pupal disappearance. Having quantified this mortality operating at the puparial stage, the next question is "What factors are responsible for this mortality, and how do they operate?.
The objectives in this section were, therefore, :-

1. to determine the causes of puparial mortality and the way in which they act, thus better understanding the factors influencing the population dynamics of the species at Nguruman, and

2. to quantify tne major density dependent and density independent mortality factors for tne construction of a predictive tsetse population model in collaboration with the ICIPE Nguruman Tsetse Ecology Research Team working in tne same area.

Tne factors causing puparial mortality were assessed from :-

1. Natural incidence and frequency of predation and parasitism in field-collected empty puparial cases;

2. Causes of mortality of field-collected live puparia which failed to emerge, and key factor analysis of tnese factors;

3. Relationship between pupal loss rate (log. tenerals-log. puparia in previous month) and climatic and biotic factors; and

4. Relationship between generation mortality from Moran curve and climatic factors.

7.2 MATERIALS AND METHODS

7.2.1 DETERMINING NATURAL RATES OF INCIDENCE OF PREDATION AND PARASITISM FROM EMPTY PUPARIAL CASES OF G. PALLIDIPES AND OTHER INSECTS COLLECTED IN THE STUDY AREA.

In the course of the field surveys large numbers of empty puparia were found, some of which showed signs of predation and parasitism. For determining the incidence of predation and parasitism in empty puparial cases, the puparia collected monthly from the field were carefully examined under the binocular microscope and were considered damaged if they showed oviposition or feeding punctures, tears, scratches or mandible markings. In the classification of causes of mortality, the following patterns were used as evidence of: -

(a) Predation by chewing predators - large or small rugged holes showing biting, chewing or mandible imprints.

(b) Apparent parasitism due to Syntomosphyrum species - small round clean holes (Mulligan, 1970) and presence of parasite's pupal cases within the tsetse puparia. However, adults of this genus were not recorded emerging from collected puparia. Emergence holes caused by the parasitoid Exhyalanthrax could not be distinguisned from normal tsetse emergence holes so were excluded from mortality estimation in empty puparial cases.

(c) Tear or bursting signs - cases torn at several places with some of the separated parts folding slightly backwards. This damage was probably caused by pupal searchers or trampling by other creatures;

(d) Adult emergence - typical emergence holes made by tsetse.

The percent predation and parasitism due to these apparently arthropod-induced damage patterns were determined in puparia of both tsetse and other insects. Since only a proportion of empty shells was

removed on each sampling occasion, predation rates estimated from empty cases reflect predation rates over the previous two to three months.

7.2.2 AGE GRADING DISSECTIONS FOR DETERMINING AGE AT DEATH OF FIELD- COLLECTED PUPARIA WHICH FAILED TO EMERGE.

A modified Bursell's method for age determination of Glossina puparia was employed in the formulation of classification categories used in ageing field-collected puparia which failed to emerge into adults. The age categories were based on certain distinguishing developmental features such as the appearance of different adult body parts and the degree of pigmentation in the eyes, appendages, wings and the general body surface. The formulation was based on the assumption that recognizable characters on which ageing are based are well preserved in the puparial case, and hence remain relatively unchanged after death.

Prior to dissection of field-collected puparia, 300 laboratory -reared puparia were kept in the laboratory at temperatures ranging between 25°C and 28°C, 60-70% RH and 12L:12D photoperiod. Ten puparia were dissected daily until all the 300 puparia had been dissected. The front half of each puparium was embedded in a block of plasticine and carefully dissected to expose the content for examination under a binocular microscope (Wild M5, 10 x 25 magnification). The features of the developing pupa or imago inside the puparium were then noted and assigned to the appropriate age category which was related to the duration of the pupa at each developmental phase. Table 19 gives the summary of the characteristics of the developing puparia-imago inside the puparia used in ageing puparia of G. pallidipes. This ageing method can be used to determine the age of dead puparia at time of death or age of live puparia at time of collection from the field. It is also a useful

Table 19 - Classification categories for determining the age of puparial stages of G. pallidipes (A = age from day of larviposition in days, B = duration of developmental phase in days, C = estimated mean age of puparium in days).

Phase	Classification category	A	B	C
1.	From formation of puparium until the three body regions corresponding to head, thorax and abdomen could be distinguished. The content of puparium remaining watery and creamy white in colour.			
	a. Quiescent stage with watery contents intimately associated with puparium at all points	2	2	1
	b. Contents still watery and creamy white but bounded by a fine membrane	3	3	3.5
	c. Head, thorax and abdomen distinguishable	4	2	6
2.	No pigmentation but form of imago and appendages discernible			
	a. legs clearly discernible	5	1	7.5
	b. wing buds separating from rest of the body	8	1	8.5

Table 19 - (cont'd)

Phase	Classification category	A	B	C
3.	From time pigment first appeared as pale yellow in the eyes until body bristles become pigmented though body colour remained creamy-white			
	a. Only the eyes pigmented			
	(i) Yellow tint in eyes	11	2	10
	(ii) eyes light yellow in colour	15	6	14
	(iii) eyes of mustard colour	20	5	19.5
	b. Pigmentation in bristles on proboscis, legs, antennae and general body surface	22	2	23
	c. Sexes could be differentiated	23	1	24.5
	d. Characteristic banding on abdomen discernible	25	2	26
	e. eyes brownish	27	1	27.5
	f. eyes reddish-brown or purplish-brown	28	2	29
4.	From body pigmentation to completion of development of the imago in the puparial case.			
	a). body heavily pigmented and pupal skin still moist	29	1	30.5
	b). Pupal skin dry and adhering to puparium, ptilimum protruding and pulsating, pharate adult moving slightly and preparing to emerge	30	1	31.5

technique for comparing relative ages of puparia collected at different times in the same locality or from different localities provided the live puparia are not needed for other studies. In this present study it was used in determining the age of puparia at time of death.

7.2.3 DETERMINING NATURAL CAUSES OF MORTALITY OF PUPARIA COLLECTED FROM THE FIELD

For determining the type of parasites and parasitoids and their rates of parasitization, the live puparia collected monthly from the field were placed singly in 6.3 x 2.8 cm ventilated plastic containers, and under conditions described in the previous chapter (see 6.2.1) for eclosion and subsequent identification of adult parasites or parasitoids which emerged. Puparia from which neither tsetse nor parasites had emerged 80 days after the day of collection were dissected and examined under the binocular microscope to determine possible causes of death. The causes of mortality were classified as follows : -

(a) Dead parasitised puparia - A few puparia were found to contain dead parasitoids, and were included with the parasites which emerged for quantification of this mortality factor;

(b) Developmental abnormalities - all instances of developmental and emergence failures. The developmental failures refer to puparia which failed to develop beyond the pupal stage. They included puparia which showed no development and hence were hollow and puparia containing a shrivelled mass of tissues of different colours. Emergence failures were characterised by puparia which had retained mature flies which failed to emerge, thus representing successful development but failure to emerge, or small adults which could not survive the "spider

stage" of emergence.

(c) Pupal tissue degeneration - dead puparia which had the cases lined with rotten tissue representing decomposed puparia.

(d) Diseased puparia or fungal infections - all puparia with mycelia inside. These included hollow cases, shrivelled tissue or retained adult flies covered with mycelia.

Total mortality in each season was expressed as a percentage of total of puparia examined.

7.2.4 KEY FACTOR ANALYSIS OF CAUSES OF NON-EMERGENCE MORTALITY OF PUPARIA COLLECTED FROM THE FIELD.

The levels of all the submortalities defined above, expressed in k-values, were estimated by subtracting log N_{t+1} from log N_t, where N_t is the number of puparia on which the factor acted and N_{t+1} is the number surviving that mortality factor. Total puparial loss (K) in each month was determined by summing k-values of all submortalies , k_1, k_2, k_3 etc. or by subtracting log. number of adult emerging from log. number of puparia collected in that month. Varley and Gradwell's method (1960, 1970) was then used in partial generation key factor analysis. Recognition of key factors was assesssed by visual correlations, in which total mortality (K) and sub-mortalities (k_1 to k_3) were plotted against months.

Quantitative evaluation of the role of each k-value was carried out using Podoler and Rogers' method (1975). The relative importance of each factor was taken to be proportional to the regression coefficient of k-values of each submortality against total mortality (K). These coefficients also gave the estimates of the role of each mortality in contributing to changes in total mortality (Taylor, 1979).

The various K-values were then tested for density dependence by plotting each against the log. puparia density on which it acted, and then calculating the regression coefficient to determine how each factor acts on the population. To detect any delay in density dependence, the K-values were plotted against log. initial puparia density and the points joined in a time sequence plot (Varley, 1947, 1958; Morris, 1959; Varley and Gradwell, 1960). The K-values were also related to climatic factors.

7.2.5. DETERMINING THE RELATIONSHIP BETWEEN LOSS RATES AND PUPAL DENSITY AND CLIMATIC FACTORS.

The pupal loss rate between puparia and teneral female flies, demonstrated in the previous chapter, were related to pupal density to determine if loss rate was density dependent.

For determining the climatic factors partly responsible for the pupal loss experienced between puparia and teneral flies, the index of pupal loss rates were correlated to climatic factors in the same or previous month.

7.2.6 DETERMINING THE RELATIONSHIP BETWEEN GENERATION MORTALITY AND CLIMATIC FACTORS AND PUPAL DENSITY

Associations between the changes in the generation mortality estimated from the Moran curve and climatic factors of the same or previous month were investigated by multiple regression analysis.

7.3 OBSERVATIONS AND RESULTS.

7.3.1 INCIDENCE OF ARTHROPOD-INDUCED DAMAGE IN PUPARIA OF GLOSSINA PALLIDIPES

The proportion of damaged puparial cases was used as an indirect measure of the intensity of predation of puparia of G. pallidipes in the natural situation. This represents only the attacks which did not involve complete consumption of puparia. Seasonal fluctuations in the incidence of damaged puparia are given in Table 20 and the monthly fluctuations are shown in Fig. 20. Out of 2,848 cases examined 25 (0.88%) had apparently been parasitized by Syntomosphyrum and 630 (22.1%) had been predated. Parasitism in cases was relatively low and trend in relation to season or density of cases could not be demonstrated.

Table 20 - Seasonal fluctuations in arthropod-induced damage in puparial cases of G. pallidipes collected from the field.

Months	Seasons	1984 - 1985			1985 - 1986		
		Cases obs.	% paras.	% pred.	Cases obs.	% paras.	% pred.
Oct-Dec	Short rains	410	2.4	16.3	288	0	21.2
Jan-Mar	Hot dry	643	1.6	26.3	255	0.4	20.0
Apr-June	Long rains	454	0.4	17.2	154	0	20.1
July-Sept	Cold dry	470	0	11.3	171*	1.2	32.2

* Based on only July and August data. Obs. = observed, paras. = parasitised, pred. = predated.

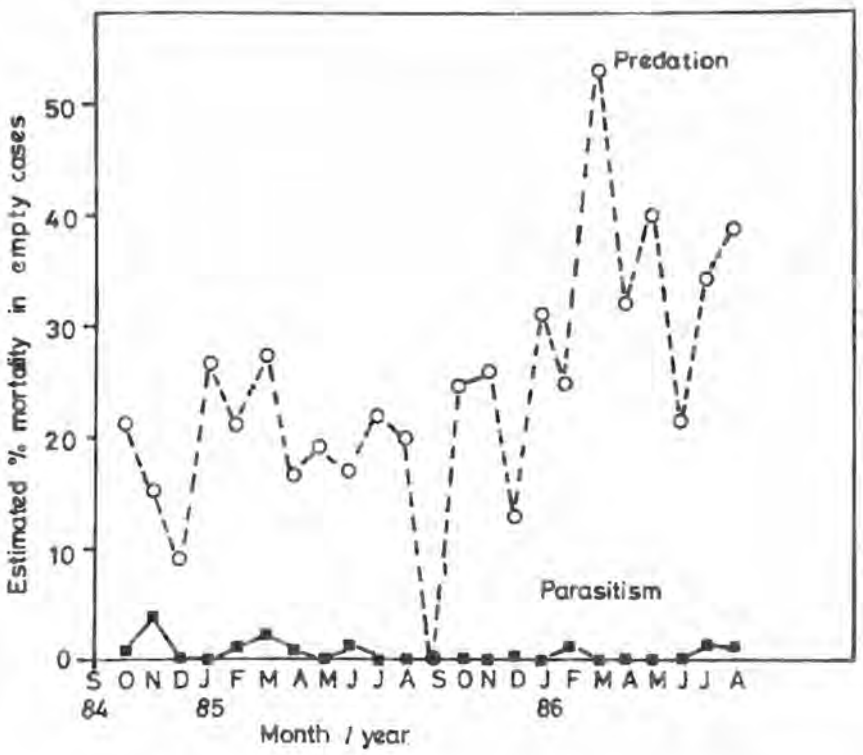

Fig. 20 - Seasonal variations in arthropod-induced damage assessed from empty puparial cases collected from the field.

Monthly predation in the cases ranged from 0.5 to 53.2% (mean = 24.0 ± 2.3%). In general, predation intensity was higher in 1985-86 than in 1984-85, and peaks of percentage predation in the two successive years occurred in the hot dry seasons, indicating that predation is perhaps more important in the dry season than in the wet seasons.

Table 21 (A) gives the incidence of damaged specimens from fourteen different sites over Transect I. Mean percent damage was 29.4 ± 2.6%. There was no significant relationship between percentage damage and density of the pupal cases (Fig. 21). This indicates that predation intensity does not vary in relation to density, but rather varies in relation to seasons. Similar observations were made in different vegetation types [Table 21(B)]. The average incidence of damaged puparia from 14 sites in the riverine thicket was 26.6% as compared to 24.7% from the 2 sites in the valley woodland. This difference was not significant (X^2 = 0.36, P> 0.10), indicating that predation intensity did not vary significantly between the two vegetation types.

Predated and non-predated puparial cases of G. pallidipes were compared with similar categories in non-tsetse puparia using Chi-squared test. The difference was found to be insignificant (X^2= 0.43, P> 0.05) In all 2,473 Glossina and 1,053 non-tsetse puparial cases were analysed for damage patterns (Table 22). Damage patterns in the two groups of puparial cases were similar suggesting that the predators attacking Glossina puparia also attacked puparia of other Dipteran and Lepidopteran insects occurring in the tsetse habitats. Damage intensity, however, varied in the two groups. The mean percentages of chewed, torn and holed cases in Glossina puparia were 19.4, 13.1, and 0.5 respectively, while the non-tsetse puparia had 17.4% chewed, 9.1% torn and 7.5% holed cases. The relatively high incidence of chewing imprints indicated that

Table 21 - Observational studies on natural predation in empty puparia of G. pallidipes collected at Nguruman, Kenya (March 1985 to August 1986).

(A) Site variations in arthropod-induced mortality in puparia

Site No.	No. of cases examined	No. damaged	% damaged
1	125	31	24.8
2	53	20	37.7
3	264	59	22.3
4	141	31	22.0
5	60	15	25.0
6	81	21	25.9
7	75	27	36.0
8	59	7	11.9
9	82	31	37.8
10	19	7	36.8
11	4	4	50.0
12	59	19	32.8
V1	281	64	22.8
V2	327	86	26.3

V1 and V2 are sites found in the Valley Woodland.

(B) Variations in arthropod-induced mortality in puparia in relation to vegetation types.

Vegetation type	No. of cases examined	Number damaged	% damaged
Riverine Thicket	1,022	272	26.6
Valley Woodland	608	150	24.7

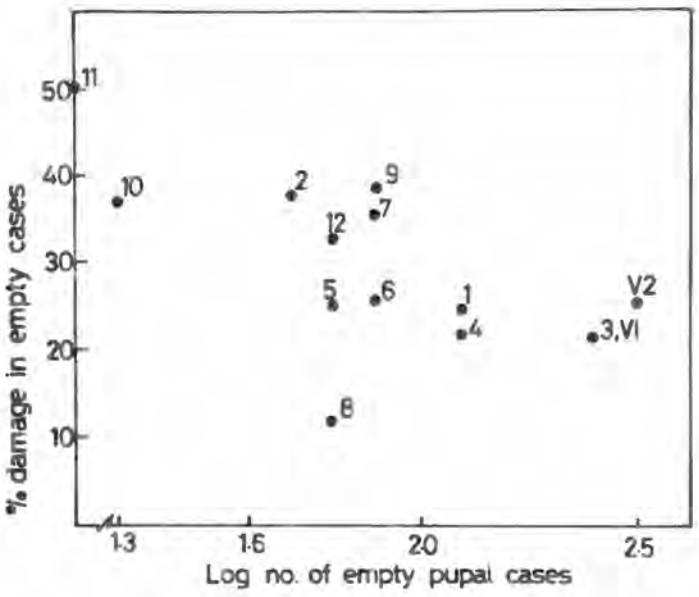

Fig. 21 - Relationship between arthropod-induced damage and density of pupal cases. Numbers refer to sites.

Table 22 - Damage patterns in empty puparial cases of G. pallidipes and other insects collected from December 1984 to August 1986. GP = Glossina pallidipes, OP = Puparia of other Dipteran and Lepidoptera insects.

Year/Month	Season	Puparia type	Cases examined	% chewed marks	% split marks	% Cases parasitised
1984						
Dec.	Short	GP	38	0	0	0
	rains	OP	6	0	16.7	33.3
1985						
Jan-Mar	Hot	GP	643	26.3	11.2	1.6
	dry	OP	160	2.5	11.9	5.0
Apr-Jun	long	GP	454	17.2	6.3	0.4
	rains	OP	65	4.6	9.3	6.2
Jul-Sept	Cold	GP	470	11.3	26.1	0
	dry	OP	158	25.9	12.0	7.6
Oct-Dec	Short	GP	288	21.2	17.2	0
	rains	OP	101	42.6	8.9	4.0
1986						
Jan-Mar	Hot	GP	255	20.0	15.7	0.4
	dry	OP	219	18.3	6.8	3.2
Apr-Jun	long	GP	154	20.1	9.7	0
	rains	OP	159	13.2	2.5	5.7
Jul-Aug	Cold	GP	171	32.2	4.7	1.2
	dry	OP	185	20.5	4.3	4.9

most of the predators attacking puparia were chewing predators.

Analysis of the locations of attack on damaged puparia of G. pallidipes did not reveal any definite pattern other than a preponderance of damage to the side and the anterior end, away from the polypneustic lobes, suggesting it is more difficult to damage the lobes.

7.3.2 CAUSES OF MORTALITY IN FIELD-COLLECTED PUPARIA OF G. PALLIDIPES

(i) PUPARIAL PARASITISM DUE TO EXHYALANTHRAX PARASITOIDS.

The puparia parasitoids were of the genus Exhyalanthrax (formerly named Thyridanthrax) of the family Bombyliidae. The two species found were E. lugens (Lw.) (78 %) and E. beckerianus Bezzi (22 %) (Plate 5).

Monthly fluctuations in apparent rates of parasitism along transect I are shown in Fig. 22 (A). The mean level of parasitism was between 10 and 12%. A close look at Table 11 and Fig. 22 (b) shows that monthly parasitism was generally low when host population was high. Although there were higher oscillations in host populations there was some degree of synchronization between the host and the fluctuations in percent parasitism, particularly between April and November 1985.

Table 23 suggests that parasitism rate was higher in the rainy seasons than in the dry seasons. It has been demonstrated in section 5.3.3 that the flies shift their sites from low-lying sites in the riverine thicket to valley woodland during the rainy season. There was considerable variations in rates of puparial parasitism in different years. The ranges were 0 - 11.5% for 90 puparia in 1984; 0 - 100% in 1985 from 251 puparia, while there was no parasite from 109 pupae collected in 1986. In general parasitism rate was higher in 1984-85 than in 1985-86.

There were also site variations in the rate of parasitism [Table 24

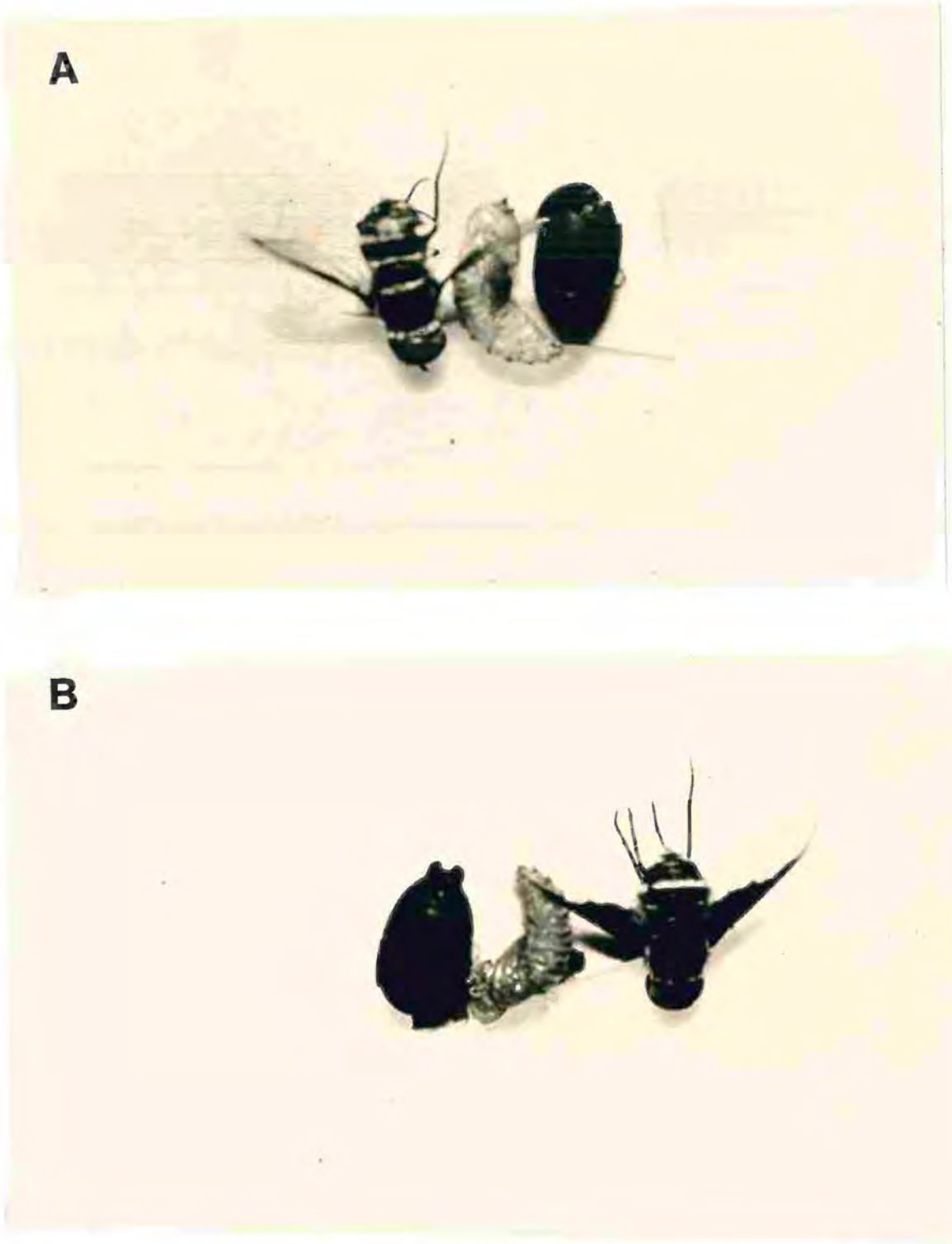

Plate 5 - Pupal parasitoids of G. pallidipes. (A) Exhyalanthrax lugens (Lw) and (B) Exhyalanthrax beckerianus Bezzi.

Table 23 - Seasonal fluctuations in percentage puparial parasitism due to Exhyalanthrax parasitoids over Transect I (October, 1984 to August, 1986)

Months	Seasons	1984 - 1985		1985 - 1986	
		puparia collected	percent parasitism	puparia collected	percent parasitism
Oct. - Dec.	Short rains	90	7.8	9	33.3
Jan. - Mar.	Hot dry	197	4.6	23	0
Apr. - June	Long rains	21	14.3	15	0
July - Sept.	Cold dry	24	12.5	71*	0

* Based on data for only July and August.

(A)]. Site 3 with a total of 48 puparia had 10.4% parasitism, while incidence in 32 puparia collected from site 8 was 12.5% and that in 23 puparia from site V2 was 21.7%. Variations between sites ranged from 0.0 to 21.7% with a mean of 5.8 $\pm$ 2.0%. There was no relationship between percentage parasitism and puparia numbers per site ($r = -0.24$, $P > 0.05$). Intensity of parasitism also varied in different vegetation habitats [Table 24 (B)]. While the incidence in 57 puparia from the valley woodland was 14.0%, that for the 393 puparia collected from riverine thicket was 3.6%. Mean parasitism for the two vegetation habitats was 8.8 $\pm$ 5.2%. The difference in level of parasitism in the two vegetation types, as compared by Chi-squared test, was significant ($X^2 = 5.03$, $P < 0.05$).

The relationship between percent parasitism and puparia density over three months periods was found to be inversely density dependent with a significant regression coefficient of $r = -0.50$, $P < 0.05$ [Fig. 22 (B)].

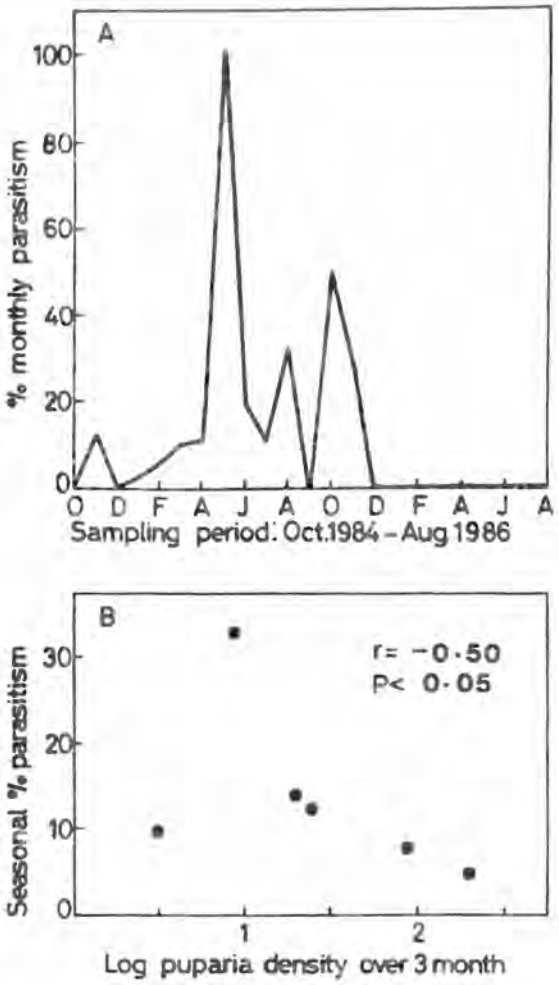

Fig. 22 - Pupal parasitism due to Exhyalanthrax parasitoids.
(A) Monthly fluctuations (B) Relationship with puparia density.

Table 24 - Fluctuations in rate of parasitism due to Exhyalanthrax species illustrating variations in different sites and different vegetation types.

(A) Site variations in % parasitism in puparia.

Site No.	Number of puparia collected	Number of parasites emerged	percent parasitism
1	47	2	4.3
2	24	0	0
3	48	5	10.4
4	46	0	0
5	29	0	0
6	41	0	0
7	64	0	0
8	32	4	12.5
9	25	0	0
10	6	1	16.7
11	1	0	0
12	30	1	3.3
V1	34	4	11.8
V2	23	5	21.7
Total	450	22	

(B) Variations in parasitism in different vegetation types.

Vegetation types	No. puparia collected	No. parasites emerged	% parasitism
Riverine thicket	393	14	3.6
Valley woodland	57	8	14.0
Total	450	22	

$X^2 = 5.03^*$

* $P < 0.05$

(ii) CAUSES OF NON-EMERGENCE OF FIELD-COLLECTED PUPARIA.

The causes and seasonal fluctuations of neither tsetse nor parasitoid emerging from puparia are summarised in Table 25. Non-emergence was due to developmental failures, emergence failures, pupal tissue degeneration and fungal infections. A small number of the dead parasitoids were found.

(a) Developmental failures.

Out of 134 dead puparia, 28 (20.9%) exhibited developmental failures which were encountered in all seasons. However, the percentage mortality due to this factor was higher in the long rainy seasons than in the dry seasons, whether hot or cold.

(b) Emergence failures.

Out of 134 dead puparia dissected, 24 contained adult flies which failed to emerge. Emergence failures were more commonly found in the hot dry seasons than in the wet seasons. The estimated ages of these unemerged adults, using the developmental ageing categories in Table 19, were as follows:-

Estimated age	No. in each group
14.0	1
19.5	3
23.0	4
26.0	6
28.0	10

(c) Pupal tissue degeneration

Seventeen (12.7%) of the 134 dead puparia contained degenerated tissue, most of which were found in the long rainy seasons and in the following dry seasons.

Table 25 - Seasonal fluctuations in causes of non-emergence and mortalities in puparia of G. pallidipes collected from the field from Nov. 1984 to Dec. 1985. Percentages in parenthesis.

Seasons	Number dissected	Developmental failures	Emergence failures	Pupal tissue degeneration	Fungal infections	Dead parasites in puparia
Short rains (Oct.- Dec.)	9	0	1 (11.1)	0	6 (66.7)	2 (22.2)
Hot dry (Jan.- Mar.)	107	23 (21.5)	17 (15.9)	12 (11.2)	52 (48.6)	3 (2.8)
Long rains (Apr.- June)	3	2 (66.7)	0 (0)	1 (33.3)	0 (0)	0 (0)
Cold dry (July - Sept.)	15	3 (20.0)	6 (40.0)	4 (26.7)	2 (13.3)	0 (0)
Total	134	28 (20.9)	24(17.9)	17 (12.7)	60 (44.8)	5 (3.7)

(d) Fungal infections

The total apparent loss due to fungi was 44.8% as compared with 20.9% developmental failure, 17.9% emergence failure and 12.7% pupal tissue degeneration (Fig. 23). The incidence of fungal infections was relatively higher in the latter part of the rainy season and early part of the dry season. In the short rains (Oct.- Dec.) 66.7% (N = 9) of the puparia were found with fungal infections, whilst one or two months after the rains in Jan. - March, 48.6% of the puparia (N = 107) had fungal infection.

It was not known whether the puparia died from the infection or the infection set in only after the death of the puparia. The fungal spores were isolated and cultured for identification by Dr. Kaaya and Mrs. Ochieng of the Microbiology Section at ICIPE. The species composition of fungi found infecting puparia of G. pallidipes at Nguruman comprised of Aspergillus niger, A. flavus, three Penicillium species, Rhizopus spp., Trichoderma spp. and one unidentified species. Prepupal stages of tsetse were exposed to the fungi in an attempt to determine their infectivity and their role in control of tsetse. At the time of writing this thesis, none of the fungi had as yet shown any significant effect on the puparia of tsetse.

(e) Puparia containing dead parasites.

Only 5 (3.7%) of the 134 puparia which failed to emerge contained dead parasites. Four of these were parasitoids of the Exhyalanthrax species, the remaining one was ?Syntomosphyrum species.

7.3.3 KEY FACTOR ANALYSIS OF MORTALITY RATES OF PUPARIA OF G. PALLIDIPES AT NGURUMAN, KENYA.

The life table data recorded in Table 26 assumed that mortalities

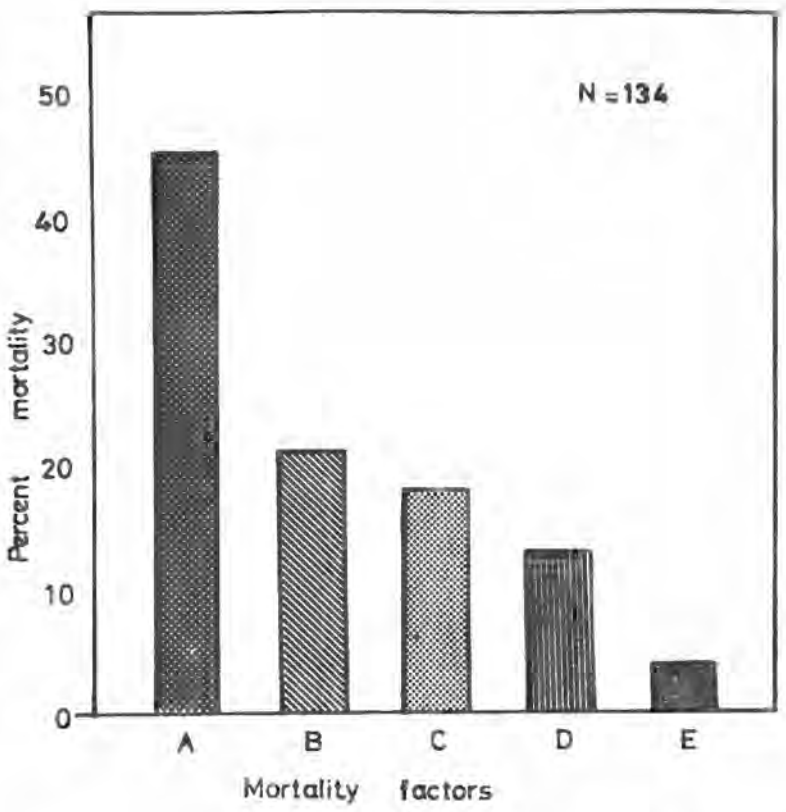

Fig. 23 – Overall percentage mortality in puparia of G. pallidipes due to (A) Fungal infections, (B) Developmental failures, (C) Emergence failures, (D) Degenerated puparia, (E) Dead parasites.

due to developmental and emergence failures (k_1), puparia tissue degeneration (k_2), parasitoid parasitism (k_3) and fungal infections (k_4) were sequential. Fig. 24 depicts the seasonal fluctuations in puparial mortality factors in which the submortalities expressed in k-values were plotted against months. The pattern of k_4 due to fungal infections was similar to that of total mortality from November 1984 to April 1985 indicating that this factor contributed greatly to the total population mortality during this period.

The role of each submortality factor was quantitatively evaluated by calculating the regression coefficient of the k-values of each submortality against the total mortality. Results of the analysis showed that mortality due to fungi (k_4) was the most significant factor ($r = 0.63$, $P < 0.05$; mortality due to puparia degeneration (k_2) was just significant ($r = 0.49$, $P = 0.05$), while mortality due to parasitization by Exhyalanthrax parasitoids (k_3) was not significant ($r = 0.13$, $P > 0.05$). Mortality due to developmental and emergence failures was also not significant ($r = 0.32$, $P > 0.05$).

Fig. 25 depicts the relationships between the k-values and the puparia densities on which they acted. A positive slope indicates a density dependent factor, while the values of the regression coefficients estimate the importance of their roles. With the exception of k_3, there was no relationship between the mortality estimates and pupal densities. Parasitised puparia (k_3) showed an insignificant curvilinear inverse density dependent relationship ($r = -0.43$, $P > 0.05$).

Fig. 26 shows the various k-values with the points joined in time sequence. Mortalities due to developmental and emergence failures (k_1), pupal degeneration (k_2, Fig. 26a) and to fungal infections (k_4, Fig. 26b) showed irregular zigzag patterns indicating that these are density independent factors. Pupal parasitism (k_3, Fig. 26b), on the other hand,

Table 26 - Apparent partial life table data of G. pallidipes at Nguruman.
(N = No. observed, k = k value.

Year	Montn		Puparia collected	Developmental & emergence failures	Puparia tissue degeneration	Parasitised puparia	Fungal infections	Adults emerging	Stage mortality
1984	Nov.	N	33	1	0	8	0	24	
		k		0.01	0	0.13	0		0.14
	Dec.	N	8	0	0	0	5	3	
		k		0	0	0	0.42		0.42
1985	Jan.	N	105	17	3	2	18	65	
		k		0.08	0.01	0.01	0.11		0.21
	Feb.	N	134	10	5	6	13	100	
		k		0.04	0.01	0.03	0.05		0.13
	Mar.	N	51	13	4	4	21	9	
		k		0.13	0.05	0.05	0.53		0.76
	Apr.	N	4	0	0	1	0	3	
		k		0	0	0.12	0		0.12
	May	N	2	0	0	2	0	0	
		k		0	0	0.30	0		0.30

Table 26 (cont'd)

Year	Month		Puparia collected	Developmental & emergence failures	Puparia tissue (k_2) degeneration	Parasitised puparia	Fungal infections	Adults emerging	Stage mortality
1985	June	N	10	2	1	2	0	5	
		K		0.10	0.05	0.15	0		0.30
	July	N	9	4	0	1	0	4	
		K		0.25	0	0.10	0		0.35
	Aug.	N	12	3	3	2	1	3	
		K		0.13	0.17	0.18	0.12		0.60
	Sept.	N	7	2	1	0	1	3	
		K		0.15	0.10	0	0.12		0.37
	Oct.	N	3	0	0	2	1	0	
		K		0	0	0.48	0		0.48
	Nov.	N	5	0	0	2	0	3	
		K		0	0	0.22	0		0.22
	Total	N	383	52	17	32	60	222	
		K		0.06	0.02	0.05	0.10		0.23

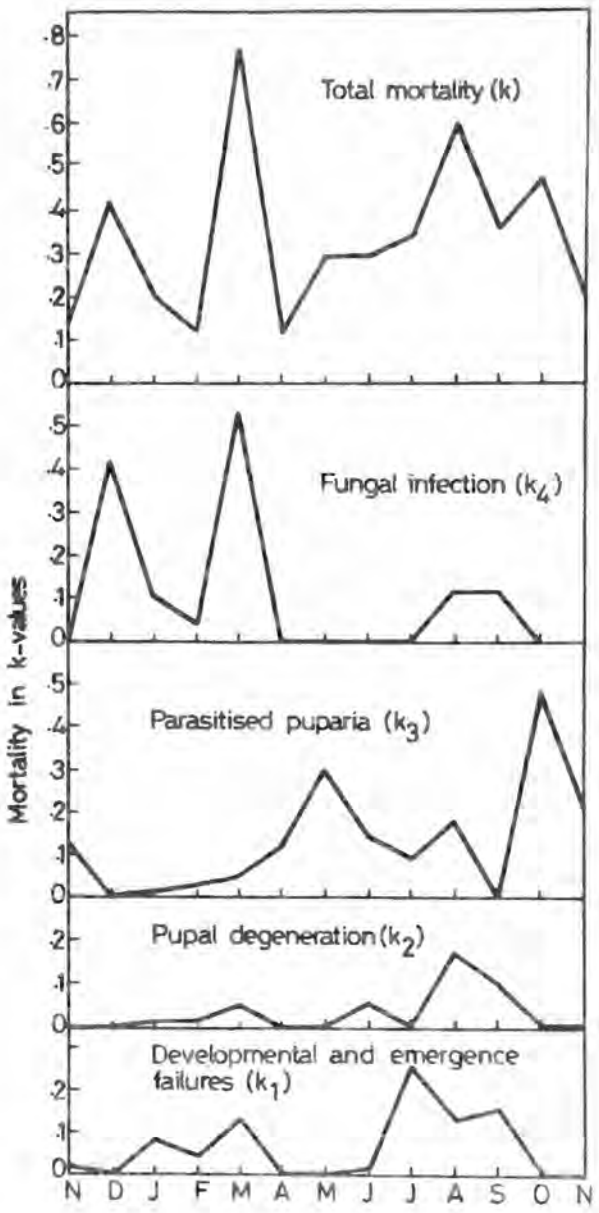

Fig. 24 - Recognition of key factor in seasonal variations in puparial mortalities (November, 1984 - November, 1985).

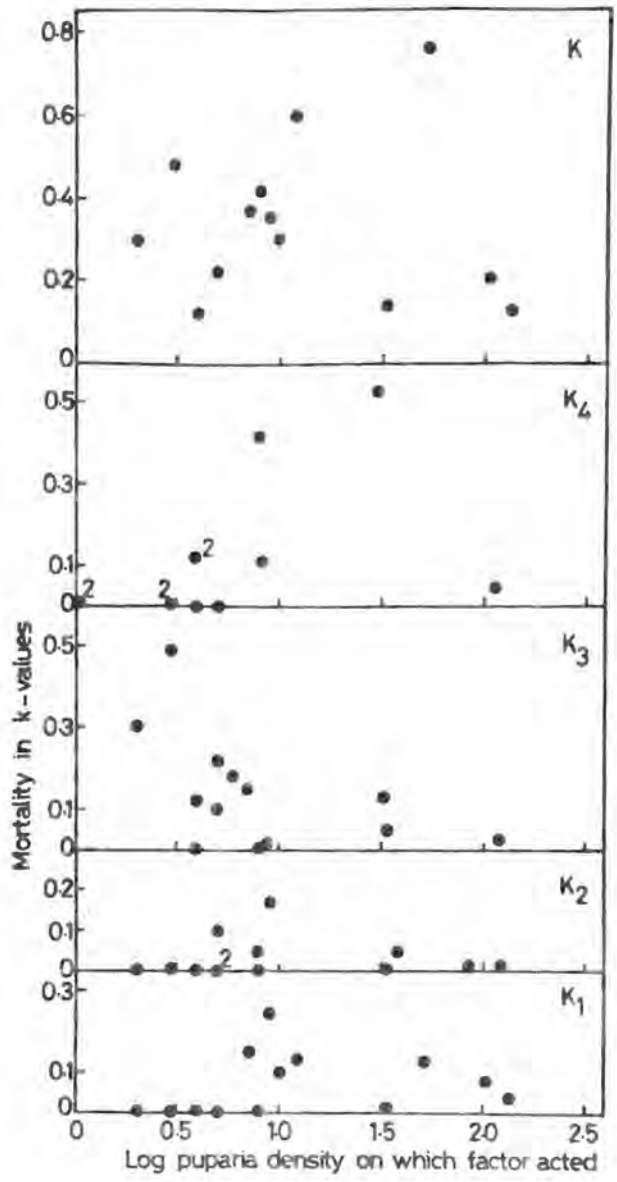

Fig. 25 - Relationship between k-values of submortalities and puparia densities on which they acted.

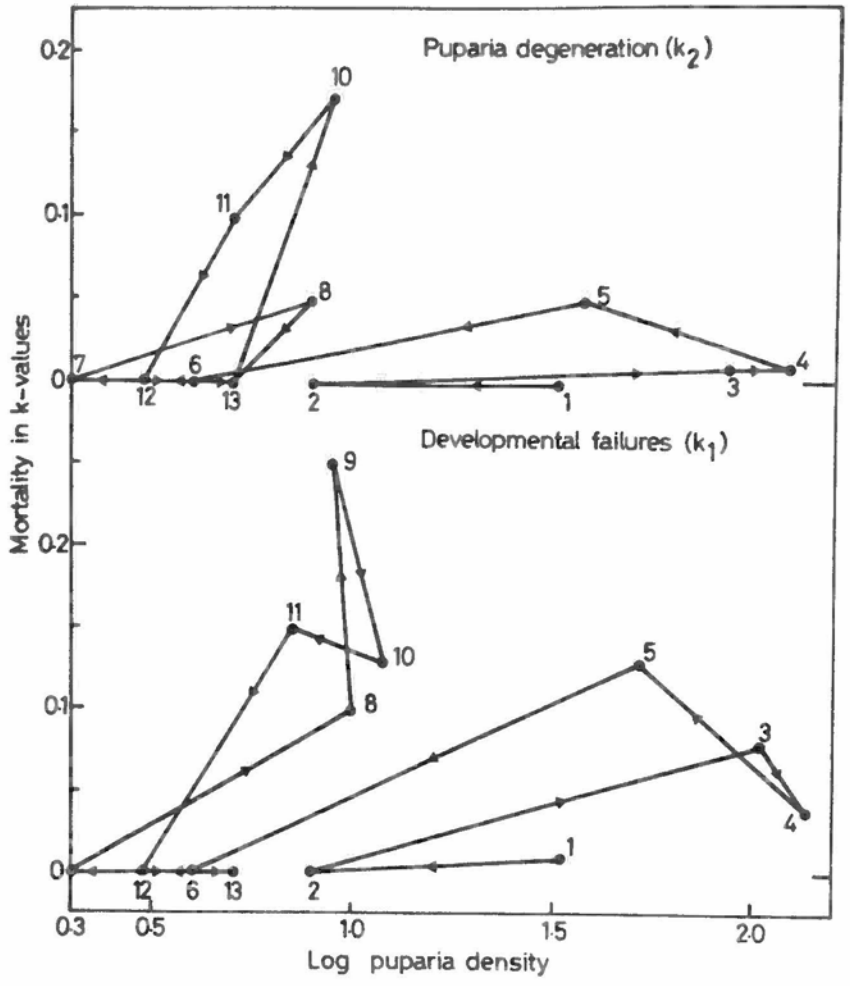

Fig. 26a - Relationships between k-values of developmental/emergence failures and puparia degeneration and puparia density with points joined in time sequence.

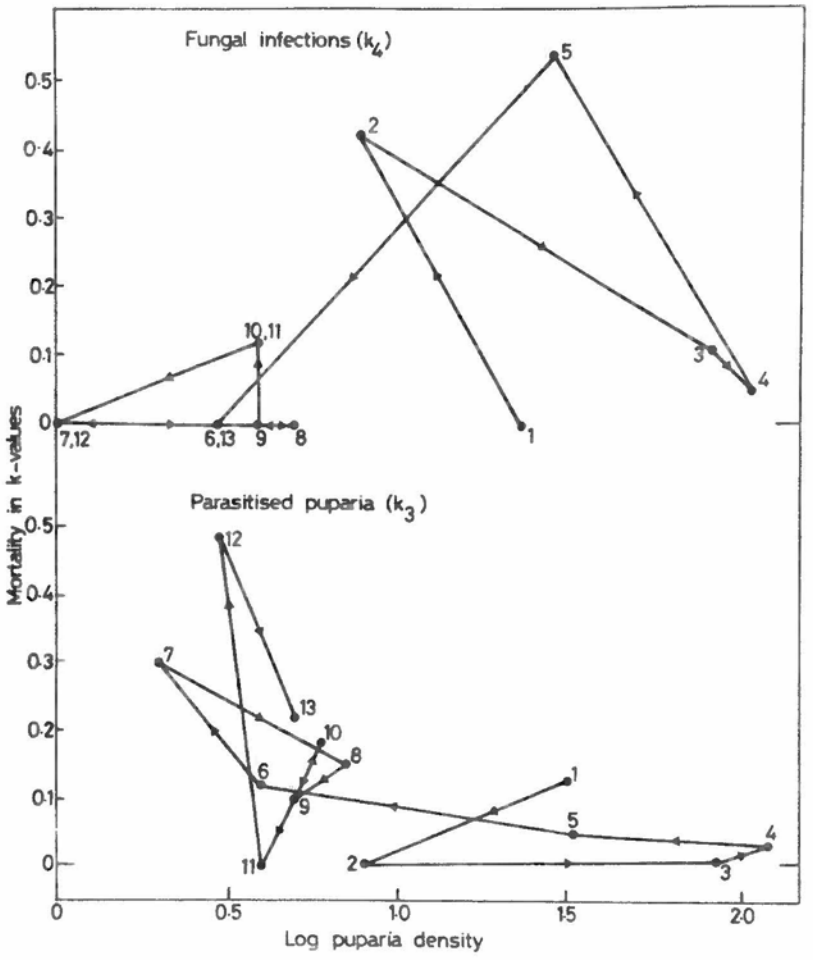

Fig. 26b - Relationships between k-values of parasitized puparia and fungal infections and puparia densities with points joined in time sequence.

showed an imperfect anticlockwise spirals during the first six months, indicating that parasitism due to Exhyalanthrax parasitoids might have a delayed density dependent component.

7.3.4 RELATIONSHIP BETWEEN PUPAL LOSS RATE, ESTIMATED FROM RELATIVE DENSITIES OF PUPARIA AND TENERAL FEMALE FLIES, AND PUPARIA NUMBERS.

Fig. 27 shows how pupal to teneral losses were positively related to pupal density in the previous month. This relationship is significant ($\ln Y = 1.26x - 1.63$, $r = 0.93$, $P < 0.001$), and demonstrates for the first time that there is a density dependent factor acting at a point between the puparial stage and the age when teneral flies become available to biconical traps. This may well be a major factor in the regulation of density of tsetse flies.

7.3.5 RELATIONSHIP BETWEEN K-VALUES FROM KEY FACTOR ANALYSIS AND CLIMATIC FACTORS.

Of all the climatic factors investigated, only RH of the same month was significantly related to mortality estimated from key factor analysis data ($r = -0.55$, $P < 0.05$).

7.3.6 RELATIONSHIP BETWEEN LOSS RATE BETWEEN PUPARIA AND TENERAL FLIES AND CLIMATIC FACTORS

None of the climatic factors in the same month was related to pupal loss rate estimated from relative densities of puparia and teneral flies of the following month. Only mean temperature of the previous month was significantly related to pupal loss rate ($r = 0.67$, $P < 0.05$).

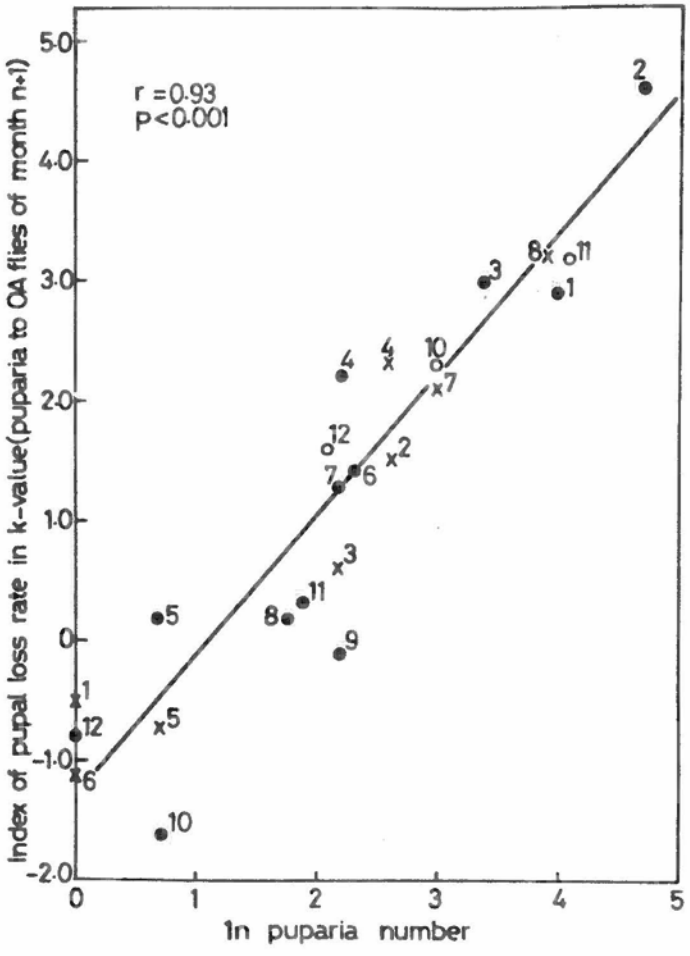

Fig. 27 - The relationship between monthly index of pupal loss, estimated from relative densities of puparia and teneral female flies, and puparia density. Numbers refer to months. O for 1984; ● for 1985; X for 1986.

7.3.7 RELATIONSHIP BETWEEN GENERATION MORTALITY AS ESTIMATED FROM MORAN CURVE AND CLIMATIC FACTORS

Rainfall, both in the same month ($r = 0.53$, $P < 0.05$), and in previous month ($r = -0.47$, $P < 0.05$) were significantly related to generation mortality estimated from the Moran curve, indicating that rainfall is an important density independent mortality factor.

7.4 DISCUSSIONS AND CONCLUSIONS

Predation as estimated from empty puparial cases averaged 22.1%. This value is quite high considering the protective nature of the puparia habitat. Disadvantages of estimating predation levels from empty cases are two-fold. First, levels of predation recorded were perhaps over-estimated because of damage that could have been caused during hand-searching for the cases. On the other hand, it is possible that the frequency of damaged puparia in natural populations was higher than observed because some predators devour the whole puparia without leaving any traces or evidence of their activities. Nevertheless, the results presented here give direct evidence of natural damage due to predation and parasitism, and the values are comparable to those observed by Lloyd et al.,(1927), who found that the proportion of damaged cases in their collections of puparia of G. palpalis on an island in Lake Victoria ranged from 3.1 to 31% in different spots. In Uganda, Fiske (1920) estimated a mean loss of 7% (N = 9000) with variations of 0 - 31%. In Tanzania, Nash (1933a) observed Melyris pallidiventris (Coleoptera; Melyridae) predating puparia but did not give estimation of the predation intensity.

The peaks of percentage predation in the two successive years under study occurred in the dry seasons, indicating that predation is perhaps more important in this season. The absence of any relationship between predation intensity and density of empty pupal cases suggests that the agents responsible for the damage are not specific to tsetse and thus do not respond to changes in the puparia density. The difference observed in predation intensity in the riverine thicket and valley woodland was not significant. This suggests that predation is perhaps more related to seasons than to habitats.

Exhyalanthrax lugens and E. beckerianus were the most important dipteran parasitoids recovered from puparia of G. pallidipes. The former has also been found in G. tachinoides and G. morsitans in Nigeria (Taylor, 1932); in G. palpalis in Tchad; in G. swynnertoni in Tanzania (Mulligan, 1970), and in G. morsitans and G. pallidipes in Kenya (Hursey, 1970). E. lugens is also widely distributed in Kenya, Zimbabwe, Tanzania, Malawi and Zambia, and has been found in G. pallidipes, G. austeni and G. brevipalpis (Laird, 1977). The mean percentage parasitism was 12.3 ± 4.5. This is lower than 18.4% parasitism due to E. abruptus found in Glossina pallidipes in Machakos, Kenya (Hursey, 1970). In Tchad, incidence of E. beckerianus in G. tachinoides was between 4 and 25% (Gruvel, 1975b). The general low levels of pupal parasitism due the Exhyalanthrax parasitoids found at Nguruman are comparable to those recorded by Saunders (1960), and Minter (1971) in other tsetse species including G. pallidipes in various parts of East Africa. The higher rates in the rainy seasons could be due to artifact resulting from the longer time spent within the tsetse puparia by the parasitoids, for after the healthy tsetse hatched only the parasitised puparia remained.

There are several possible reasons for the low rates of parasitism. It could be due to differences in host and parasite fecundity which prevent the parasites from catching up with the host population. Exhyalanthrax also probably only parasitize larvae which have just been larviposited or found burrowing into the soil. The difficulty experienced by the parasitoids in locating the buried puparia may, at least, partly account for the low rates of parasitism. It is likely that the ability of the parasitoid larvae to penetrate tsetse puparia will be reduced after complete sclerotization. These parasitoids were found commonly parasitizing other Diptera at Nguruman. Heaversedge (1970) and Hursey

(1970) have also observed these parasitoids in other insect pupae in various soil habitats. These parasitoids are therefore not specific and other members of Diptera and Lepidoptera in the area are probably more susceptible to parasitism.

Another probable important factor in the dynamics of the puparia and the rates of parasitism is the large proportions of predatory arthropods found in the sites. These may be exerting some degree of pressure on the early pupal stages and thus reduce the numbers available for parasitization. The full potential effect of Exhyalanthrax could have been masked by these predators, since they would consume parasitised and non-parasitised puparia indiscriminately and consequently deny the parasite its full numerical response potential.

At Nguruman, with seasonal extremes of temperature and saturation deficit, it was suspected that climatic stress would be strong. The notable seasonal variation in rates of dead puparia in field samples supported this. All causes of non-emergence observed in the present study have been reported in the literature for laboratory colonies and in natural populations of Glossina species (Buxton, 1955; Mulligan, 1970; Laird, 1977; Challier, 1982). The developmental failures could be due to larvae being deposited prematurely, effects of adverse environmental conditions, or occured as a result of endogenous physiological disabilities or hormonal imbalance (Jack & Williams, 1937; Jack, 1939; Vanderplank, 1948a). Emergence failures, on the other hand, could have resulted from hormonal disorders, climatic factors, diseases or a combination of these factors which prevented the puparia from successfully completing their development up to emergence of adults. Rotten or degenerated puparia could be attributed to effects of flooding which caused death probably through drowning, and asphyxia which ultimately led to tissue degeneration/ decomposition.

Fungal infection was the major cause of non-emergence of puparia, and its rate was high in the rainy seasons which provided the favourable humidity for fungal growth. Similar facts were presented for puparia of G. tachinoides in Gadau, Nigeria (Nash, 1933b, 1939) and by Pomeroy (1930) for both G palpalis and G. tachinoides in the Volta basin in Northern Ghana. Most of the fungal species are generally saprophytic in nature suggesting that infections might have occurred after the death of the puparia. However, A. flavus produces aflatoxin, a very potent toxin which could cause death in live puparia, it is therefore possible that some of these fungi may be facultative pathogens. It has been suggested that conditions experienced by field-collected puparia during maintenance in the laboratory cause mortality. This possibility cannot be ignored. Thus although proportion of dead puparia varied in different sites and in different seasons, their levels could have been increased because of further mortality which could have occurred in the pupal room.

The key factor analysis carried out on causes on non-emergence sheds some light on the main causes of mortality and the way in which they were acting. Fungal attack was identified as the key factor but until fungal pathogenicity is tested more thoroughly, the cause of this mortality must remain uncertain. It was apparent that parasitism due to Exhyalanthrax species was low, patchy and inversely density dependent. It therefore did not appear to be significant in puparia population regulation. Some level of delayed density dependence was detected, and because this parasitism was not a key factor, any tendency for oscillations due to this factor will tend to be obscured by other important factors due to changes in climate, diseases etc.

The most likely reason for the inverse density dependent relationship is the accumulation of parasitised puparia because of the longer

pupal duration of the parasitoid. When the rains come and tsetse switch their larviposition sites this will result in very high proportions of parasitised puparia in the former sites. Other possible hypotheses have been presented by various authors for changes in density dependent parasitism in relation to host densities. Morrison et al. (1980) showed that by manipulating the distances between the leaves bearing eggs of the host, they found the relationship between per cent parasitism by Trichogramma and the host density varied from inverse density dependent to density independent as separation distance was increased. It has been pointed out in Chapter 4 of this thesis that densities and distances between puparia differ in different sites of different sizes and this situation could also help to explain the complex density relationships shown by Exhyalanthrax species to the variable densities of tsetse puparia in the field. It follows that the percent parasitism will vary from density dependent relationship in small sites with short distances between the puparia to density independent or inverse density dependent in large sites with long distances between the puparia.

Although none of the non-emergence mortalities were density dependent, the pupal loss rate estimated from the relative densities of puparia and teneral female flies was found to be significantly density dependent. The mortality slope of the pupal losses was found to be close to one which indicates that the degree of control exercised by the natural density dependent mortality at the puparia stage compensates for the changes in population density. The conclusion drawn from this mortality curve is that density dependent mortalities at the pupal stage are extremely important in regulating the population of G. pallidipes at Nguruman. The question then is "At what point is the density dependent process operating?. Could it be before the larvae burrowed into the

soil; while the puparia were buried in the soil; or while the teneral flies were emerging from the soil?. To answer this question further investigations are required on the larviposition behaviour of adult females, the burrowing behaviour of the larvae and the emergence behaviour of the teneral flies in the larviposition sites. This should reveal the actual stage in the cycle on which the density dependent factor operates. What could be causing this density dependent mortality at the pupal stage?. At this stage the agents responsible for this mortality are unknown, but attempts will be made in the next two chapters to identify predators which attack tsetse in their natural environment.

CHAPTER EIGHT

8. TRAPPING STUDIES ON POTENTIAL PREDATORS OF GLOSSINA PALLIDIPES AT NGURUMAN

8.1 INTRODUCTION

Data presented in the previous chapter suggested that predation was an important component of the overall mortality of tsetse puparia at Nguruman. Here results are given of trapping studies on the various potential predators of both pupal and adult tsetse. Numerous instances of predation on tsetse have been reported by different tsetse ecologists in the past, and the literature on the subject has been reviewed by Saunders (1960), Glasgow (1963), Jenkins (1964), Mulligan (1970), Gruvel (1975b), Laird (1977), Herting (1978) and Challier (1982). All these reviews indicate that Glossina species have numerous natural enemies which may contribute more or less to the natural regulation of tsetse. A list of natural enemies known to attack G. pallidipes is given in Appendix 4 with references, and the families given here were used to define potential predators.

Although these predators fall in the class of natural control factors, they have not received serious attention because they are generally polyphagous. The failure to consider such predators in population suppression of tsetse species reflects the interest in control that is biased toward a monophagous species which show high specificity and has a reciprocal density dependent relation with its host (Huffaker and Messenger, 1964; Huffaker and Kennett, 1966). However, a study on the regulatory role of predators is needed for the development of ecologically safe management strategy for control of tsetse in the

rapidly changing African environment. The suppression of insect vectors by chemical and other means inevitably interferes with the natural control and regulation processes, and it is only when such processes are fully understood that they can be manipulated in vector control programmes to maximize suppressions while at the same time minimizing cost and environmental hazards.

The present study was therefore carried out to study major predators influencing the population of G. pallidipes at Nguruman, South-west Kenya.

The objectives are :-

1. to develop a simple trapping methodology for sampling the natural enemy complex;

2. to study the prevalence, distribution and abundance of major potential predators in relation to climatic factors; and

3. to study the relationship between densities of the various potential predators in relation to densities of tsetse puparia and adults.

8.2 MATERIALS AND METHODS

8.2.1 TRAPPING OF POTENTIAL PREDATORS IN LARVIPOSITION SITES OF G. PALLIDIPES

Faunal surveys were carried out to determine which groups of potential predators were prevalent in the study area. The populations were then monitored between October 1984 and August 1986 in sixteen larviposition sites and in some sections of the riverine thicket and the valley woodland on Transect 1. (refer to Fig 2).

A network of 8 unbaited pitfall traps, 4 banana-baited pitfall traps and 4 water traps were positioned inside larviposition sites to capture predators which either attack puparia or larvipositing or emerging adults. The pitfall traps consisted of 1 liter capacity glass jars sunk in a vertical position into the soil so that the mouths were level with the soil surface. They contained water to which detergent and formalin had been added to kill insects that fell into the traps. The banana-baited traps were used to trap live predators which were used in the laboratory predation studies. The water traps consisted of metal enamelled trays measuring 35 x 26.5 x 4 cm mounted at a height of 30cm from the ground on wooden stands. They contained water to which approximately 10 ml of a wetting agent (detergent) and about 5 ml of preservative (picric acid or formaldehyde) had been added. In the dry season additional water was added to compensate for evaporation and in the wet season extra detergent and formaldehyde were added to prevent dilution. All the sites were chosen at the beginning of the investigations and were in general maintained throughout the trapping period. Sampling took place at monthly intervals and traps were allowed to catch samples continually for 72 hours every month. All traps were emptied at 24 hour intervals in the same order on every occasion.

Possible predators and parasitoids were removed with forceps and placed in 80% ethanol to which glycerol had been added.

In addition to trapping, leaf litter, vegetation and soils at sampling sites were searched for two man-hours and all predators that were found were counted. The gut contents of some predators were dissected out for subsequent detection of tsetse in their diet by the serological technique described by Ouchterlony and Nilsson (1979). Counts of samples from all the different traps were combined and used for estimating fluctuations in the relative densities of the different predators in different months. Catches of different traps were compared to find their relative efficiency in trapping the predators.

8.2.2 TRAPPING METHODOLOGY IN GENERAL HABITAT FOR POTENTIAL PREDATORS OF ADULT G.PALLIDIPES

Populations of potential predators of adult tsetse outside the larviposition sites were monitored using stationary biconical traps and moving parties using hand-nets. Two areas of Transect 1 both running close to watercourses, one in the riverine thicket and the other in the valley woodland were selected for monthly hand-netting of predators. A group of 5 catchers with hand-nets moved along a defined path of known lengths of the habitat (1 km in the woodland and 0.80 km in thicket) and stopped occasionally and captured predators seen either actively flying or resting on rocks, vegetation in the footpaths, or grasses from tracks in the vegetation near larviposition sites. Approximately 7 1/2 man-hours and 5-man hours were spent in the valley woodland and riverine thicket respectively every month and predators captured in different habitats were kept separately and counted. Gut smears of the predators were taken for serological analysis. Data analyses were the same as for the pupal predators.

8.2.3. IDENTIFICATION OF POTENTIAL PREDATORS

Some identification of predators were carried out by the author. Other predators were stored in 80% alcohol with glycerol or pinned dry until they could be identified by comparison with a reference collection in the National Museum of Kenya in Nairobi (NMK). Both the identified and the unidentified specimens were sent to staff of the Museum for identification and/or verification of identification. The following persons provided identification services in NMK and Commonwealth Institute of Entomology, Britain (CIE) : Solifugae - Ali Mohammed (NMK) and D. MacFarlane (CIE); Asiliidae - Robert Lavigne, Univ. of Wyoming, USA (temporarily at NMK); Coleoptera - John Ngoroge (NMK); Orthoptera - Micnael Mungai (NMK); Lepidoptera - M. Clifton (NMK); Araneae - M. Ritchie and Susan Wangari Kimani (NMK); Diptera and Hymenoptera - Joseph Munhagani (NMK).

8.2.4 DETERMINATION OF THE RELATIONSHIP BETWEEN PREDATOR ABUNDANCE AND CLIMATIC FACTORS AND TSETSE NUMBERS.

For each of the potential predator groups selected for detailed study, the changes in their relative densities were related by regression analysis to climatic indices.

Changes in log transformed data on puparia numbers (N + 1) from monthly hand-searching method were related separately to changes in population numbers of ants and crickets, and densities of adult tsetse flies were related to spiders and asilids. The objectives were first to demonstrate their effect on the population, and secondly to identify the manner in which their influence was exerted.

8.3 OBSERVATIONS AND RESULTS

8.3.1 PREDATORS IN LARVIPOSITION SITES OF G. PALLIDIPES AT NGURUMAN.

(i) Species composition.

In the larviposition sites the natural enemies most likely to predate on G. pallidipes are : -

(a) those that attack puparia in the soil. These include Carabidae and Elateridae (Coleoptera); Formicidae (Hymenoptera); Gryllidae (Orthoptera); immature stages of soil-inhabiting arthropods and birds;

(b) those that attack the emerging tsetse on ground or gravid females larvipositing their larvae. These include Attidae and Lycosidae (Araneae); Scorpionidae and Solifugae (Arachnida); lizards (Reptilia), toads (Amphibia) and birds; and

(c) those that attack adult tsetse resting on tree trunks and branches, which include ants, spiders, wasps, asiliids, lizards and birds.

The species composition of potential predators caught in the larviposition sites is listed in Table 27. Many of the predators could only be identified to generic level. A few predatory bug, Physorhynchus erythroderus Schaum. (Hemiptera : Reduviidae) were caught, but because these were found in very small numbers they were not considered important predators. Many amphibians (mainly toads) were also collected. The amphibians were found in relatively low numbers throughout the study period except in the rainy seasons when a peak of 35 was reached in June 1985. They are therefore considered potential adult predators only within that period, though I failed to find positive evidence from examination of stomach contents of 74 toads.

Table 27 - Species composition of potential predators caught in larviposition sites of *G. pallidipes* at Nguruman.

POTENTIAL PUPARIA PREDATORS

INSECTA

HYMENOPTERA

Formicidae

Polyrachis spp.

Pheidole spp.

Camponotus spp.

Odontomachus spp.

Paltothyreus cibrinodis

Paltothyreus spp.

Acantholepis spp.

Viticicola spp.

COLEOPTERA

Carabidae

Campalita chlorostictum Dejean

Tefflus jamesoni Bates

Chlaenius ?paulae Gerst

Cypholoba trilunata Gerst

Elateridae

Tetralobus smuckardi Hope.

ORTHOPTERA

Gryllidae

Gryllus spp.

Gryllulus spp.

Homoeogryllus spp.

Liogryllus bimaculatus

Liogryllus spp.

Phaeophillacris spp.

Scapsipedus spp

Gryllotalpidae

Gryllotalpa africana

DICTYOPTERA

Blattaria

Epilampra spp.

?Pseudoderopeltis spp.

HEMIPTERA

Reduviidae

Physorhynchus erythroderus Schaum.

Table 27 (cont'd)

POTENTIAL ADULT PREDATORS

ARACHNIDA

ARANEAE

Lycosidae	Tetragnathidae
Salticidae	Philodromidae
Tnesiidae	Clubionidae
Araneidae	Attidae
Pholcidae	Palpimanidae
Oxyopidae	Scytodidae

SOLIFUGAE

Rhagodidae

Rhagodoca spp.

Rhagodessa spp.

Galeodidae

Galeodes spp.

Korschiidae

?*Lipophaga* spp.

Daesiidae

Biton ?*tigrinus* (Pocock)

Solpigudae

Solpuga spp.

AMPHIBIA

SCORPIONIDA

Buthidae

Parabuthus liosomoma (Hemprich and Ehrenberg)

Buthotus trilineatus (Peters).

(ii) Comparison of trapping systems

Relative densities of predators caught in unbaited and baited pitfall traps, water traps and during constant time searches are recorded in Tables 28, 29, 30 and 31 respectively. Unbaited pitfall traps (Table 28) were effective in capturing predators like Gryllidae, Formicidae, Araneae and Amphibians found walking, crawling or hopping within the larviposition sites. A few Formicidae and Araneae may also have fallen from the overhead vegetation. The catches from these traps were of course a measure of both activity and density. In general, the pitfall traps caught the highest numbers of Formicidae and Gryllidae, and mean catches of these two predators differed significantly from that of other predators. Baited pitfall traps (Table 29) which used banana captured Formicide ants, Gryllidae and other arthropods which were naturally attracted to odour of decaying fruit. Though the catches were similar to those from unbaited traps in species composition, they contained lower proportions of all predator groups. Since these traps contained no killing agent and thus caught live arthropods, the low incidence of Hemiptera and larvae/grubs in these traps were attributed to predation by ants, beetles and spiders which were also found in the traps. The bait had no significant effect on the catch sizes over that of unbaited traps, but they did supply live predators for further experimental work.

It was hoped that water traps (Table 30) would be useful for sampling Asiliidae, Exhyalanthrax species and other predatory Diptera and Hymenoptera, but very few of these insects were caught. However, various species of dipteran insects which visit animals in the larviposition sites either to feed on their blood (Tabanids, Stomoxys, Glossina, Haematobia, Hippoboscids and mosquitoes of the Aedes and Anopheles species), or on their secretions (Muscids and scarabid beetles) were caught in the

Table 28 - Relative abundance (total numbers) of potential predators of *G. pallidipes* caught in unbaited pitfall traps.

Year	Month	Formicidae	Gryllidae	Araneae	Amphibians
1984	Oct.	40	29	11	0
	Nov.	12	12	6	0
	Dec.	11	16	15	0
1985	Jan.	71	26	16	1
	Feb.	0	0	0	0
	Mar.	19	40	17	0
	Apr.	3	3	7	1
	May	1	1	4	4
	Jun.	6	11	10	19
	Jul	32	21	10	9
	Aug.	30	23	7	1
	Sep.	32	23	5	0
	Oct.	75	153	13	0
	Nov.	2	115	11	2
	Dec.	11	58	10	1
1986	Jan.	32	52	21	3
	Feb.	39	85	19	0
	Mar.	265	59	22	1
	Apr.	78	79	11	0
	May	-	-	-	-
	Jun.	36	11	17	2
	Jul.	68	19	20	0
	Aug.	61	12	9	0
	Total	924	848	261	44

Table 29 - Relative abundance (total numbers) of potential predators caught in banana-baited pitfall traps.

Year	Month	FORMICIDAE	GRYLLIDAE	ARANEAE	AMPHIBIANS
1984	Dec.	10	2	4	0
1985	Jan.	0	0	0	0
	Feb.	3	3	2	0
	Mar.	12	3	1	0
	April	5	0	0	0
	May	0	9	2	0
	June	1	3	4	6
	July	3	2	5	4
	Aug.	7	14	1	1
	Sept.	0	5	2	0
	Oct.	1	13	1	0
	Nov.	4	28	0	0
	Dec.	15	44	5	0
1986	Jan.	2	16	6	0
	Feb.	8	15	7	0
	Mar.	23	11	4	0
	April	18	13	3	0
	May	-	-	-	-
	June	17	8	4	0
	July	2	0	2	0
	Aug.	14	0	2	0
	Total	145	189	55	11

Table 30 - Relative abundance (total numbers) of potential predators of G. pallidipes caught in water traps.

Year	Month	Formicidae	Grylliidae	Araneae	Hymenoptera
1984	Oct.	0	19	8	19
	Nov.	0	1	2	7
	Dec.	0	1	0	19
1985	Jan.	0	3	1	7
	Feb.	0	2	0	1
	Mar.	0	20	5	7
	April	0	7	3	6
	May	0	0	0	1
	June	0	2	2	2
	July	0	1	0	5
	Aug.	0	1	7	15
	Sept.	0	8	1	10
	Oct.	0	0	2	18
	Nov.	0	1	0	6
	Dec.	0	0	4	4
1986	Jan.	0	1	1	0
	Feb.	1	4	1	10
	Mar.	3	2	2	8
	April	1	1	2	2
	May	-	-	-	-
	June	2	1	0	0
	July	2	0	2	2
	Aug.	0	0	0	2
	Total	9	75	43	151

Table 31 - Relative abundance (total numbers) of potential predators of Glossina pallidipes from 2-man hour searches in the larviposition sites at Nguruman, Kenya.

YEAR	MONTH	FORMICIDAE	GRYLLIDAE	ARANEAE	LARVAE[1]	CHILOPODA	BLATTERIA
1984	Oct.	1	3	0	1	0	0
	Nov.	3	0	1	21	1	0
	Dec.	8	3	3	266	3	1
1985	Jan.	1	5	2	31	4	2
	Feb.	2	7	1	18	5	1
	March	2	14	3	110	9	3
	April	3	11	6	139	8	6
	May	0	6	3	4	8	4
	June	0	1	5	8	10	2
	July	0	1	1	0	3	0
	Aug.	0	1	4	8	0	0
	Sept.	0	0	3	3	0	0
	Oct.	1	2	0	0	0	0
	Nov.	0	1	1	0	0	0
	Dec.	8	6	9	376	7	3
1986	Jan.	7	20	14	45	12	1
	Feb.	7	41	10	68	4	0
	March	18	28	14	5	0	1
	April	6	12	8	10	1	3
	May	28	18	7	83	15	5
	June	159	20	29	57	24	2
	July	30	12	7	9	3	2
	Aug.	31	8	5	0	0	1
Total		315	220	136	1,262	117	37

1 Larvae = Dipterous and Coleopterous larvae.

traps. Araneae were found in all traps in high numbers, while toads were caught only in unbaited and baited pitfall traps which gave evidence of traps sampling different levels of the habitats.

The pitfall traps were the most effective for Gryllidae and Formicidae, while the constant time searches were best for Coleopteran grubs and larvae. With the exception of Coleopteran grubs and Blatteria, the catches from constant time searches (Table 31) were comparable to catches from the baited and unbaited pitfall traps. Comparison of mean catches of different predators in various traps by Duncan's Multiple Range Test are given in Table 32. The trap type effect was significant ($F = 6.61$, $P < 0.001$).

Table 32 - Comparison of mean catches in the larviposition sites.

Trap type	Formicidae	Gryllidae	Araneae
Unbaited pitfall traps	43.9 a	38.5 a	11.9 b
Baited pitfall traps	7.3 b	9.5 b	2.8 b
Water traps	0.2 b	3.4 b	2.0 b
Constant time search	13.7 b	9.6 b	5.9 b

Means followed by the same letter are not significantly different at $P < 0.05$.

(iii) Spatial and temporal variations in densities of predators caught in the larviposition sites.

Fig. 28 shows monthly fluctuations in the relative abundance and distribution of Formicidae, Gryllidae and Araneae caught in various traps (combined data of all traps), in the larviposition sites.

Seasonal fluctuations in the relative densities of Gryllidae, Formi-

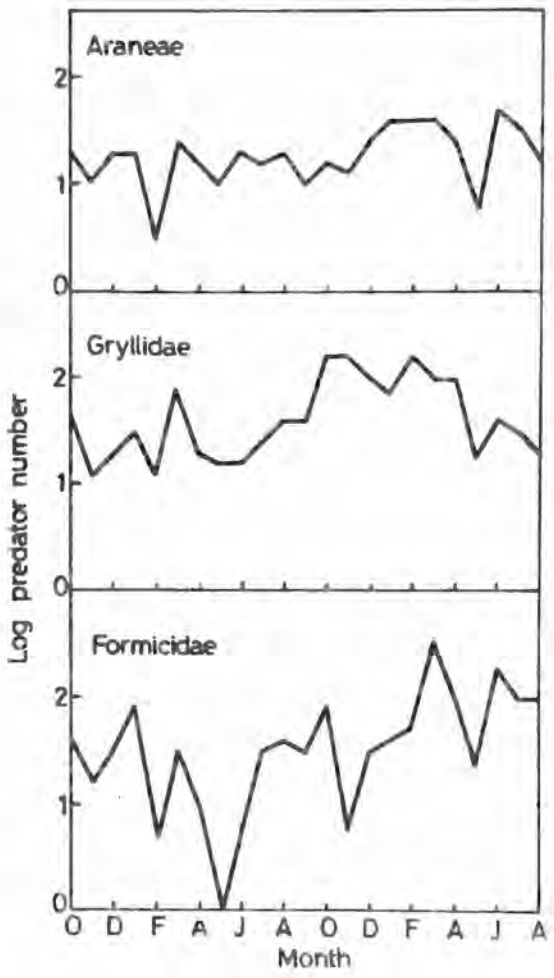

Fig. 28 - Monthly fluctuations in population of potential predators caught in the larviposition sites.

-cidae and Araneae in the larviposition sites are summarised in Table 33. All the predators were more numerous in 1985-86 than in 1984-85. In 1984-85, the numbers of Formicidae and Gryllidae were generally higher in the

Table 33 - Seasonal fluctuations in the abundance of potential predators trapped in the larviposition sites. All traps combined.

Season	Months	Total numbers of predators from all traps					
		Formicidae		Gryllidae		Araneae	
		a	b	a	b	a	b
Short rains	Oct-Dec.	85	117	86	421	50	56
Hot dry	Jan-Mar.	110	405	123	334	48	121
Long rains	Apr-June	18	344	54	163	46	81
Cold dry	July-Sept.	104	208	100	51	46	47

a - 1984-85 b - 1985-86.

dry seasons than in the rainy seasons, while the Araneae showed no clear trends. In 1985-86, numbers of all predators showed no clear trends.

8.3.2 PREDATORS IN GENERAL TSETSE HABITAT AT NGURUMAN.

(i) Species composition

The most dominant predatory dipteran group was the Asilidae. The genera represented were Alcimus spp., Promachus binucleatus Bezzi., Promachus spp., Lamyra gulo Loew., Hoplistomerus mobilis Loew., Ommatius spp., Hoplistomerus spp., Sticnopogon spp., Stenopogon spp., Proagonistes spp. There were also 11 unidentified species.

The Odonata were identified only to the generic level. The most abundant groups included Hadrothemis, Brachythemis, Crocothemis, Trithemis, Olpogastria, Philonomon, Palpopleura, Orthethrum (Libellulidae); Petalia (Petaluridae); Phyllomacronia (Corduliidae); Chlorocypha and Platycypha (Chlorocyphidae); Phaon (Agriidae); Lestes (Lestidae).

Hymenoptera were dominated by members of Eumenidae, Sphecidae and Vespidae. The Eumeniidae comprised of Eumenes maxillosus f. fenestralis Sauss, E. campiformis f. formusus Sauss, E. maxillosus de Geer and Synagris abyssinica Gaerin. The Sphecidae were made up of Bembex moebii Handl., B. forcipata Handl., B. olivata Dahl., Tachytes melancholicus Arn. T. observabilis, Tachysphex sericeus Sm., Cerceris nasidens Schltt., Sphex umbrosum Christ., S. lanutus Moes., Sceliphron spirifex L., Stizus lugnensis Mayr., Liris spp., Ammophila spp., Oxybelus spp., Trypoxylon spp., Pison spp.and Pacedonia spp. Belanogaster spp. were the major group of Vespidae found in the area. There were some members of Pompiliidae also. These were dominated by Cyphonomyx species.

(ii) Comparison of trapping systems

Relative densities of Hymenoptera captured using time constant hand nets sampling were compared with catches from the biconical traps (Table 34). The hand-netting catches gave better results for all Hymenoptera considered. However, if the intention is simply to catch Sphecidae and Eumenidae then the trap is adequate. Very few Asiliidae were captured in the biconical traps.

(iii) Spatial and temporal variations in relative density of adult predators in two vegetation habitats.

Seasonal fluctuations in the predators in the general tsetse

Table 34 - Comparison of catches from hand-nets and biconical traps

Trapping method	Sphecidae	Vespidae	Pompiliidae	Eumenidae
Hand-nets	173	26	26	74
Biconical traps	178	0	0	106

habitat are given in Table 35. With the exception of the Asiliidae, all the other predators were more abundant in 1984-85 than in 1985-86. Peaks of Asiliidae coincided with low numbers of Anisoptera and vice versa. Fluctuations in densities of Asiliidae and Anisoptera (except for the three months in 1985) were less than those of Hymenoptera and Zygoptera. These were due to differences in the species composition of the samples. The 1985 peak in Hymenoptera, for example, was mainly due to increase in populations of Bembex spp. and other Sphecidae, while that in 1986 was due to Sphex spp. Cyphonomyx spp., Pompillids and Eumenes spp.

Monthly fluctuations in apparent densities of predators in the riverine thicket and the valley woodland are shown in Fig. 29. Peak numbers of different predators in different vegetation types occurred in different months. In most cases the peaks in the valley woodland preceded those in the riverine thicket. Catches in the riverine thicket declined during the long rainy season and remained low throughout that season in contrast to valley woodland, where catches were highest during the rains and the early dry season. Catches from both vegetation habitats indicate that numbers of all predators increased soon after the start of the long rains in February 1984. Although the catches showed the same basic trends for all predator groups, the relative distribution of the

Table 35 - Seasonal fluctuations in hand-nets catches of potential predators of adult G. pallidipes in the two vegetation types. (Riverine thicket and Valley woodland combined).

Season	Months	Asiliidae		Anisoptera		Zygoptera		Sphecidae		Vespidae etc.	
		A	B	A	B	A	B	A	B	A	B
Short rains	Oct-Dec.	-	74	-	82	-	45	-	23	-	26
Hot dry	Jan-Mar.	27	179	72	28	20	4	29	22	4	13
Long rains	Apr-Jun.	64	78	64	50	84	6	59	3	54	5
Cold dry	Jly-Aug.	101	32	144	64	113	8	25	7	11	1

A - 1984-85 B - 1985-86.

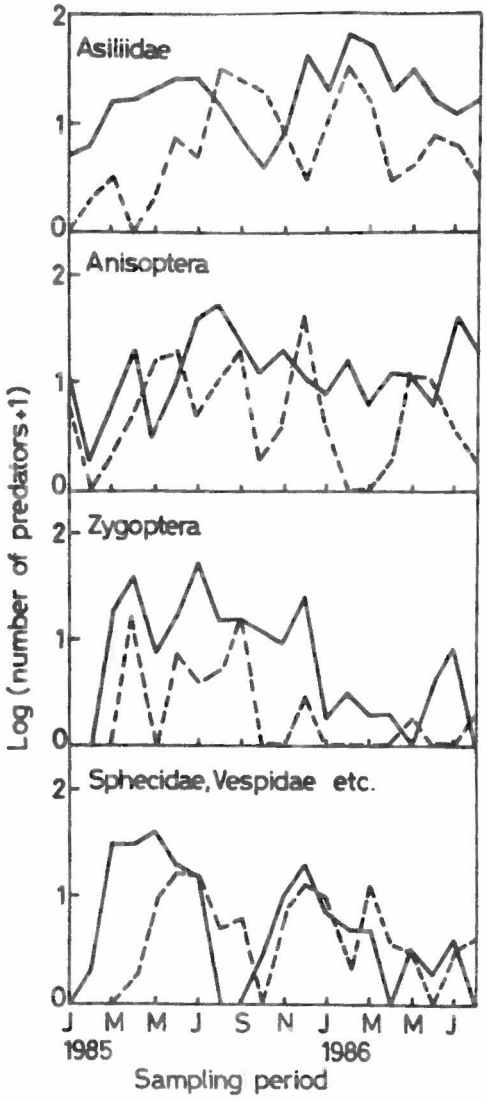

Fig. 29 - Monthly fluctuations in population of adult predators caught in hand-nets in two vegetation types. Solid line - Valley woodland, Broken line - Riverine thicket.

peak densities in the vegetation types varied with time of year. Asiliids and Wasps (Vespidae) started declining around July, while Odonata remained high until end of October before the population began to decline again. Bembex species were relatively unavailable throughout the study, except from July to September 1985 when they became abundant, particularly in the riverine thicket.

Summary of analysis of variances of catches in the two vegetation types and comparison of the means by Duncan's Multiple Range Test are given in Table 36. The difference between the two vegetation habitats was significant ($F = 4.95$, $P < 0.001$), but variations between months were not significant ($F = 0.73$, $P > 0.05$). Catches of Asilids in valley woodland were significantly different from those of wasps, but variations between dragonflies, damselflies and wasps were not significant.

8.3.3 RELATIONSHIP BETWEEN APPARENT PREDATOR DENSITIES AND CLIMATIC FACTORS.

Relationships between predator densities in the larviposition sites and climatic indices were determined by multiple regressions. A significant positive relationship of log. density with any climatic index suggested that density or activity is directly affected by that index. The abundance of Formicidae was directly related to saturation deficit (Reg. coeff.= 6.87; $t = 2.48$, $P < 0.05$), but showed no significant relationship with any of other climatic factors investigated. The gryllid catches were positively related to saturation deficit (Reg. coeff. = 8.85; $t = 4.60$, $P < 0.001$) and rainfall, and inversely related to mean temperature (Reg. coeff.= - 23.20; $t = - 3.12$, $P < 0.001$). Abundance of Asiliidae was inversely related to minimum temperature of the same month (Reg. coeff.= - 30.37; $t = - 4.88$, $P < 0.001$), mean temperature of the previous month (Reg. coeff.= -14.3; $t = - 3.28$, $P < 0.001$), and RH of the

Table 36 - Comparison of hand-net catches of predator in the two vegetation types.

Predator type	Mean catches in different vegetation types	
	Valley woodland	Riverine thicket
Asilids	19.5a	8.3b c d
Dragonflies	15.7a b	9.6b c d
Damselflies	12.2a b c	2.5d
Wasps	9.4b c d	4.7c d

Summary of ANOVA Table.

Source of variation	SS	df	MS	F ratio
Between months	1507	3	502.20	0.73
Between habitat	2740	4	685.09	4.95***
Residual	20758	150	138.39	
Total	25005	157		

*** $P < 0.001$ Means with same letters are not significantly different at $P < 0.05$. LSD = 7.35, Sx = 2.63, n = 20.

same month (Reg. coeff.= - 11.35; t = - 3.47, $P < 0.001$), implying that the cool dry season provided optimum conditions. None of the relationships was statistically significant for the Araneae and Zygoptera. Anisoptera showed a significant negative relationship mean temperature of the previous month (Reg. coeff.= - 34.80; t = - 2.53, $P < 0.05$).

8.3.4 PREDATOR ABUNDANCE AND TSETSE NUMBERS.

Since entomophagous predators and parasitoids seldom, if ever, achieve their major control by virtue of their functional responses alone, other parameters or derivatives of functional response were sought for insight into the control potential of some of the predators found in the study area. One such response is numerical response which consists of two principal components: aggregation and reproduction.

Evidence of numerical responses of predators to prey numbers was based on regressions and correlation analyses between field data on monthly fluctuations in prey and predator populations, both during the same and previous month intervals. Populations of ants and crickets were related to puparia, while asilids and spiders were related to adult G. pallidipes.

At Nguruman, correlations between predator abundance and tsetse puparia numbers were not significant (Table 37), indicating the pupal predators are not tsetse-specific. The situation was similar with the adult predators except that the Asilid numbers seem to decrease in response to increase in numbers of adult G. pallidipes (Fig. 30a), resulting in a significant inverse density dependent relationship ($r = - 0.78$, $P < 0.05$). There is some evidence for a delayed density relationship, at least for 1986, in Fig. 30b which shows the points joined in time sequence. There was no relationship between abundance of Araneae, Hymenoptera and numbers of adult G. pallidipes at Nguruman.

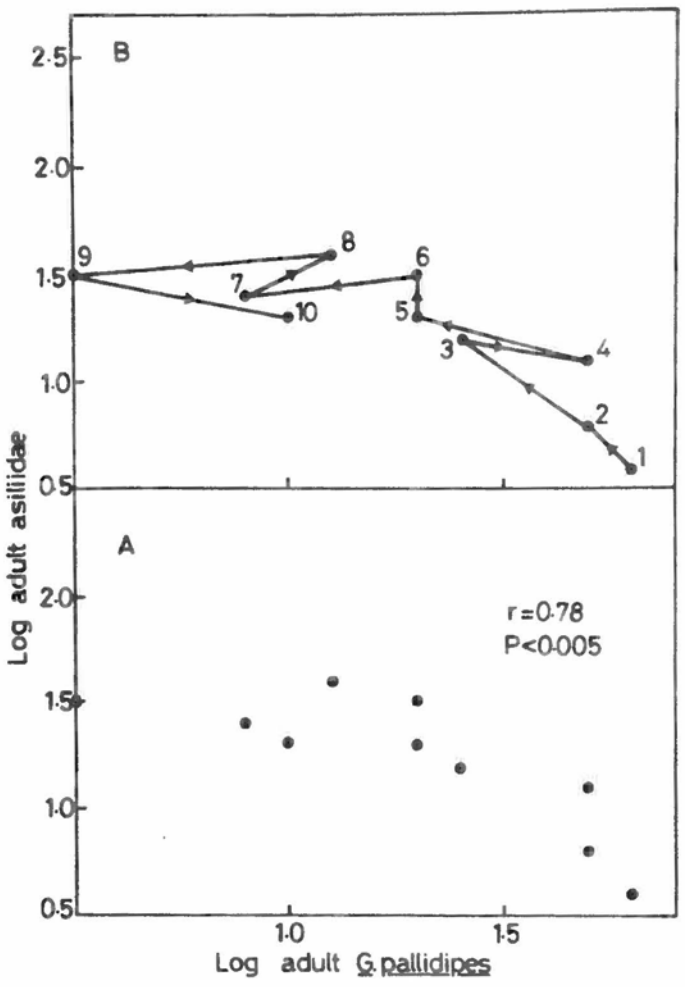

Fig. 30 - Relationship between relative densities of Asiliidae and adult G. pallidipes.

Table 37 - Values of regression coefficient and Student's t in the regression analysis on log. numbers of predators and potential prey.

Predator type	prey type	Reg. coeff.	t value
PUPAL PREDATORS			
Formicidae	Puparia	- 0.08	-0.37
Formcidae[1]	"	- 7.48	-0.72
Gryllidae	"	- 0.56	-1.76
Gryllidae[1]	"	537.5	0.12
Coleoptera	"	0.16	0.60
Coleoptera[1]	"	134.79	0.12
Grubs/larvae	"	- 0.19	-1.08
Grubs/larvae[1]	"	465.60	0.56
ADULT PREDATORS			
Asiliidae	Adult tsetse	- 1.05	-3.56***
Asiliidae[1]	"	- 1.01	-1.39
Araneae	"	- 0.21	-0.35
Araneae[1]	"	- 0.72	-0.92
Anisoptera	"	- 0.28	-0.99
Anisoptera[1]	"	- 0.62	-2.12*
Hymenoptera	"	- 0.03	-0.11
Hymenoptera[1]	"	0.17	0.61

*** $P < 0.001$, * $P < 0.05$.

8.4 DISCUSSION.

Potential predators found in the larviposition sites were dominated by Formicidae, Gryllidae, Araneae, Coleopteran larvae and grubs which were found foraging in the leaf litter, on the soil and among the vegetation in the sites. These predators have been reported in tsetse habitat in other parts of Africa. In Uganda, Fiske (1920) reported that adult and larval Coleoptera of the families Caraoidae and Elateridae found in the habitat of G. fuscipes and G. morsitans may destroy large numbers of puparia. The gryllids found in the area were dominated by members of the genera: Gryllus, Gryllulus, Homeogryllus, Liogryllus, Pnaeophillacris and Gryllotalpa. In Burkina Faso, Challier (1971), while studying G. palpalis gambiensis noted the presence of large crickets on the larviposition sites and considered them to be occasional predators of puparia. He however did not give the name of these crickets. Species of Pheidole, Polyrachis, Camponotus, Odontomachus, Paltothyreus, Acantholepis and Viticicola were found at Nguruman. Other ants species are often mentioned wandering in the breeding areas of tsetse, and are considered enemies of tsetse larvae or puparia. For example, Paltothyreus tarsatus and Euponera senaarensis have been observed carrying larvae of G. morsitans and G palpalis (Carpenter, 1912). In Tanzania, Ford (1940) observed Pheidole ants carrying puparia of G. swynnertoni into their nests. Several investigators have also reported observing various species of wasps, ants, asilids and spiders in tsetse habitat. In Zaire, Bouvier (1936) frequently noted the presence of G. palpalis in nests of Sphex, Synagris and Bembex species.

The fact that composition of predators varied according to methods of collection is further evidence that the four different methods sampled

different levels of the habitat. For while the water traps sampled flying insects, the unbaited and baited traps sampled the ground and the constant time searches concentrated on samples from the soil and vegetation. With stationary traps like the pitfall and water traps, the predators have to be sufficiently mobile to go to the traps and get captured, whereas the searches were dependent on searching and catching skills of the predator collectors. The most likely factor attracting dipteran and hymenopteran insects to the water traps was the white colour which contrasted sharply with the blue sky, the brown soil and the green vegetation of the background.

Changes in trap catches probably do indicate actual changes in predator density rather than just availability and specific responses to various trap types because trap catches increased with increase in numbers of the predators.

As regards the sampling of predators in the general breeding area, the biconical traps in collapsible forms are exceedingly easy to transport and erect, but the catches are few. Concerning the representative catches of many different species, the hand-netting gave better results. It appears that, if the intention is simply to catch Sphecidae and Eumenidae, the appropriate trap is the biconical, but for a wide array of predators the best method is handnetting for a constant time period.

Of all the climatic factors investigated, only saturation deficit was related to abundance of Formicidae, while Gryllidae were affected by temperature, rainfall and saturation deficit. This difference in reactions of predators to climatic factors was responsible for the temporal variations in abundance of the predators in the larviposition sites. Other predators in the larviposition sites showed no significant relationships with climatic factors.

Within the larviposition sites, Gryllidae, Formicidae, various larvae and Araneae were most abundant indicating that these were probably the main predatory species feeding on puparia and adult tsetse. However, none of the predators showed clear numerical responses to tsetse densities and are therefore almost certainly facultative predators.

Active fliers like Asiliidae, Anisoptera, Zygoptera, Sphecidae, Vespidae, and Pompillidae were the most abundant predators found in the general area. The numbers of these predators caught in traps located in larviposition sites were negligible indicating that probably these predators do not actively hunt for tsetse in the larviposition sites, but rather stayed in the general breeding area and captured tsetse on the wing when they ventured out to feed. This gives the impression of a mosaic spatial distribution in which different predators occupied different niches with foraging ranges which overlap. Such mosaic distribution could be responsible for the species diversity in predator groups found in the different areas. This ensured the co-existence of the wide array of predators in the area.

With the exception of Asiliidae, most of the potential predators of adult tsetse investigated did not show significant relationships with climatic factors. Adult asilids were abundant in cool conditions following the rains when prey like crickets, butterflies, grasshoppers etc. were also abundant. The increase in asilid numbers with increase in prey density suggests a numerical response to these prey. Asilids are known to lay their eggs attached to vegetation, in the soil or in decaying wood (Lavigne and Holland, 1969; Dennis and Lavigne, 1975). It is therefore possible that the heavy rains washed away some of the eggs resulting in decrease in the asilid numbers observed during the rains, although this could have resulted from lower activity levels.

The apparent delayed density dependent relationship between Asiliidae and tsetse numbers does suggest that Asiliidae would be important predators. In the final Chapter, serological analysis is used to positively identify predators and experiments on predation are carried out.

CHAPTER NINE

9. SEROLOGICAL IDENTIFICATION OF TSETSE PREDATORS AND LABORATORY AND FIELD EXPERIMENTAL WORK ON PREDATION.

9.1 INTRODUCTION

It has been shown in Chapter 7 that predation is likely to be an important cause of tsetse mortality, and temporal and spatial variations in density of potential predators were then considered. There was however little evidence for numerical responses, although this is not unexpected with polyphagous species. In this chapter, serological identification of the main tsetse predators as well as laboratory and field experiments on predation are described.

Predation studies on tsetse in the past have focussed, to a large extent, on the polyphagous predatory insects and spiders. In spite of the interest, very little is known of quantitative nature of their diet. This is due to their method of feeding which involves predigesting and sucking out prey contents, thus leaving no visibly recognisable prey remains in the gut or faeces. Diet analysis of predators is thus restricted to observations where possible. For chewing predators, gut contents can often be examined visually for prey remains (Phillipson, 1960; Penny, 1966; Sunderland, 1975), or the remains of the prey left by the predators can be counted (Turnbull, 1960; Robinson and Robinson, 1970). For sucking predators, more sophisticated techniques are required which involved protein analysis of the gut contents using either serology (Oniagu and Boreham, 1978) or electrophoresis (Giller, 1984, 1986). A review of techniques available for analytical evaluation of invertebrate prey-predator interactions has been published by Boreham and Oniagu (1978).

Serological analysis has been used extensively in entomology for blood meal identification (Weitz, 1952, 1960; Boreham, 1972; Boreham and Gill, 1973; Tempelis, 1975; Service et al., 1986), and for prey-predator studies (Dempster, 1958, 1960; O'Rourke, 1958; Loughton and West, 1961; Rothschild, 1966; Pickavance, 1970; Sutton, 1970; Service, 1973; Ashby, 1974; Giller, 1986). The analysis is based on the concept that each prey species possesses one or more proteins with antigenic determinants unique to that species (Ouchterlony, 1958). Thus identification of the source of predator diet will depend on the ability of the antisera to recognise only the unique proteins in the prey. A particular prey species can, therefore, be identified from gut macerates of different predator species on the basis of specific reaction between the antigen(s) of the prey in the gut macerates and antisera raised in rabbits against the prey antigen(s). In recent years, the serological approach has been preferred to other methods of identification of predators on insect pests and vectors since such methods have been found to be accurate and consistent.

Literature on predation shows that intensity of predation depends on several important components and factors. These include prey density, predator density, characteristics of the environment, presence or absence of variety of alternate prey, the attack technique of predators and characteristics of prey in relation to defense mechanisms (Leopold, 1933; Southwood, 1966; Holling, 1959a, b; Hassell, 1966, 1976; Hassell, et al., 1976, 1977). Of the many aspects of predator behaviour relevant to predator- prey interactions, the functional response of the predator to changes in prey density is one of the most important. These are best measured in the laboratory. Information of functional responses is essential for a clear understanding of the predator-prey interactions.

Although predation on tsetse by predators is not often observed in

the field, such a process has been reported by several authors (Carpenter, 1913; Fiske, 1920; Nash, 1933a; Swynnerton, 1936; Buxton, 1955; Glasgow, 1963; Gruvel, 1974a; and Challier, 1982). A few experiments have also been conducted to estimate predation intensity (Ford, 1940; Rogers, 1974), but clearly more are required. The purpose of the work presented in this chapter is to identify which of the potential predators are significant tsetse predators and then to evaluate their effectiveness in the laboratory and field situations.

The main objectives were :-

1. to use serological analysis of gut smears of field-collected invertebrate predators to identify tsetse predators.

2. to quantify the impact of some of these predators on tsetse in the laboratory by determining their functional responses to changes in prey densities;

3. to quantify the impact of natural predators on both the puparia and adults in the field and to determine whether such predation is density dependent.

9.2 MATERIALS AND METHODS

9.2.1 Immunological determination of predators of G. pallidipes at Nguruman: Incidence of tsetse diet in gut smears of predatory arthropods collected from the field.

The agar gel double immunodiffusion method, as described by Ouchterlony and Nilsson (1979), was used to identify tsetse protein in the gut contents from predators. Test runs using macerates of tsetse, gut macerates of starved predators and predators fed on tsetse were carried out to determine whether immunized rabbits produced antibodies which formed reaction precipitin lines with these macerates on gel plates. Gut smears from field-collected predators were then analysed to determine which predators had fed on tsetse in nature.

(a) Collection of predator meal samples.

The guts of insects and other arthropods hand-netted from the general tsetse habitat or collected from larviposition sites were dissected out and subsequently smeared on 15cm diameter qualitative filter papers (Whatman No. 1). The filter papers were divided radially into 8 sectors so that each paper could take 8 gut smears from different predators. The smears were then stored in glass dessicators containing dessicant at room temperature until required for serological analysis.

(b) Determination of protein content of tsetse extracts.

The potential for gel precipition of antigen-antibody complexes for prey identification in predator's gut was recognised some time ago. However, the results are affected by the amount of proteins being detected. For this reason, the protein contents of tsetse puparia and adult were determined. Some laboratory-raised puparia and field-collected adult G. pallidipes were separately homogenised in cold phosphate-buffered saline

(PBS; 0.1M Na-phosphate, 0.85% NaCl, pH 7.2) in 0.5ml Eppendorf tubes. The homogenates were centrifuged in an Eppendorf centrifuge (Model 5415S) at 10,000g for 10 minutes, and the supernatants aliquoted and stored at -20°C until needed. The standard method of Bradford (1976) was used to measure the protein content of the extracts. Ten ul of each extracts was pipetted into clean, dry standard test-tubes and 90 ul of PBS was added to each sample (i.e. 1:10 dilution). Five ml of the protein reagent[a] was then added under constant stirring. After a period of 2 minutes, the absorbance of the resulting mixture was measured at 595 nm. The protein contents in the unknowns were then calculated from a standard curve that had been established with 20-100 ug Bovine Serum Albumin (BSA; 1mg/ml) in 0.9% NaCl (Bradford, 1976).

(c) **Production of tsetse anti-sera.**

A number of adult tsetse were starved for 2 to 3 days to empty the gut and then killed by freezing. Puparia and adult G. pallidipes were separately homogenised in cold PBS using a polytron (Kinematica) at setting 7 for 1 minute, 3 times with 1 minute interval. Ten ml of the buffer was used for 40 puparia and 200 ml for 80gm of adult tsetse. The homogenate was centrifuged in a Beckman Ultracentrifuge (Model L5-50) at 20,000 g for 30 minutes at 4°C. The supernatant was carefully removed and stored at -20°C in small aliquots until required for the preparation of emulsions for immunization of rabbits.

In order to raise rabbit Glossina anti-sera, two five-months old male rabbits weighing about 1 kg each were injected at multiple intra-

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a = 100 mg Coomassie Brilliant Blue G 250 dissolved in 50 ml 95% ethanol, and 100 ml 85% (w/v) phosphoric acid was added. The resulting solution was then diluted to a final volume of 1 litre).

muscular sites with 500 ul (4 mg/ml) of tsetse extracts emulsified with an equal volume of Freund's Complete Adjuvant (FCA). Another two rabbits of the same sex, age and weights were similarly injected with the same amount of tsetse adult antigens emulsified with equal volume of FCA. The antibody responses were boosted with three injections of the same amounts of tsetse extracts emulsified with incomplete Freund's adjuvants given via the same route at two weekly intervals. Ten days after the third booster injection, 10 ml of venous blood was collected from the ear of each rabbit. The blood in 30 ml plastic tubes was allowed to clot at 37^{o}C for two hours and then left overnight at 4^{o}C. The sera were collected with a pasteur pipette and centrifuged to remove the remaining red blood cells. The clear sera were stored at - 20^{o}C in 5 ml aliquots until required for tests. Antisera against pupal and adult antigens were raised separately. A stage-non-specific (general) antiserum of G. pallidipes was prepared by simply mixing equal volumes of pupal and adult antisera. This general antiserum was used in screening the gut smears of predators collected from the field. The specificity of the antisera was determined by agar gel immunodiffussion technique described by Ouchterlony (1958). Cross reactivity tests were carried out between Glossina-antiserum and antigens of Promachus binucleatus (Diptera : Asillidae); Atylotus agrestis (Diptera: Tabanidae); Periplaneta americana (Dictyoptera : Blaterria); an acridid grasshopper (Ortnoptera: Acrididae); Phaeophillacris sp. (Ortnoptera : Gryllidae); Musca domestica and Stomoxys sp. (Diptera: Muscidae) and G. longipennis (Diptera: Glossinidae).

(d) **Extraction of predator gut smear proteins.**

Portions of filter paper containing gut smears were cut out into smaller pieces, and soaked overnight in 50-100 ul of PBS depending on the size of the smear. The filter paper eluates were centrifuged and stored

at -20°C until needed for the test. Eluates were thawed prior to testing and then kept on ice until required.

(e) **Determination of maximum period of prey detection in predator gut**

Experiments to determine the maximum period of time by which antigens from a single G. pallidipes could be detected within the gut of a predator were conducted. This was done since prey detectability depends on both the size of the meal and the rate of its breakdown due to digestion (Titova, 1974; Giller, 1984, 1986; Service et al., 1986). The insects used as predator models in this study were the robberflies, Promachus binucleatus and Alcimus sp. (representing adult predators), and the crickets, Liogryllus bimaculatus and Phaeophillacris sp. (representing pupal predators).

All predators were first starved for 48 h to empty their guts, and then allowed to feed on a single tsetse. In one series of the experiment, the previously starved crickets were allowed to feed on one puparium each and then were killed at 1, 2, 3, 4, 6, 9, and 12 hours postfeeding. Smears of gut contents were taken on filter papers which were dried in dessicator at room temperature. The smears were eluted in PBS as described above and used for detection of the prey. The relationship between digestion rate and prey detectability for the robberflies was also determined in similar manner using adult tsetse as prey. These experiments were carried out to test the sensitivity in detecting tsetse diet which was substantially digested. The gut contents from predators which were deliberately fed on tsetse in the laboratory were used as positive control samples and were tested alongside gut smears from field collected predators.

(f) **Agar-gel immunodiffusion test.**

Ouchterlony's double immunodiffusion technique was used to detect

tsetse antigens in predator gut smear eluates. The gel plates for tests were prepared by pouring 20 ml of molten 1% agarose in PBS (pH 7.2) containing 0.85% sodium chloride and 0.05% sodium azide (NaN_3) on to the entire surface of 8 cm^2 glass plates on a level surface. After the agarose gel had solidified, a desired pattern of 3 mm diameter wells spaced 3 mm apart were punched with a gel punch, and the agar plugs removed by gentle suction. The prepared plates were stored in a humidified box at room temperature until required for test. When needed, the wells were then filled with 10 ul of each antigen sample using an Eppendorf pipette without spilling samples on surrounding agar or interfering with the shape of the wells. The filter paper eluates of predator gut smears were placed in the outer wells. Ten ul of positive control material consisting of either a general tsetse antigenic solution prepared by mixing equal volumes of pupal and adult antigens, or tsetse protein which had passed through the gut of the cricket, Liogryllus bimaculatus, was placed in one well of each pattern. A negative control well contained PBS. Once the reactants (serum and antigens) were added to the wells, the test plates were incubated in the humidified chamber for 24 hours at room temperature. They were then observed for the presence of precipitin lines against a dark background. In order to have stained records, excess unprecipitated protein was washed away from the gel by soaking it in two changes of 0.85% NaCl for 12 h each, and then in several changes of distilled water. The gel was then covered with a pad of Whatman No.1 filter paper and pressed under a weight, on a level surface, overnight, and then dried at room temperature. The dried gels were stained in a staining solution (0.1% Coomassie Brilliant Blue R-250 in methanol, acetic acid, water 25:10:65, v/v/v)) for 15 minutes, and then washed in two changes of destaining solution (1: 2.5 : 6.5, acetic acid,

methanol, distilled water, v/v/v) to clear the background stain. The diagrams of resulting precipitate patterns were then drawn. Photographic records of the Ouchterlony's were also made.

9.2.2 COLONISATION OF PREDATORS IN THE LABORATORY

(i) Colonisation of puparia predators

Prior to any predation experiments, attempts were made to establish colonies of potential predators collected from the field to provide enough materials for both field and laboratory experiments. The rearing cages (Plate 6) made of perspex and measuring 21.5 x 15 x 15 cm, had a netting sleeve on one side to allow cleaning of cages whenever necessary. The top of the cages was made of netting material to allow adequate ventilation. Each cage was provided with black plastic cylindrical cups in which immatures could hide, a feeding dish containing vegetables, dead insects and a water fountain. The sterilised soil on the floor of the cage and the water fountains were occasionally sprinkled with water to maintain high relative humidity inside the cage. Two major species of crickets of the family Gryllidae (Pnaeophillacris and Liogryllus spp.) were established with adults reared from immature samples collected from the field in October 1984. The crickets were maintained on vegetables comprising of lettuce, carrots, cabbage and also dead insects. The vegetables were offered in cut pieces and were replaced with fresh ones every other day. Rearing was carried out in laboratory conditions of 25-28^{o}C, 60-80% RH and 12L:12D photoperiods.

(ii) Colonisation of predators of adult tsetse.

Attempts were made to establish colonies of spiders collected from the larviposition sites. Adult female spiders carrying egg cocoons were kept singly in perspex cages and fed on Musca domestica (houseflies),

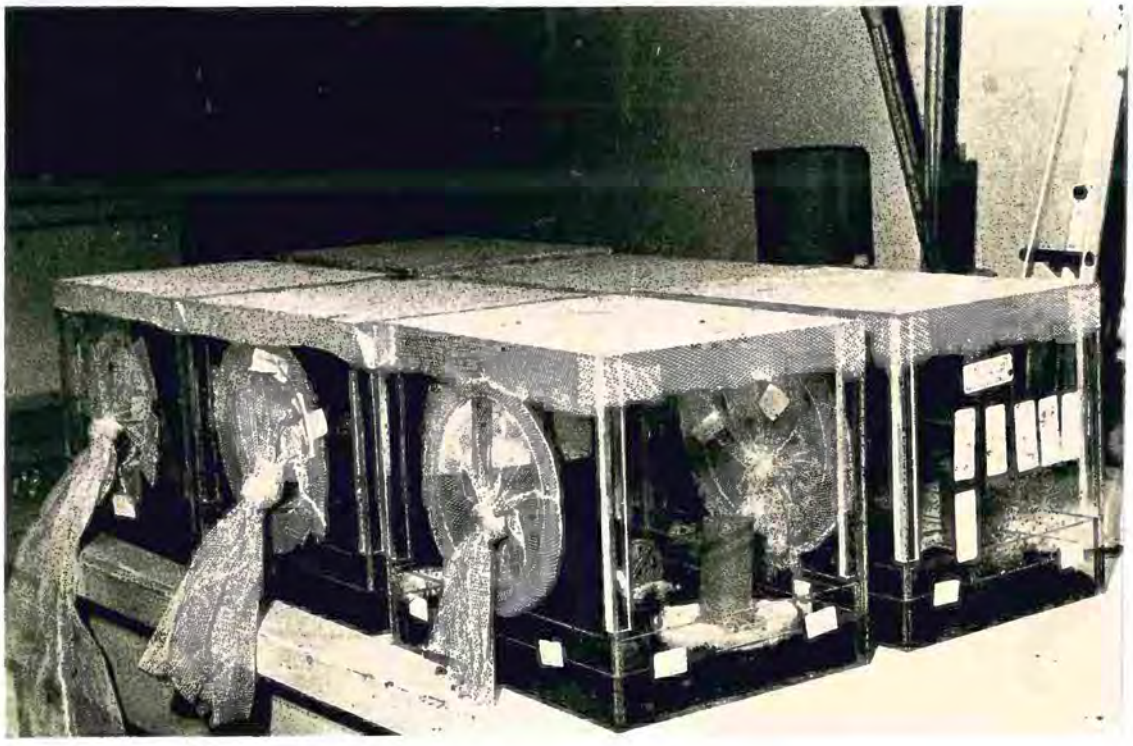

Plate 6 - Rearing cages for predators in the laboratory.

of total numbers of puparia exposed. Similar study was carried out using 30 adult Bembex moebii Handl. (Hymenoptera:Sphecidae) which were individually exposed to 5 live adult G. pallidipes in oblong PVC cages for 72h. Flies found paralysed were kept singly in plastic vials, and the time taken for them to die was noted and used to determine how long the paralysis lasted before the flies died.

9.2.4. HANDLING TIMES AND CHOICE AND NO-CHOICE EXPERIMENTS

The handling time was defined as the period of time spent in catching and completely consuming the prey or discarding the unwanted parts of the prey. For handling time studies, individual predators were starved for 24 hours and then given variable numbers of prey species. The handling time per prey species was recorded. In choice situations, the puparia of houseflies, dead insects and vegetables were given to the crickets (pupal predators) in addition to the tsetse puparia, but in the no-choice tests only tsetse puparia were given as food source. Crickets chewed puparial cases and emptied their content, and the discarded 'husks' were easily distinguished from 'exuviae'(puparial cases from which tsetse had emerged), so the numbers of puparia consumed were estimated by summing up the numbers of damaged puparia and the number of puparia which were completely eaten up.

Colonies of Solifugids and Spiders could not be successfully established so samples used in these experiments were collected from the field, hence ages were unknown, and the experiments could only be replicated as often as new materials were obtained from the field. Each predator was tested three times at each prey density studied, and those brought from the field were allowed time to acclimatize to the laboratory conditions before being used. For handling studies, individual spiders,

Lycosa sp. (Araneae:Lycosidae) were given adult Stomoxys sp., Glossina morsitans and G. pallidipes, and the handling time per species was recorded. In the "Choice" experiments they were given Atylotis agrestis (Diptera:Tabanidae), Stomoxys sp., and Musca domestica (Diptera:Muscidae) in addition to puparia and adult of G. pallidipes. The Musca were reared on cow dung, sour milk and sugar water, while the other prey species were collected from the field. Whenever possible the prey species were fed before being introduced into the experimental cages. Most of the spiders were extero-digesters and suck out the prey's liquified tissues leaving 'husks' which were easily distinguished from flies which had died naturally. Other spiders and solifugids chewed, sucked out the liquified tissues and discarded a mass of the chewed parts. The numbers of prey eaten were estimated by summing the flies that were completely eaten and the discarded remains or husks left in the cages.

To determine prey preference of the asilid, Promachus binucleatus Bezzi (Diptera:Asilidae), thirty adults caught in the field were put singly in rectangular cages covered with muslin cloth and provided with wet cotton wool to keep the inside of the cages relatively humid. Each asiliid was given one of each of the three prey species comprising of G. pallidipes, G. longipennis and Atylotis egrestis and left undisturbed to allow the tsetse to predate on the prey of its choice. The cages were checked at regular interval to note the type of prey captured and to remove other prey which were not attacked in order to prevent second feeding. Percent prey preference was then calculated.

9.2.5 FUNCTIONAL RESPONSE STUDIES OF PREDATORS IN THE LABORATORY.

Predators which had a high proportion of them feeding on tsetse were selected for functional responses studies. All functional response

experiments were performed in controlled conditions (mean ± S.E.) of 27 ± 0.8 °C, 70.0 ± 2.5% RH and 12L:12D photoperiod in an insectary in Nairobi, thus avoiding the possibility of diurnal cycles affecting the results. All predators were first left in superabundant prey for 48h and then starved for 48h prior to predation experiments in order to minimize differences in individual hunger levels which might affect the results (Nakamura, 1977). Predators studied included two species of crickets (Liogryllus bimaculatus and Phaeophillacris sp.), two species of Solifugids (Galeodes sp. and Rhagodoca sp.) and six species of spiders, Nephila sp., Lycosa sp. etc.

For the responses of crickets, the specimens were obtained from stock cultures started from field-collected specimens maintained in the insectary. Thirty adult crickets were put singly in perspex cages and given tsetse puparia at densities of 1, 2, 3, 4, up to 30 sequentially for 24h periods. In the first experiment the puparia were put on the surface of the soil on the floor of the cages; in the second, the puparia were buried in the soil at different depths ranging from 1 to 5 cms, and in the third, some of the puparia were put on the surface of the soil and equal numbers were buried in the soil at constant depth of 3 cm. The cages were subsequently re-examined every 24h to determine level of mortality in puparia due to predation, and to note the condition of the predator. All the damaged puparia were removed and replaced with fresh ones of equal or greater numbers depending on the density to be tested.

9.2.6 EXPERIMENTAL STUDIES ON PREDATION IN THE FIELD.

(i) Studies on predation of puparia

A latin square design was used to quantify puparial losses and damage due to predation at six densities in six different sites and in

six different months. Test areas measuring one square meter each were searched thoroughly to remove all live and empty puparia cases prior to the experiments. Puparia of varying ages produced by small colonies of field-collected flies of G. pallidipes were arranged at densities of 1, 4, 9, 16, 25 and 36 per test site and buried at 2 cm depth. The puparia at different densities had different spacings within the square meter (see Table 48). White-painted wooden boards with holes made at precise positions where puparia were to be buried at various densities were used to locate each puparium within the test areas, the corners of which were marked with short lengths of wooden pegs.

The buried puparia were left in the field under a layer of leaf litter for two weeks, after which they were dug up and surviving, predated and missing puparia were counted. Potential predators found at the sites during puparia burying and scoring of predation were also noted.

(ii) Studies on predation of adults

Prior to field experimentation on predation in the adult tsetse, the method of tethering the flies proposed for the study was tested for its feasibility in the field study and to determine survival/mortality rates in the tethered flies. Laboratory-reared flies with nooses around their neck were individually tethered on a meter square wooden board and left undisturbed for several days and survival of the flies determined at 24h intervals for a period of ten days.

The adult flies used in the studies were wild flies captured from the field using biconical traps, and were tethered to trees within one square meter and up to a meter from the ground. Nooses at one end of different lengths of light brown cotton threads were placed round the

neck of the flies, and the other end pinned to the tree trunks and branches. The lengths of the threads allowed flies to rest in fairly natural position, walk about on the trunk or seek shelter in the vegetation and also allowed limited flight but prevented them from flying off. The flies were tethered in the late afternoon and this allowed the flies to settle down before darkness and were left over a period of 24 hours after which level of predation by different predators, particularly ants, spiders and birds, were recorded. According to Rogers (1974) ants usually removed all traces of flies and sometimes chewed the noose attached to the flies, while the spiders, on the hand, sucked out the predigested prey's body and discarded the 'husk' still attached to the thread. Head of decapitated flies were found hanging from the nooses which showed no sign of chewing characteristic of damage by ants or other chewing predators. These were attributed to avian predation. The above criteria were used to estimate predation intensity due to the different predators.

9.3 OBSERVATIONS AND RESULTS.

9.3.1. INCIDENCE OF TSETSE DIET IN PREDATORY ARTHROPODS BASED ON SEROLOGICAL ANALYSIS OF GUT SMEARS.

Typical antigen-antibody reaction patterns of starved predators, Phaeopnillacris species (C_1, C_2), those fed on tsetse puparia (P_1, P_2) and those fed on tsetse adults (A_1, A_2) are shown in Plate 7a. The antiserum raised against the pupal stage of G. pallidipes reacted with adult antigen and vice versa. However, the precipitin lines formed with the pupal and adult stage antigens showed partial identity (Plate 7b). When the general anti-serum (GA) was tested for antibodies against pupal and adult antigens (PE and AE in Plate 7b), three lines formed between general antiserum and general antigens (GE), two lines formed between the antiserum and the pupal antigen, but only one line was visible between the anti-serum and adult antigen or gut content of crickets fed on adult tsetse. The results of these tests have demonstrated that the general anti-serum is reactive with both pupal and adult antigens, and could therefore be used for routine testing of Glossina antigens in predators.

(a) Sensitivity of test

The dilutions of pupal antigen eluate ranging from 1:10 to 1:320 gave positive reactions for tsetse antiserum, while positives for the adult antigen were obtained with a dilution of 1:640 and that for the general antigen between 1:320 to 1:640 (0.6 to 70 ug of protein/ ml). The protein contents of puparia, adult and general antigens were 4.0 $\pm$ 0.4, 3.7 $\pm$ 0.2 and 3.7 $\pm$ 0.4 gm/ml respectively, showing that these samples contained enough proteins for easy detection by precipitin test.

Although the stability of antigens on the filter paper was not tested, it was later found that all the antigen eluates from the filter

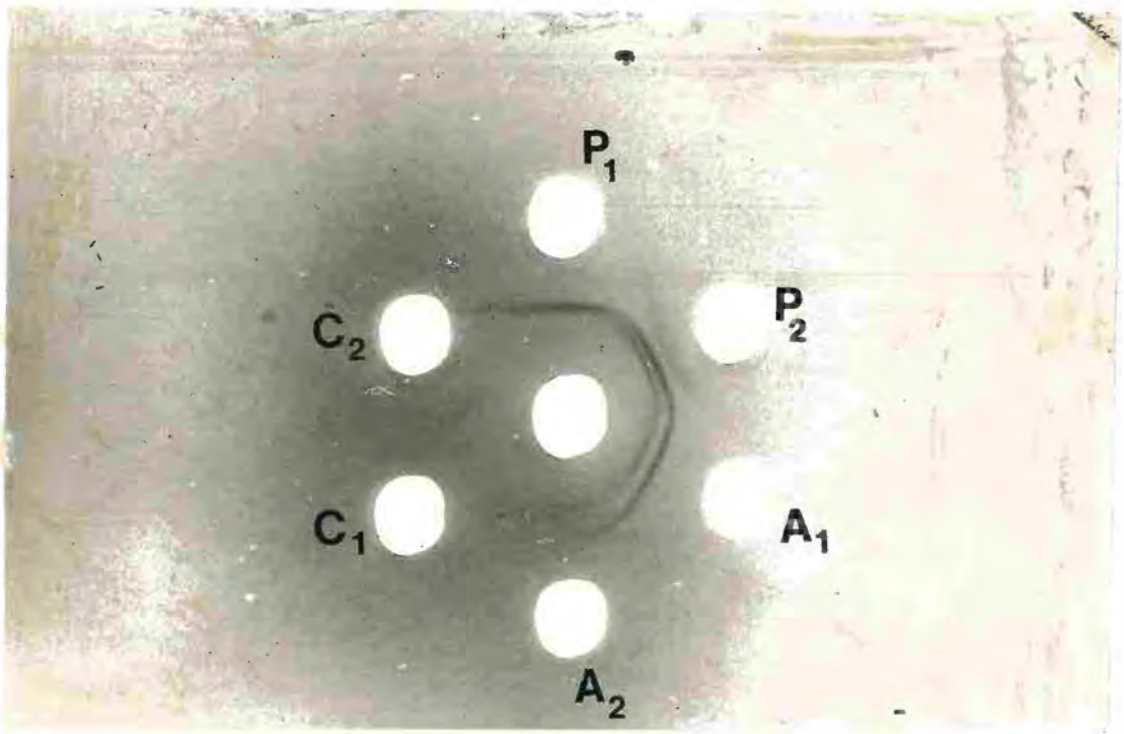

Plate 7A - Reaction patterns of tsetse antigens and antisera raised in rabbit. C_1, C_2 = starved predators, P_1, P_2 = predators fed on puparia, A_1, A_2 = predators fed on adult.

Table 38 - Detection periods in three different predators fed on single pupa (P) or adult (A) G. pallidipes using gel precipitin test.

Predator type	Hour after feeding(a)	% prey detectable/
Liogryllus bimaculatus	1	100.0
(Orthoptera : Gryllidae)	2	100.0
(P).	3	100.0
	4	100.0
	6	66.7
	9	0
	12	0
Phaeophillacris sp.	0	100.0
(Orthoptera : Gryllidae)	1	100.0
(A)	3	100.0
	6	100.0
	9	100.0
	12	100.0
	16	100.0
	24	66.7
	48	33.3
	72	0
Promacnus binucleatus	1	100.0
(Diptera : Asilidae)	3	100.0
(A).	6	100.0
	9	100.0
	12	66.7

a - at mean temp. 27°C b - per three replicates.

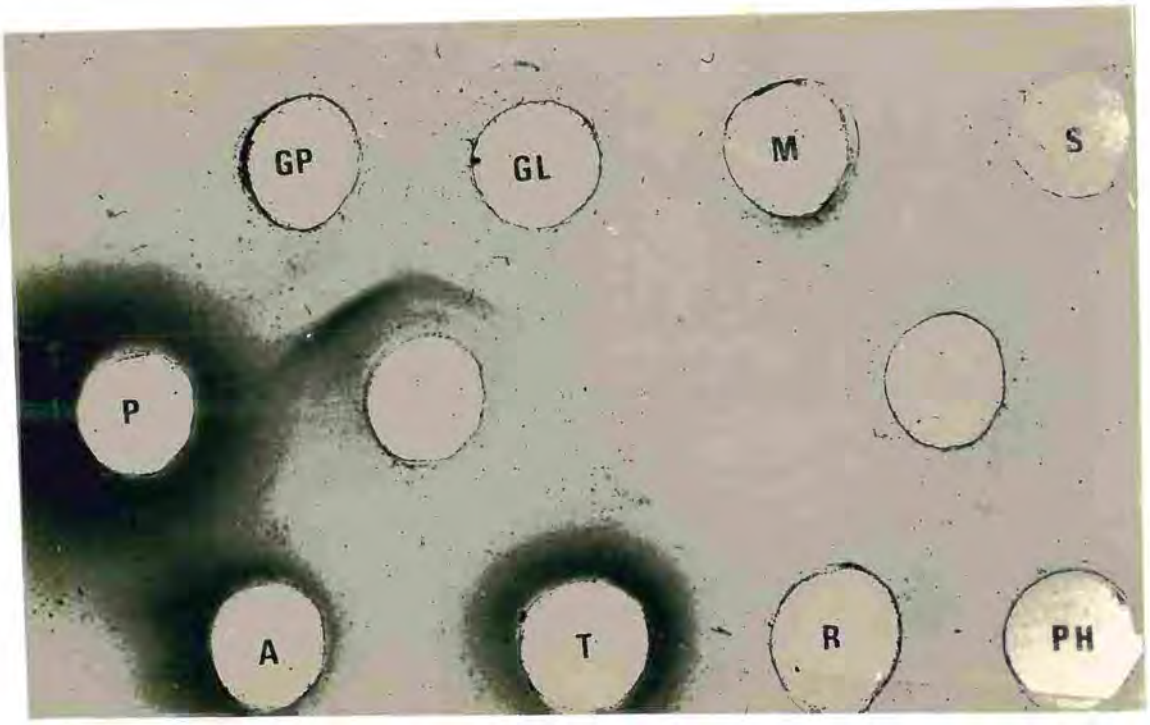

Plate 8 - Results of cross reactivity tests between pallidipes - antiserum and antigens of insects from different families. M - Musca domestica; GL - G. longipennis; PH - Phaeophillacris sp; S - Stomoxys sp.; P - Promachus binucleatus; T - Atylotus agrestus; R - Periplaneta americana; GP - G. pallidipes; A - Acridid grasshopper.

Table 39 - Incidence of tsetse diet in field-collected arthropods, based on results of immunological analysis of their gut contents using gel precipitin test.

SUSPECTED PUPAL PREDATORS	Number tested	Number positive	% positive
ORTHOPTERA			
GRYLLOTALPIDAE			
Gryllotalpa africana	4	0	0
GRYLLIDAE			
Gryllus sp.	35	10	28.6
Gryllulus sp.	84	6	7.1
Phaeophillacris sp.	12	5	41.7
Liogryllus bimaculatus	15	1	6.7
Liogryllus sp.	14	0	0
Scapsipedus sp.	10	0	0
Total Orthoptera	174	22	12.6
DICTYOPTERA			
BLATTERIA			
Epilampra sp.	39	1	2.6
HEMIPTERA			
REDUVIIDAE			
Physorhynchus erythroderus Schaum	7	0	0
HYMENOPTERA			
MUTILIIDAE			
Mutilla sp.	7	0	0
FORMICIDAE			
Platythyrea cibrinodis	12	0	0
unidentified ants	45	0	0
Total Hymenoptera	64	0	0
COLEOPTERA			
CARABIDAE	40	3	7.5
ELATERIDAE	12	0	0
LAGRIIDAE	1	0	0
Total Coleoptera	53	3	5.7

Table 39 (cont'd)

SUSPECTED ADULT PREDATORS	Number tested	Number positive	% positive
CHILOPODA	31	0	0
NEUROPTERA	11	1	9.1
DERMAPTERA	6	0	0
DIPTERA			
ASILIDAE			
Promachus binucleatus Bezzi	215	54	25.1
Promachus sp.	100	34	34.0
Alcimus sp.	107	20	18.7
Hoplistomerus mobilis Loew.	13	4	30.8
Hoplistomerus sp.	7	1	14.3
Ommatius sp.	9	1	11.1
Stenopogon sp.	7	2	28.6
Lamyra gulo Loew.	5	2	40.0
Proagonistes sp.	1	0	0
Unidentified asilids	8	0	0
Total Asilidae	472	118	25.0
ARANEAE			
LYCOSIDAE			
Lycosa sp.	7	0	0
Unidentified spiders	46	10	21.7
Total Araneae	53	10	18.9
HYMENOPTERA			
SPHECIDAE			
Ammophila sp.	71	4	5.6
Tachytes melancholicus Arn.	16	1	6.3
Tachytes observalis Kohl.	2	0	0
Bembex moesii Handl.	24	8	33.0
Bembex olivata Dahl.	1	0	0
Spnex umorosum Cnrist.	1	0	0
Spnex lanutus Moes.	1	0	0
Total Spnecidae	116	13	11.2
VESPIDAE			
Belanogaster sp.	18	10	55.6

Table 39 (cont'd)

SUSPEDTED ADULT PREDATORS	Number tested	Number positive	% positive
SCOLIIDAE			
Scolia sp.	1	1	100.0
POMPILIIDAE			
Cyphononyx sp.	20	3	15.0
Hemipepsis codoptera St.	1	1	100.0
Total Pompiliidae	21	4	19.0
EUMENIIDAE			
Eumenes maxillosus de Geer	20	6	30.0
Eumenes maxillosus f. *fenestralis* Sauss.	27	10	37.0
Synagris abyssinica Gaerin	3	0	0
Total Eumenidae	50	16	32.0
MEGACHILIDAE			
Chalicodoma felina Gerst.	2	1	50.0
Chalicodoma sp.	1	0	0
Euaspis sp.	1	0	0
Unidentified hymenoptera	12	1	8.3
Total Hymenoptera	222	46	20.7
ODONATA: ANISOPTERA			
LIBELLULIDAE			
Hadrothemis spp.	14	3	21.4
Brachythemis spp.	4	1	25.0
Trithemis spp.	12	3	25.0
Olpogastria spp.	6	1	16.7
Philonomon spp.	20	2	10.0
Palpopleura spp.	4	1	25.0
Crocothemis spp.	2	0	0
Orthetrum spp.	195	14	7.8
PETALURIDAE			
Petalia spp.	19	3	5.3
CORDULIIDAE			
Phyllomacronia spp.	4	3	75.0
Unidentified anisoptera	120	12	10.0
Total Anisoptera	396	43	10.9

TABLE 39 (cont'd)

SUSPECTED ADULT PREDATORS	Number tested	Number positive	% positive
ODONATA: ZYGOPTERA			
AGRIIDAE			
Phaon spp.	10	0	0
LESTIDAE			
Lestes spp.	17	5	29.4
CHLOROCYPHIDAE			
Chlorocypha spp.	6	2	33.3
Platycypnan spp.	15	4	26.7
Unidentified spp.	126	33	26.2
Total Zygoptera	174	44	25.3

in the larviposition sites, high percentages of gut smears from the gryllids of the genera *Phaeophillacris* (41.7%, N = 12) and *Gryllus* (28.6% of 84 tested) and in the Araneae 18.9% (N = 53) reacted positively with tsetse anti-sera. In the general tsetse area positive results were mainly obtained with gut antigens from Odonata, Diptera and Hymenoptera species, and ranged from 10.9% in Anisoptera (N = 396) through 25.0% in Asiliidae (N = 472) to 55.6% in Vespidae (N = 18). In the Anisopteran group, members of the family Libellulidae (*Hadrothermis*, *Brachythermis*, *Tritnermis*, *Palpopleura*, *Olpogastria* and *Orthetrum* species) appeared to be the important predators of tsetse, while species in the genera *Chlorocypha* and *Platycypha* (Chlorocypnidae) and *Lestes* (Lestidae), were important among the Zygopteran Odonata. *Promachus*, *Alcimus* and *Hoplistomerus* were the most important among the Asiliidae.

Seasonal fluctuations in the incidence of tsetse diet in arthropods

Table 40 - Fluctuations in incidence of tsetse diet in gut smears of arthropods collected from the field at Nguruman.

(A) Seasonal fluctuations

Seasons	Months	Asiliidae				Anisoptera				Zygoptera				Hymenoptera			
		1		2		1		2		1		2		1		2	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Short rain	Oct-Dec	-	-	58	34.5	-	-	77	15.6	-	-	43	30.2	-	-	28	7.1
Hot dry	Jan-Mar	22	0	179	16.2	71	5.6	28	36.0	20	20.0	4	25.0	31	6.5	26	19.2
Long rain	Apr-Jun	57	42.1	75	16.0	40	12.5	32	0	29	17.2	3	0	67	17.9	0	0
Cold dry	Jly-Sept	57	49.1	24	22.7*	99	12.5	39	17.9*	78	28.2	7	0*	30	26.7	3	0*
Total		136	38.2	336	19.6	210	10.0	179	11.4	127	24.4	57	24.6	128	17.2	57	12.3

(B) Fluctuations in the two vegetation types.

	Asiliidae				Anisoptera				Zygoptera				Hymenoptera			
	1		2		1		2		1		2		1		2	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Riverine thicket	40	45.0	99	23.2	97	9.3	52	5.8	14	28.6	3	0	31	29.0	23	8.7
Valley woodland	96	35.4	237	18.1	113	11.5	124	13.7	113	23.9	54	25.9	97	13.4	34	14.7

1 - 1984-1985, 2 - 1985-1986; Hymenoptera = Sphecidae + Vespidae + Eumenidae; No. - Number tested

% - percentage of smears reacting with pallidipes-antiserum; * - Values based on only July-August data.

and variations in the two different vegetation types are given in Table 40. There was no clear relationship between incidence of tsetse diet in gut smears and season. Many gut samples of Asiliidae from the riverine thicket reacted positively with pallidipes-antiserum than those from the valley woodland, the opposite is true for the Anisoptera.

9.3.2 COLONISATION OF PREDATORS

Mass rearing of spiders was difficult because of the long incubation period of the eggs and the cannibalistic habit among the spiderlings.

Rearing the crickets was more successful. The field-collected adult Pnaeophillacris readily laid eggs in moist soil and the nymphs were successfully maintained on vegetables and dead insects. Adults appeared within one to two months and usually survived for several months. The winged males were never observed flying. This could be attributed to the small size of the cage, and the presence of abundant food and females which made flight in search for both food and mate unnecessary.

9.3.3 PALATABILITY STUDIES, HANDLING TIMES AND HOST PREFERENCE OF TSETSE PREDATORS.

Levels of palatability of tsetse to any predator group were measured by the numbers which readily fed on tsetse. Table 41 shows that puparia and adult G. pallidipes are palatable to a wide range of predators. Those found to prey on puparia of G. pallidipes included members of Gryllidae, Gryllotalpidae, Carabidae and Dermaptera (Forficulidae). Individuals of all Hemiptera, Dictyoptera, Formicidae, larvae of Elaterid and Carabid beetles investigated died without feeding on the puparia offered to them. Several species of velvet ants (Hymenoptera: Mutillidae) have been reported to be important parasites of Glossina puparia, but in the present

Table 41 - Results of palatability tests for different arthropods collected from larviposition sites of G. pallidipes. Arthropods marked with * fed readily on dead adult tsetse.

Predator spp. tested	Number tested	Number which fed on G. pallidipes		% of predators attacking tsetse
		Puparia	Adults	
DERMAPTERA*				
Forficulidae	4	3	0	75.0
ORTHOPTERA*				
Gryllotalpidae	7	1	0	14.3
Gryllidae	93	30	0	32.3
DICTYOPTERA*	21	0	0	0
HEMIPTERA*	34	0	0	0
COLEOPTERA *				
Carabidae *	57	4	0	7.0
Grubs*	33	0	0	0
Elateridae *	45	0	0	0
SOLIFUGAE				
Rhagodidae	1	0	1	100.0
Galeodidae	1	0	1	100.0
HYMENOPTERA				
Mutillidae*	7	0	0	0
Formicidae*	25	0	0	0
Wasps				
Bembex spp.	30	0	30	100(paralysis)
Other sphecidae	15	0	0	0
ODONATA				
Anisoptera	6	0	0	0
Zygoptera	4	0	0	0
DIPTERA				
Asilidae	30	0	15	50.0
ARACHNIDA				
Scorpionida	7	0	4	57.1
Araneae	30	0	16	53.3
MYRIAPODA				
Chilopoda	19	0	0	0

Table 42 - Results of palatability tests for determining predatory potential of different arthropods collected from larviposition sites G. pallidipes at Nguruman, Kenya.

Predator type	Subject No.	No. of prey given	No. of prey eaten	% prey eaten	Mean % prey eaten
PUPAL PREDATORS					
ORTHOPTERA					
Gryllotalpidae	1	13	5	38.5	
(Gryllotalpa africana)	2	3	0	0	
	3	3	0	0	
	4	3	0	0	5.5
	5	2	0	0	
	6	7	0	0	
	7	3	0	0	
Gryllidae					
Liogryllus bimaculatus	1	25	8	32.0	
	2	36	32	88.9	63.3
	3	45	31	68.9	
Pnaeopnillacris sp.	1	15	2	13.3	
	2	13	7	53.8	
	3	13	2	15.4	20.3
	4	15	1	6.7	
	5	10	1	10.0	
	6	8	2	25.0	
B. ADULT PREADATORS					
SOLIFUGAE					
Rhagodidae	1	62	45	72.6	67.3
Galeodidae	1	42	26	61.9	
ARANEAE					
Nephila spp.	1	161	105	62.2	
	2	568	377	66.4	64.3
Lycosidae	1	95	91	95.8	
Lycosa spp.	2	126	85	67.5	
	3	152	131	86.2	84.6
	4	60	46	76.7	
	5	29	28	96.6	

study, none of the puparia exposed to the mutillids were parasitized.

Most spider, asiliid, scorpions and solifugid species fed readily on adult tsetse, but all the dragonflies, wasps, damselflies, and centipedes tested did not do so. Only Bembex moebii attacked adult tsetse under laboratory conditions without actually consuming them. They stung the flies and caused paralysis which lasted for five or more days.

Results of a more detailed evaluation of some of the predators are given in Table 42. Among the potential pupal predators, the highest predation intensity of 63.3% was found in Liogryllus species. Predation intensity in adult predators ranged from 64.3% for Nephilid spiders, 67.3% for solifugids to 84.6% for Lycosid spiders. In general, the adult predators had higher predation intensities.

Twenty individuals of Liogryllus bimaculatus were offered tsetse puparia and the average handling time after three replicates (N = 60) was found to be 2.9 ± 0.1 minutes. For thirty replicates, Galeodes sp. (Solifugae : Galeodidae) had a mean handling time of 2.3 ± 0.1 minutes when fed on adult tsetse. For thirty asiliids, Promachus binucleatus and Alcimus sp. (Diptera : Asiliidae), the average handling time was 1.48 ± 0.2 hours, much longer than that recorded for other predators. Table 43 shows that Lycosa sp. (Araneae : Lycosidae) had different handling times for different prey at different densities. More time was spent on relatively bigger prey like G. pallidipes than on G. morsitans, and at low prey densities the spider spent more time on each prey caught.

Results of feeding preference of asilids to adult prey species are given in Table 44. In choice situations, the asilids showed an 87.5% preference for G. pallidipes and 12.5% preference for G. longipennis, but did not attack Atylotus agrestis (Tabanidae).

Table 43 - Handling times of a Lycosa sp.in relation to prey types

Prey type	Number given	Number eaten	Handling time per prey (min.)
G. morsitans	29	16	12.0 ± 2.2
Stomoxys sp.	2	2	15.5 ± 0.5
G. pallidipes	2	2	42.0 ± 9.0

Table 44 - Prey Preference of Asilidae

Feeding condition	No. of Asilids tested	Prey type given	No. of prey given	No of G. pallidipes eaten	% predation on G.pallidipes
No choice situation	12	G. pallidipes	3 each	10	100.0
Choice Situation	10	G. pallidipes G. longipennis Atylotus agrestis	1 each	8	87.5

9.3.4 FUNCTIONAL RESPONSES OF DIFFERENT PREDATORS.

(a) Functional responses of Gryllid species.

It was observed that only puparia found on surface of the soil were eaten by the gryllids, those buried in the soil at depth of 2cm or more were not attacked. Phaeophillacris sp. never burrowed into the soil in search of puparia. Though Liogryllus sp. burrowed into the soil they did not appear to search actively for puparia while in the soil. The crickets can only be considered facultative or occasional puparia predators.

The functional responses of two cricket species to puparia of G. pallidipes are given in Table 45. The feeding performance of Phaeophillacris sp. (Fig. 31a) is curvilinear and is similar to Holling's Type II functional response curve. It could therefore be represented by the disc equation of Holling (1959a) in which the number killed increased at progressively reduced rate as prey density increases until a constant level plateau is reached, where numbers killed does not change with any further increase in prey density.

Fig.31b illustrates functional response of L. bimaculatus which is a sigmoid curve indicating a Type III response (Holling, 1959a). The cricket took a long time to accept the puparia as food source, but discovery of palatability of the puparia stimulated them to search for similar puparia, so as the puparia numbers increased the contacts came at shorter intervals resulting in functional response with an initially increasing slope. As the crickets became satiated and more time was spent handling prey the slope decreased to produce an S-shaped curve. This satiation component exerted its effect probably by affecting the ratio of successful captures to prey contacts.

(b) Functional responses of Solifugid species.

Feeding responses of the solifugid species investigated are given

Table 45 - Functional Responses of Cricket species to different densities of puparia *G. pallidipes*.

Species tested	Density of prey given	Mean number eaten per 3 replicates
Liogryllus bimaculatus	1	1.0 ± 0.0
	2	2.0 ± 0.0
	3	2.5 ± 0.5
	4	3.5 ± 0.5
	5	4.5 ± 0.5
	7	6.3 ± 0.5
	12	11.0 ± 0.3
	16	14.0 ± 0.2
	25	19.0 ± 0.3
	28	25.0 ± 0.4
	30	26.0 ± 0.5
Phaeophillacris sp.	1	0.4 ± 0.1
	3	0.8 ± 0.5
	4	1.5 ± 0.5
	5	1.0 ± 1.0
	8	3.0 ± 0.5
	10	2.0 ± 0.6
	12	5.0 ± 0.1
	18	5.0 ± 0.3
	20	6.0 ± 0.4
	26	6.0 ± 0.5

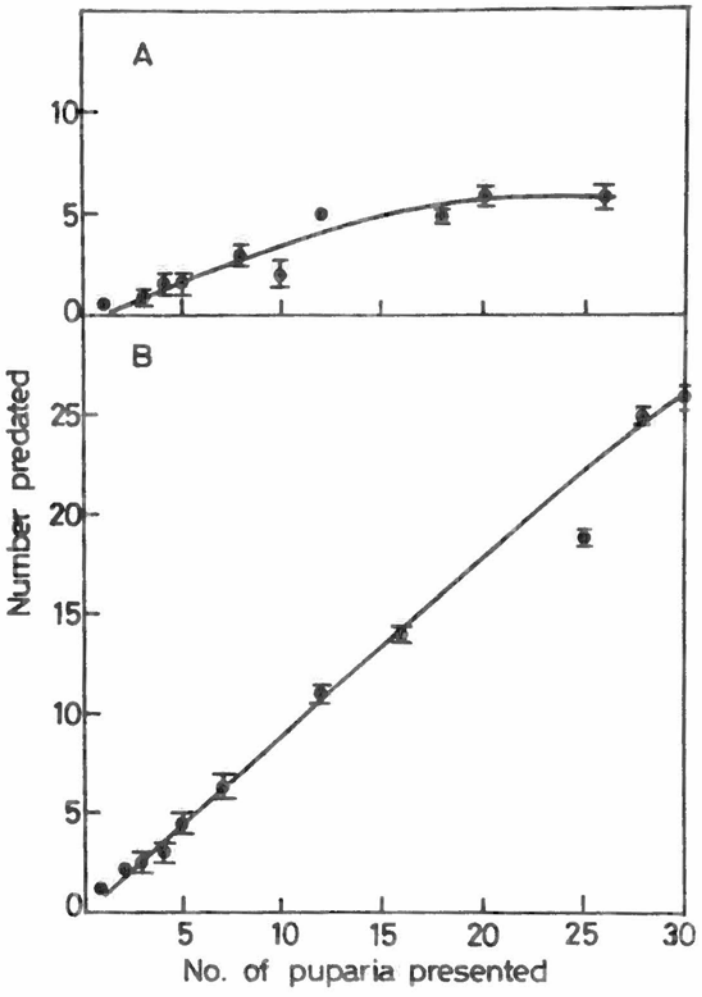

Fig. 31 - Functional responses of Gryllidae species: (A) Phaeophillacris sp. (B) Liogryllus bimaculatus.

in Table 46. The Galeodes sp. had a curve similar to Holling's Type II response curve (Fig. 32a). Rhagodoca sp., on the hand, exhibited a sigmoid response to changes in densities of adult tsetse flies (Fig.32b). At higher densities this solifugid captured and killed the flies without eating them, even when completely satiated, and also captured other flies when still feeding on previously captured prey. This wasteful killings apparently resulted in the second rise in the performance curve.

(c) Functional responses of Spider species.

Table 47 and Fig.33 illustrate functional responses of six different spider species. Two species showed curvilinear Holling's Type II curve, one of them showed sigmoid responses, while the remaining species showed density dependent responses in which increasing steepness of the curves indicate increasing percentage kill as prey density increases.

9.3.5 PREDATION ON PUPARIA BURIED AT DIFFERENT DENSITIES IN FIELD SITUATION.

Table 48a gives the average percent predation in puparia buried at different densities in the field, and the corresponding relationship between puparia density and percent predation is shown in Fig. 34. Out of the total of 545 puparia buried, 23.8% could not be found and were assumed to have been eaten completely; 14.7% emerged while still buried; 10.4% were partially eaten; 0.2% contracted fungal diseases and the remaining 50.9% were exhumed intact after the exposure period and kept in the laboratory for emergence. All that emerged were tsetse adults indicating that none of them was parasitised within the time the puparia were exposed to the field conditions. Mean percent partially eaten puparia ranged from 4.2 to 33.3%, while that for combined partially eaten and missing puparia

Table 45 - Functional Responses of Solifugid species to different densities of adult G. pallidipes

Species tested	Density of prey given	Mean number eaten per 3 replicates
Galeodes sp.	1	1.0 ± 0.0
	5	5.0 ± 0.0
	6	6.0 ± 0.6
	10	10.0 ± 0.8
	18	18.0 ± 1.3
	20	18.0 ± 2.1
	24	18.0 ± 3.7
Rhagodoca sp.	1	1.0 ± 0.0
	6	6.0 ± 0.0
	10	5.0 ± 1.0
	15	15.0 ± 3.4
	18	18.0 ± 2.0
	20	18.0 ± 1.3
	24	24.0 ± 0.5

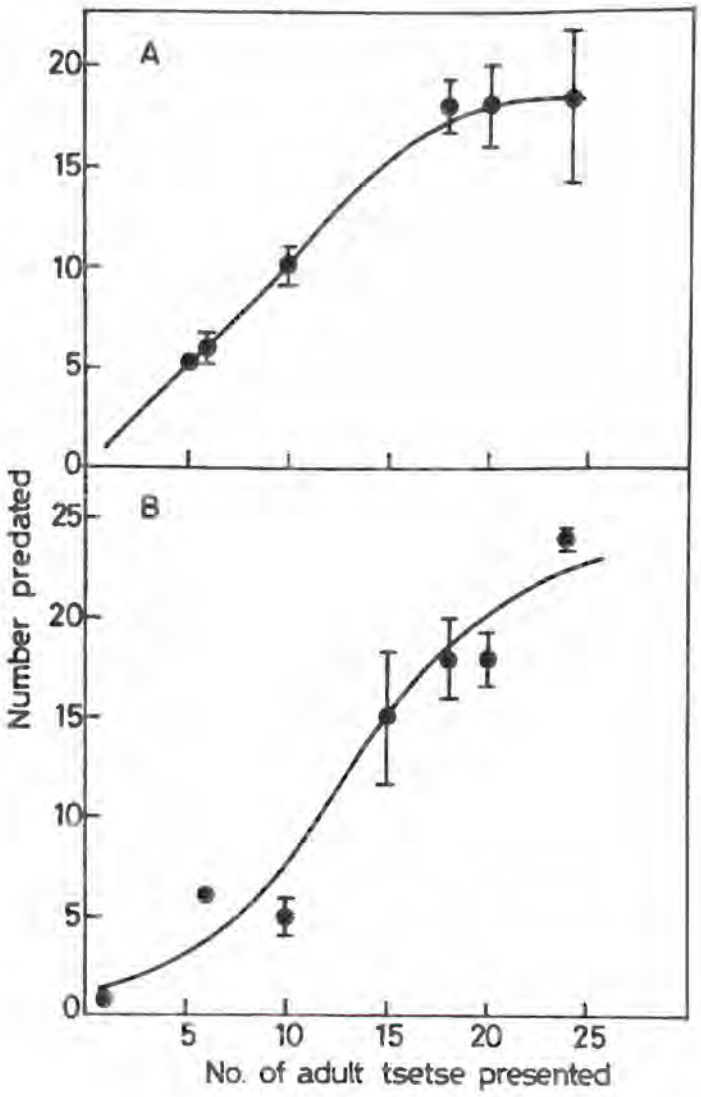

Fig. 32 - Functional responses of Solifugae species:
(A) Galeodes sp. (B) Rhagodoca sp.

Table 47 - Functional Responses of Spider species to different densities of adult G. pallidipes

	Species tested	Density of prey given	Mean number eaten/3 reps.
A.	Lycosa sp. 1	1	1.0 ± 0.0
		2	2.0 ± 0.0
		4	4.0 ± 0.0
		7	5.0 ± 1.0
		8	7.0 ± 1.0
		12	10.0 ± 0.5
		14	14.0 ± 0.0
		15	15.0 ± 0.0
		28	20.0 ± 0.5
B.	Nephila sp. 1	1	1.0 ± 0.0
		2	1.5 ± 0.5
		3	3.0 ± 0.0
		4	4.0 ± 0.0
		5	5.0 ± 0.0
		8	5.6 ± 0.5
		10	6.5 ± 2.4
		12	7.0 ± 1.2
		14	5.5 ± 2.4
		20	17.0 ± 1.7
		25	20.3 ± 2.5
		32	19.0 ± 0.0
		34	28.0 ± 0.0
		35	29.0 ± 0.5
		40	28.0 ± 0.1

Table 47 - (cont'd) Functional Responses of Spider species

	Species tested	Density of prey given	Mean number eaten per 3 replicates
C.	Lycosa sp. 3	2	2.0 ± 0.1
		3	2.6 ± 0.2
		4	3.0 ± 0.2
		5	4.0 ± 0.1
		7	7.0 ± 0.0
		9	8.0 ± 0.1
		12	9.0 ± 0.3
		15	12.0 ± 0.5
		22	15.0 ± 0.6
D.	Lycosa sp. 4	4	4.0 ± 0.0
		6	6.0 ± 0.0
		7	7.0 ± 0.0
		8	8.0 ± 0.0
		10	10.0 ± 0.0
		13	13.0 ± 0.0
		15	14.0 ± 0.2

Table 47 - (cont'd) Functional responses of Spider species.

	Species tested	Density of prey prey given	Mean No. eaten per 3 replicates
E.	*Lycosa* sp. 2	1	1.0 ± 0.0
		2	1.5 ± 0.1
		3	1.6 ± 0.1
		4	3.4 ± 0.1
		5	4.0 ± 0.2
		7	6.0 ± 0.2
		10	7.3 ± 0.1
		12	10.0 ± 2.3
		15	8.0 ± 3.5
		18	6.0 ± 4.3
		21	18.0 ± 3.2
		25	15.0 ± 5.5
		30	22.0 ± 3.5
F.	*Nephila* sp. 2		
		1	1.0 ± 0.0
		2	2.0 ± 0.0
		3	3.0 ± 0.0
		5	5.0 ± 0.0
		6	6.0 ± 0.0
		7	5.6 ± 0.1
		9	9.0 ± 0.0
		10	10.0 ± 0.0
		12	7.0 ± 2.5
		15	15.0 ± 0.0
		18	18.0 ± 0.0
		21	17.0 ± 0.8
		27	16.0 ± 2.3
		30	30.0 ± 0.0

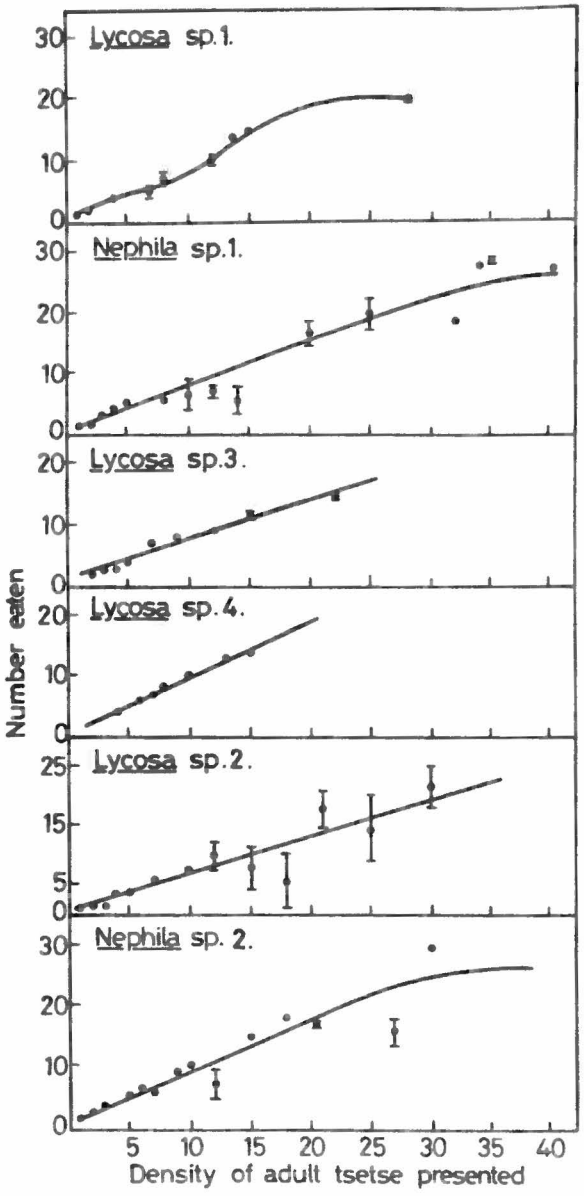

Fig. 33 - Functional responses of Araneae species.

Table 48a- Average percentage predation in puparia buried at different densities at Nguruman, Kenya. All densities replicated six times.

Density per m2	Distance between puparia (cm)	Mean percent predation (± S.E.) Number partially eaten	Number missing	Total predation
1	-	33.3 ± 21.1	16.7 ± 15.7	50.0 ± 22.4
4	50.0	4.2 ± 4.2	16.7 ± 12.4	20.8 ± 11.9
9	33.3	14.8 ± 7.8	29.6 ± 6.8	44.5 ± 11.5
16	25.0	6.3 ± 2.3	23.0 ± 12.4	27.4 ± 12.0
25	20.0	12.0 ± 4.8	15.3 ± 5.8	27.3 ± 8.9
36	16.7	11.1 ± 4.5	23.2 ± 9.6	34.3 ± 13.6

Table 48b 6 x 6 LATIN SQUARE ANOVA TABLE ON PUPAL PREDATION

Source	df	SS	MS	F
Sites	5	4367.2	873.44	2.10 NS
Months	5	2771.7	554.33	1.33 NS
Densities	5	2018.5	403.70	0.97 NS
Error	20	8330.6	416.53	
Total	35	17487.9		

NS means not significant at $P < 0.05$.

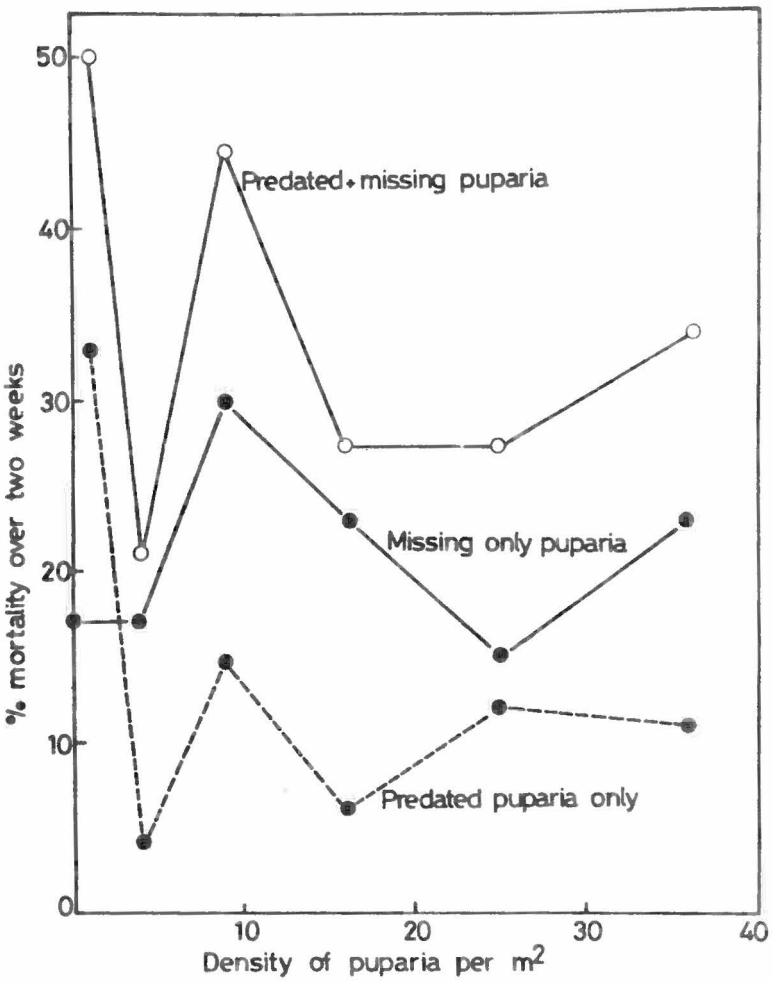

Fig. 34 - Percent predation in puparia buried at different densities. (December 1985 - June 1986).

was from 20.8 to 50.0%. Overall mean predation over 2 weeks was 34%.

Latin square analysis of the rate of predation in different sites, months and densities are given in Table 48b, the results show that effects of site ($F = 2.10$), months ($F = 1.33$) and treatment or density effects were not statistically significant ($F = 0.97$) at $P > 0.05$. There was no relationship between overall predation rate estimates and puparia density (Fig. 34).

9.3.6 PREDATION ON ADULT G. PALLIDIPES TETHERED AT DIFFERENT DENSITIES ON TREE TRUNK.

Adult mortality due to predation was estimated and the results based on 15 replicates at each density are given in Table 49. Flies were recorded to be predated upon when the fly was found missing (assumed to be completely devoured) or partially eaten. The motivation of such a study was to determine whether predation was density dependent. Predation by ants was the most important and ranged from 56.7 to 89%. The overall predation curve shown in Fig. 35a indicates that predation by the Formicidae is significantly density dependent ($r = 0.88$, $P < 0.01$).

Percent predation by spiders was very low and ranged from 0.0 to 1.7% (see Table 49). The avian predation illustrated in Fig. 35b shows that predation by birds ranged between 11.6% and 36.7% and was density-independent. Fig. 35c combines results of all predators to give an inversely density dependent mortality at low density, switching to direct density dependence at high densities.

Table 49 - Average percentage predation in tethered adult G. pallidipes at Nguruman, Kenya. All densities replicated fifteen times.

Density of flies per M3	Mean percent predation (± S.E.) due to different enemies. Invertebrates: Ants	Invertebrates: Spiders	Vertebrates: Birds	Total.
2	56.7 ± 11.8	0.0	36.7 ± 11.4	93.3 ± 5.6
4	63.3 ± 9.7	1.7 ± 1.7	15.0 ± 4.8	83.3 ± 8.3
6	66.7 ± 9.2	0.0	18.9 ± 4.6	90.0 ± 7.2
10	63.3 ± 9.8	0.1 ± 0.1	20.0 ± 6.3	84.0 ± 6.3
20	66.3 ± 6.5	0.3 ± 0.3	24.0 ± 4.0	90.7 ± 5.5
30	89.0 ± 4.7	0.0	11.6 ± 4.6	98.4 ± 1.2

ANOVA TABLE

Source	df	SS	MS	F
Densities	5	1,302	260.0	0.01
Between predators	12	225,397	18,783.09	30.78***
Residual	252	153,731	610.24	
Total	269	380,480		

*** Significant at $P < 0.001$.

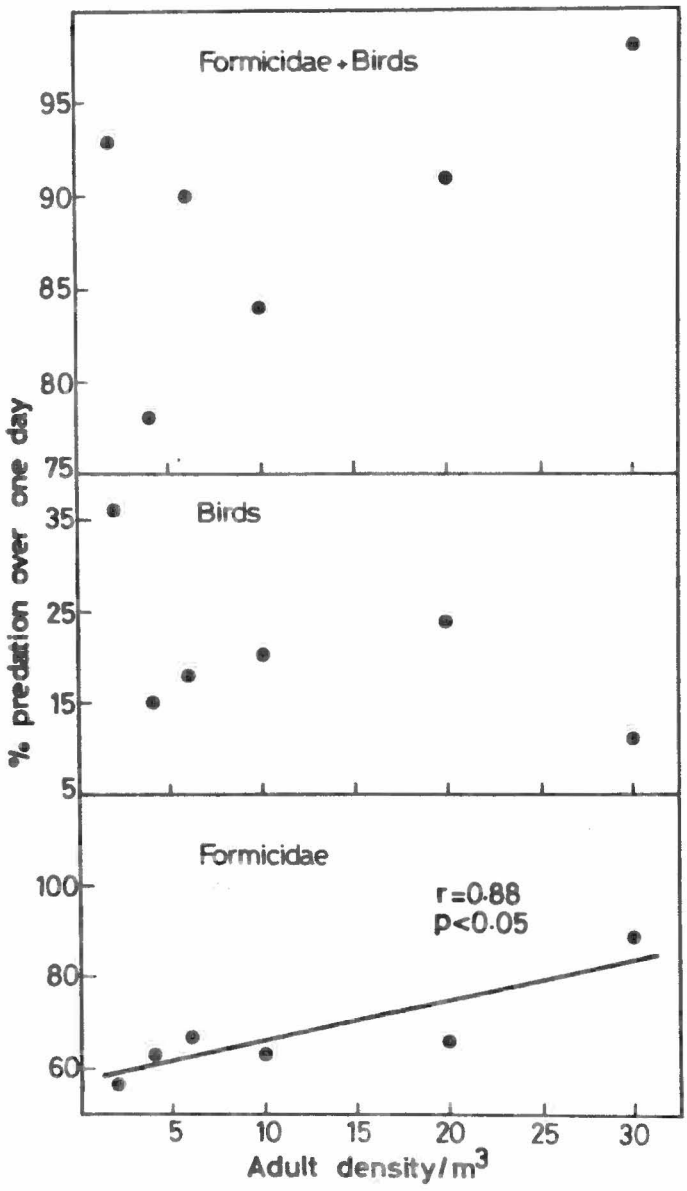

Fig. 35 - Percent predation in tethered adult G. pallidipes in natural habitat.

9.4 DISCUSSIONS AND CONCLUSIONS

Serology as a potential tool for analysing diet of invertebrate predators was demonstrated as early as 1946 by Brooke and Proske, but the usefulness was not recognised until recently. Onyeka (1983) applied it to identify natural predators of Culex pipiens L. and C. torrentium Martini in England. Calver et al., (1986) also used it to determine predators of the bush fly, Musca vetustissima Walker in south-western Australia.

The immunological precipitin test used in the present study was simple and could detect tsetse antigens at dilutions of 1 : 320 for puparia, 1:640 for the adult and 1 : 640 for general antigen with very faint band at 1:1280, indicating that it was sensitive enough to detect the small amount of tsetse diet (6 to 70 ug of protein) on a filter paper. The antiserum raised against the pupal stage of G. pallidipes reacted with adult antigen and vice versa, indicating that there are some antigenic determinants which are common to both developmental stages. The presence of both pupal and adult antigenic determinants in the general antigen was evidenced by the formation of three precipitin lines. The lack of the second precipitin line with the adult stage may have been due to either insufficient quantities, or absence of that antigen in the adult stage.

Tsetse meals at different stages of digestion could be detected for 6-48 h post-feeding. The detection periods in different predators is an indication that detectable components of tsetse are degraded faster in some predators than in others. In field situations one is likely to catch predators with only residual tsetse meal. It is therefore encouraging to note that tsetse meal could still be detected in some predator species up to 48h after feeding. The detection periods observed in the present work are comparable to that obtained by Onyeka (1983) who reported that precipitin tests could detect mosquito meal in the guts of predators from

a minimum of 8 h for the newt, Tritunus vulgaris to 24 h for the zygopteran Ischnura elegans (van der Linden). Using the gel precipitin test, Calver et al., (1986) could detect single Musca vetustissima larva in Staphilinid Leptacinus sociaus (Fauvel) up to 2 h after feeding, while the immunoelectroosmophoresis test (IEO) gave positive results up to 5 h post-feeding. They also recorded that, with the precipitin test, the same prey in the carabid, Chlaenium greyianus could be detected for up to 24 h, while with the IEO test it could be detected up to 36 h. These results show that detection times will depend not only on the size of the meal (Giller, 1984), speed of digestion (Giller, 1986) and the environmental factors determining the digestion rates (Service et al., 1986), but also on the sensitivity of the detection method.

The results of the cross reaction test indicates that the pallidipes-antiserum is specific to Glossina. Because there was no cross reactions between the pallidipes-antiserum and antigens of other dipteran genera : Atylotus, Stomoxys, Promachus, Musca and other insect taxa : Gryllidae, Blatteria and Acrididae, positive identification of Glossina diet in guts of predators was possible without the laborious process of removal of cross-reactivity by absorption. A certain degree of cross reaction was, however, present between the pallidipes-antiserum and antigens of Glossina longipennis (also found at Nguruman). This cross reaction indicates partial immunological identity in the two species in terms of the antiserum used. Although distinct separation of the two species of Glossina in the area would have been ideal, it does not significantly affect the use of this assay in work with predator-tsetse relationship. The two species generally prefer different sites for breeding, but are sometimes found within the same habitat, and it can be speculated that a predator effective against one tsetse species could

also have some impact on the other species.

The serological method used in this study has a number of advantages in the study of predator-prey relationships. Firstly, it is sensitive because dilution of antigens up to 1 : 1280 could be detected. Secondly, the assay was simple and easy to perform, and was amenable to large scale use because as many as 48 samples could be tested simultaneously on $8cm^2$ glass plates. Thirdly, it offers a means of positively identifying predators which prey on tsetse in their natural habitats and the extent of predation. There are, however, two possible sources of bias in this immunological test for identification of predators. Firstly, there is no way of distinguishing between active predation, carrion feeding and cannibalism (that is, larger predator eating a smaller one which had previously eaten the prey). Secondly, there are problems of quantification and cross-reactivity.

It has been shown previously that members of the Orders, Diptera, Hymenoptera, Odonata, and Orthoptera can be important and active predators of Glossina (Laird, 1977; Challier, 1982). In the present study positive immunological reactions were obtained with gut smears from Gryllidae (12.6%), Carabidae (7.5%), Asiliidae (25.0%), Blatteria (2.6%), Araneae (21.7%), Sphecidae (11.2%), Vespidae (55.6%), Eumenidae (32.0%), Megachilidae (25.0%), Libellulidae (9.7%), Petaluridae (5.3%), Lestidae (29.4%) Corduliidae (12.1%), and Chlorocyphidae (26.5%).

The relative proportions of predator species varied in different habitats. Gryllidae were numerous in the larviposition sites and are noted as being opportunistic, omnivorous feeders which presumably used the larviposition sites as their own feeding and breeding sites. Since they are not active predators, they may have scavenged on any of the developmental stages, particularly larvae, puparia and newly-emerged adults that

had died from other causes. Such carrion feeding could have contributed to the high incidence of positive results observed in the Gryllidae. Amongst the predators found in the larviposition sites, Formicidae and Araneae were numerous and widespread. These predatory groups may be important but since they are transient and their gut contents were difficult to collect and analyse, they were infrequent in the samples tested. They may however be more regular predators than the data suggest.

The high incidence of positive results in any particular predator group perhaps indicates that they are regular predators of tsetse. The high incidence of positive results found in Asiliidae, Araneae, Lestidae, Chlorocyphidae and various species of Hymenoptera indicate that these groups could be the regular predators which attacked adult tsetse in flight or those resting on vegetation. Different species of Asiliidae, Odonata, Araneae and Hymenoptera are effective predators and therefore potential biological agents. One of the problems of using any of these predators in control in the field is that no suitable method has so far been developed to rear them economically in large numbers. With the positive identification, as done in this study, it may be possible to develop the breeding methods of any of the important predators as biological control agents.

Handling times were generally longer for spiders, asilids and other predators which have extero-digesting feeding patterns than the predators that chew their prey. These long handling times affect predation rates by decreasing the time available for active searching and attacking of prey. At higher prey densities some spiders and solifugids killed some of the prey without consuming them. Such wasteful killings have also been reported for many vertebrate predators in the literature on predation (Buckner, 1966; Kruuk, 1972; Toth and Chew, 1972). In other cases, some

of the spiders consumed fewer prey at higher prey densities because the predators were disturbed by the large number of active uncaptured prey. Reduced killing due to this disturbance or interference component could be the explanation for the slight decline observed at higher prey densities in the sigmoid response curve. In some cases the disturbing prey is captured and added unto the already captured prey, resulting in increase in prey numbers killed.

The possible impact of predators on reducing the size of tsetse population was assessed by laboratory experiments on functional responses. Certain general conclusions can justifiably be drawn from the present study. The first is that predation tends to be of two types, Holling's Type II and sigmoid responses. The Holling's Type II functional response has also been recorded for many insect predators and parasites (Burnett, 1959; Thompson, 1975; Hassell et al., 1977) indicating that it is a widespread functional response among invertebrate predators, parasites and parasitoids. The sigmoid response was formerly known to be exhibited by only vertebrate predators which were offered the opportunity of shifting from one prey to another (Hollings, 1959a). In the vertebrates, the second steepness in the curve was attributed to improved skill in capturing prey or a shift to more abundant prey as their numbers increased. However, Haynes and Sisojevic (1966) demonstrated a sigmoid response for the spider, Philodromus rufus Walckenaer, preying on Drosophila adults. Since then similar responses have been demonstrated in predatory phytoseiid (Sandness and McMurtry, 1970); the tachinid parasite, Cyzenis albicans (Fall) (Embree, 1966); and some insects predators (Murdoch and Oaten, 1975; Hassell, 1978) indicating that such feeding responses are also widespread among invertebrate predators and parasites. According to Haynes and Sisojevic (1966), the sigmoid

relation presents the only feeding response implying inherently regulating possibility as far as functional response alone is concerned.

In summary, the two principal types of functional responses shown by predators of G. pallidipes can be explained by a combination of five predation components notably, times predator and prey were exposed; searching and attacking rates; handling time; hunger state and stimulation of the predator by each prey discovered or captured. The first three components are basic and explained those feeding responses that are best represented by Holling's Type II curve. If the hunger and stimulation of prey discovery are added to the three basic components then the sigmoid or S-shaped response results. Thus in many situations where the subsidiary factors are constant, by assuming that numerical response is immediate, predation can be completely described by combining functional and numerical responses as was done by Holling (1959b).

Pupal loss rate has been shown to be density dependent from the monitoring data (Adabie, see chapter 5 of this thesis), but this could not be corroborated by these field experiments. Observations made in the present study on predation on puparia of G. pallidipes indicated that predation intensity was density independent. Rogers (1974) however found that predation was density dependent. Three explanations could account for the differences observed. First, Rogers arranged puparia in a line, resulting in much shorter inter-puparial distances. Secondly, predation at higher densities in these experiments was probably under-estimated because some of the puparia emerged before the end of the two weeks exposure period allowed for the experiments. Such emergences obviously reduced the numbers of puparia available for predation. Lastly, Rogers physically marked the positions of the puparia in the ground which could have served as cues for vertebrate predators. Only the corners of the

square were marked in these experiments.

Rogers and Randolph (1984) found that predation of adult G. f. fuscipes by vertebrates, notably birds, in Uganda was strongly density dependent, but that caused by invertebrates was not. Results of similar predation experiments on tethered adult G. pallidipes in this study showed that predation by birds was density independent. The proportion of decapitated heads used as the only index of avian predation could have under-estimated predation due to birds, because birds sometimes tore off the entire fly without leaving any evidence of their activity. However, predation due to ants was found to be density dependent. G. pallidipes have body colour which blends with the background of their resting sites and thus make them less conspicuous. This could be one of the reasons why the flies are not easily predated upon by birds.

Natural predation damage attributable to specific predators was difficult to assess because most of the predators are nocturnal and therefore their activities could not be observed during the day. It was however estimated using serological analysis described earlier in this chapter. Based on my findings, predation of G. pallidipes appears to be an important mortality factor with regulatory role on the population in the study area. It may be worth seeking specific predators responsible for the density dependent mortalities and enhance their effectiveness by manipulating the environment (habitat) in a way that will help to improve their survival, reproduction and thereby increase their impact on the population. The conservation of predators in their natural habitat clearly deserves some attention in the execution of a program of integrated control which has application of insecticides as one of the methods to be used.

CHAPTER TEN

GENERAL DISCUSSION

Seasonal fluctuations in puparia numbers of G. pallidipes at Nguruman, Kenya were established using a constant-time hand-searching method. This method provides relative population estimates, but may not adequately reflect real changes in densities. This is partly due to difficulty in searching soils in waterlogged sites. The searching efficiency was also affected by the physical and mental states of the searchers. There is therefore a need to devise a more quantitative method for estimating puparia numbers which will minimize these problems. One approach is to use simple 'larviposition' traps consisting of 1m x 0.5m x 8mm wooden or metal trays with a wire-mesh bottom and collapsible sides, and provided with shelters. This method is now being tested at Nguruman (Muange, pers. comm.). The shelter could be as simple as black cloth over a wooden frame hinged to one side of the tray. This will induce the gravid females to congregate and drop their larvae into the soil in the tray section of the trap under the shelter. The sides of the tray should be collapsible to allow several trays to be stacked together to facilitate transportation to the field, and to allow several traps to be stored in relatively small area. Such trays could be filled with soil from natural larviposition sites and left for variable periods of time in recognised larvipositions sites in the tsetse habitat. The wire-mesh base will then allow the puparia to be sieved out of the soil on each sampling ocassion. An alternative approach is to use quadrat sampling involving a combination of constant-area search followed by sieving of the soil within the quadrat.

The presence of teneral flies (as indicated by catches in the biconical traps) in all vegetation types indicated an area-wide distribution of the flies. However, the sites selected for the monthly monitoring of the population only revealed movement of the flies along the east-west direction, with no information of what goes on in the other areas. It would therefore be desirable to select sites in all vegetation types to include a wider range of sites in future studies.

The aggregation of puparia in some sites in certain seasons suggests that the pregnant flies make an active selection of particular sites in relation to the climatic conditions. What cues are used by pregnant females in selecting larviposition sites?. They probably recognise potential larviposition site by their visual (shade and dark colour) and edaphic and olfactory characteristics (loose, dry and coarse soil) which initiate site-orientated responses. Approach to a site is probably modulated by the visual stimuli, while the entry into a site is probably mediated through a combination of visual and olfactory stimuli from the soil. Non-random site selection may also be explained by the responses of the flies to microclimate of the larviposition sites.

How can we study the factors influencing (a) the choice of larviposition sites by the female flies and (b) choice of pupariation sites by the larvae in a natural situation?. Electric screens around larviposition sites will provide information on the rate of entry of pregnant females to potential larviposition sites, while a study of the microclimatic factors of the sites selected will give an insight to the factors which govern site selection. For determining the pupariation sites, the release of radio-labelled larvae in sites with different microclimatic conditions will prove more informative, because the position of the resulting puparia can be located using a radiation

detector.

Many predators and few parasitoids were trapped in the area. In selecting an appropriate trap for sampling tsetse predators it is necessary to consider the convenience and cost-efficacy of the traps available. As regards practicability, pitfall traps containing preservative have several advantages. A single trap could provide large numbers of predators, once set the traps require little attention for a period of 3 to 5 days and samples are preserved in good conditions for later morphometric studies and identifications. Baited pitfall traps, on the otner hand, require attention if predation among the predators is to be avoided. The traps are however expensive and susceptible to breakage. The expense of the glass jars can be reduced by using discarded empty tin cans of similar capacity, which are extremely cheap and relatively damage-proof. In conclusion, the unbaited and baited pitfall traps and constant-time searches appeared to provide a reasonable picture of the changing patterns of the distribution and abundance of most of the potential predators in the larviposition sites and thus can be used for sampling predators in such habitat.

How important are the parasites, pathogens and predators in regulating tsetse population size?. Parasitism by Exhyalanthrax parasitoids was low and inversely related to puparia numbers with little evidence of delayed density dependence. The relationship between pupal loss rate (estimated from relative densities of puparia and teneral female flies) and puparia number was, however, significantly density dependent. What could be responsible for this regulation?. Serological analysis of gut smears of some of the arthropods caught in the area showed relatively nigh predation by Gryllidae, Asiliidae, Odonata and Hymenoptera. However, no numerical responses could be demonstrated

between some of these predators and tsetse numbers. In addition, field experiments on predation showed no relationship between predation intensity by spiders or birds and tsetse number. These results are not surprising since most of the predators are polyphagous and are therefore opportunist feeders, feeding on any suitable species of prey which happens to be present when the predator requires a meal. However, the fact that density-related responses of a particular predator to change in numbers of its prey is, to some degree, probabilistic in mode of action does not necessary mean that it cannot serve as a reliable density stabilizing agent (Milne, 1957). Moreover, a clear distinction should be made between the total absence of regulation and the failure to detect its presence because of sampling and technical difficulties. It is not uncommon to fail to detect density dependence with only a short run of data, as in this study. Alternatively the density dependent feature of the relationship between pupal loss and puparia density could result from emigration of very young flies or could be an artifact from variable efficiencies in sampling the puparia and the teneral flies on which the pupal loss is based.

What are the implications of the findings of the present study for tsetse control?. Can tsetse be controlled at the pupal stage?. Collection of puparia from larviposition sites is not a feasible proposition, because it is not feasible to identify all the sites which are widely scattered and are used seasonally.

Have shelters or larviposition traps any potential in tsetse control?. It is possible that if insecticide-impregnated shelters were constructed in good sites and baited with odours that are selectively attractive to the gravid females, they might prove effective in

concentrating and eliminating a good proportion of the reproductive members of the population. Insecticide application to the ground would probably have a detrimental effect on the predators. However, if the larvipositing females rest on the underside of the shelter as appears to be the case, this could be impregnated with insecticide to selectively kill the female tsetse. If non-pregnant flies use the shelters as refuges in hot weather, this would further increase the mortality.

The information on shifting of breeding sites, seasonal fluctuations in puparia numbers and diurnal periodicity of adult emergence obtained from this study could be relevant in indicating times, sites, habitats and seasons of application of insecticides or of other control measures in order to maximise their effects on the proportion of the population comprising of pregnant females entering the sites to larviposit and the emerging teneral flies. For instance, in the hot dry season the flies tend to concentrate in riverine thickets and the valley woodland where greater numbers of puparia were also found. This would be the best time to concentrate control efforts in the productive vegetation habitats.

Fungal infection was the major cause of non-emergence of puparia collected in the field. From control point of view, the fungi when released from cadaver of the dead puparia may build up in the soil to provide new sources of infection and long period of control, as long as conditions are favourable to fungal growth. Therefore, the establishment of the patnogenicity of the fungi identified and the long term effects of fungal infections and fungal ecology in the soil require further study.

It has been shown that biological control such as the sterile male technique, combined with restricted usage of selective chemicals or

insecticide-impregnated targets and screens and use of odour-baited traps and other integrative measures can, in fact, solve tsetse problem in small isolated areas without resort to polluting chemicals. For tsetse, it is obvious that weather is not sufficient natural control factor. By the same token, the natural enemies under the existing conditions are not either. However, unlike the weather the natural enemies are factors of natural control which are subject to manipulation. How then can predators be used to supplement natural control measures?. Can the action of predators, for instance, be practically enhanced by environmental manipulation or through mass rearing and releases?.

The provision of resting sites for predators is one example of modifying the habitat to enhance the beneficial effect of native natural enemies. Unfortunately, studies in this area are rare. Another obvious approach is to rear native predators in large numbers and release them at appropriate times and places. This may be related in part to the ease with which they can be mass-reared and manipulated. Unfortunately, little progress has been made in developing expertise in utilizing this approach. Aside from that, inundation programmes may not be economical for many affected countries because of the mass rearing problems.

Since past and recent empirical data on biological control programmes involving naturally-occurring enemies have not been successful, nature's own method of control through the action of parasites, pathogens and predators can be augmented by introduction of these agents from other areas. Multiple importation of natural enemies either simultaneously or sequentially may be considered. Why is it worthwhile to add any biological control agent to a complex of parasites and predators already unable to control tsetse?. It is wortnwhile if that predator will fill some functional niche not already filled, or be

more effective than other species already there. The introduction of a highly specific species is a desirable practice, but it is unrealistic to attempt to find and to pre-rank every possible candidate in order to ascertain the 'best' one to introduce. Furthermore, rarely is a specific natural enemy superior over the whole geographic range. The benefit to gain by multiple introduction is that it not only achieves diversity but establishes a combination of species that will prove better than what already exists. Such methods have been used against the California red scale (DeBach et al., 1962), the spotted alfalfa aphid (Van den Bosch et al., 1964) and Klamath weeds (Huffaker, 1967; Harris et al., 1969). There is therefore no justifiable reason why it should not be considered for tsetse control. Lack of knowledge of the ecology and biology of predators hampers the selection of the most effective biological control candidates and developing an introduction strategy. Effectiveness of candidate predators must be based on detailed qualitative and quantitative knowledge of the predator's feeding habits and the contributing roles of prospective competing predators in the area to be treated. Such basic information will not only improve the chance of selecting the best predator, but may eventually lead to development of supplementary approaches to tsetse control.

SUMMARY

1. A two year programme was carried out at Nguruman in the Kajiado District in the Rift Valley Province of Kenya, to study the ecology of puparia of Glossina pallidipes Austen and the natural enemies of both puparia and adults.

2. The study area supports an indigenous Maasai population with their cattle, goats, donkeys and sheep. There are few irrigated farm schemes producing fruits and vegetables and small rural industries producing charcoal. The area is rich in game animals, but the presence of large numbers of G. pallidipes, G. longipennis and other biting insects has rendered the greater part of the area inhospitable for high grade cattle ranching. The climate of the area is divided into two wet and two dry seasons.

2. The trends in relative abundance and distribution of puparia in different months, sites, shading regimes and vegetation habitats were established using the time-constant hand searching method. The searching efficiency of puparia collectors within $2m^2$ plots averaged 60%, thus efficiency in $42m^2$ site will be 12%..

3. Puparia numbers were highest during the dry seasons and the riverine thicket contributed most to the total puparia numbers because of its greater size and its attractiveness for larviposition. Puparia population in the riverine thicket

declined in the rainy seasons. This was attributed to shift in breeding sites from the flooded primary habitats to relatively dry secondary sites, use of scattered sites on hilly slopes unaffected by floods, difficulty in locating puparia in wet soils by searchers and to reduced availability of host animals which moved out of the thickets into other locations in the study area.

4. True primary habitats of G.pallidipes at Nguruman were found in riverine thicket and dense mixed woodland which contained evergreen and deciduous trees and shrubs providing good shade. Sites shaded by deciduous vegetation were used seasonally and often abandoned when the trees became leafless. Most of the sites have no ground vegetation cover except for layer of dry leaves falling from the shading vegetation.

5. Larviposition sites are located close to water courses where animals go to drink thus ensuring that they get blood meals. Because of the proximity of sites to these courses some of the sites get flooded every rainy season. Coolness and shade are features of effective sites and the application of insecticides to natural refuges with these features is a policy of merit.

6. Greyish-brown soils are the most preferred (59.6%), followed by black soils and the least preferred soils have light brown colour (2.1%). Though puparia are found in a wide range of

soil types, they occur more frequently in loamy-sand soils(63.8%) and less in clayey soils (4.3%).

7. Puparia duration varied monthly and ranged between 25-38 days, with a mean of 32.2 $\pm$ 0.8 days. Duration was much longer at lower temperatures but was relatively shorter at higher temperatures. Differences observed in duration of puparia from different sites were attributed to possible effect of edaphic factors and microclimatic factors.

8. Diurnal rhythm of adult emergences from field-collected puparia shows bimodal pattern with minor peak occuring around 0600h and the major peak occuring in the late afternoon between 1500 and 1800h, resulting in an irregular U-shaped curve. Diurnal emergence pattern of the pupal parasitoids, Exhyalanthrax species was similar to its tsetse host.

9. Age structure of the puparia collected from the field varied monthly but the survivorship curve indicates that mortality rate in different age groups is constant with an estimated mortality rate of 0.15, indicating a rate of 4.5% (k-value = 0.02) per day. Pupal to adult survival was high in the dry months of December-February (average 55.5%), but was low in the wet months of March-June (average 45%). The moderately high pupal to adult survival indicates that substantial numbers of puparia are protected from mortality agencies.

10. The devised age-grading dissection method for ageing field collected puparia is a useful technique for assessing the age structure of dead puparia at time of collection, and for comparing the relative age of puparia collected at different times in the same locality or from different localities.

11. Puparia were found near the surface of the soils when it was wet or covered with thick leaf litter cover, while larvae tended to burrow deeper into dry soils and soils without leaf litter cover. The general pattern of vertical distribution of puparia in the soil is (a) decreasing number of puparia with increasing depth; (b) pupal depths shallower in wet soils and deeper in dry soils, and depth shallower in shady areas than in relatively open areas.

12. In general puparia showed marked tendency to be aggregated in shades underneath horizontal branches, reflecting adult fly preference for resting on horizontal surfaces during the terminal stages of pregnancy. However, puparia are more scattered in large-sized sites than in smaller sites, making it easier to discover more puparia in smaller sites than in larger ones.

13. Because the larvae have limited powers of locomotion, the responsibility for survival of the puparia is placed on the adult. Particularly important is the selection of larviposition sites, because larvae deposited in exposed areas are unlikely to survive. The aggregation of the puparia

found in the vegetation types with adult abundance suggests that the adult makes an active selection of larviposition sites.

14. Breeding intensity in sites varied monthly and the favoured sites which are used continuously are recognised by the large numbers of puparia found in such sites throughout the year. Variations in puparia numbers found in different sites are attributed to shifts in sites in relation to the habitat and weather changes. Puparia numbers per site are not proportional to size of site and hence could not offer a useful breeding index for comparing relative densities of puparia from different sites or for predicting expected puparia yield per site.

15. While puparia numbers in thickets declined following heavy rains, those in dense mixed woodland increased suggesting the possibility of a seasonal shift in breeding sites within the same locality, resulting in changes in distribution and abundance of puparia within an area. This seasonal shift probably evolved to avoid environmental and climatic stresses experienced in different areas in different seasons.

16. Additional shading provided by artificial shelters appeared effective, especially in the dry seasons when most of the deciduous trees become leafless, in concentrating puparia by offering good shade. The dark appearance of the interior probably attracted and induced gravid females to larviposit

in the soil under the shelters. The numbers of puparia collected under the shelters were 7X greater than those collected from natural unsheltered sites. Such artificial shelters have trapping potential and can be developed further to form larviposition traps.

17. Of all the climatic factors of larviposition sites investigated, only rainfall over 80mm and associated increase in soil water content, waterlogging or flooding of low-lying sites along river banks caused drastic density independent catastrophic changes in puparia population by making some sites unsuitable for larviposition for two or more months. Soil temperatures at 2 and 4cm depths, ambient temperature and relative humidity and light intensity are relatively constant within the sites and seem to have little or no effect on changes in puparia population.

18. There is clear evidence that vegetational and climatic changes, availability and movement of game animals and seasonal shift in breeding sites play major part in determining local abundance and distribution of adult tsetse as well as the puparia.

19. Potential predators of tsetse were sampled by several methods. Baited- and unbaited pitfall traps and constant time searching of vegetation and soil were effective for capturing predators in the larviposition sites, while hand-nets and biconical traps proved suitable for sampling potential predators in the general tsetse area.

20. Attempts at rearing some of the potential predators, particularly crickets and spiders are discussed. In contrast to the rearing of spiders, rearing of crickets was easier and more successful because field collected adults readily laid eggs in moist soil and the nymphs also readily fed on vegetables and dead insects.

21. Pupal mortality rate, estimated from relative densities of puparia of a particular month and teneral female flies of the following month, is significantly density dependent and thus serve to regulate population size.

22. Natural puparial mortalities due to non-emergence are caused mainly by developmental failures, emergence failures, degeneration of puparial tissues and fungal infections. Developmental failures took the form of empty pupal cases, puparia containing shrivelled mass of tissue of different colours ranging from cream to dark brown, while the emergence failures took the form of puparia with retained adult flies which failed to emerge.

23. Drowning of puparia brought about by floods provided favourable conditions for fungal growth, and puparia mortality due to fungal infections was a significant key factor ($r = 0.63$, $P < 0.05$) in causing changes in puparia population. However, it failed to be an important density dependent factor. Since it is seasonal in nature it fits with Howards and Fiske's category of density independent catastrophic agencies. The isolated fungi are generally saprophytic in nature suggesting

that the infections could have occurred after the death of the puparia. However, some species like Aspergillus niger and A. flavus isolated from the puparia are known to produce very potent toxin called aflatoxin and it is possible that some of the fungi may be facultative pathogens. The k-values for this mortality factor vary slightly from year to year and so in simple population models its action can be represented by a constant.

24. Incidence of arthropod-induced damage in empty puparial cases varied monthly with mean of 24.0% and peaks occurring in dry seasons. The relatively high incidence of chewing imprints in predated puparia indicated that most of the arthropods attacking puparia are chewing predators. Invertebrates found in the soil, on vegetation and among the leaf litter in the larviposition sites, which could be responsible for these damage, include Gryllidae, Formicidae, Coleoptera and immature stages of insects and other arthropods. However, levels of predation showed no relationship with puparia density.

25. Puparia of G. pallidipes collected from the field gave seasonal fluctuations in rate of parasitization by two species of parasitoids, Exhyalanthrax beckerianus Bezzi and E. lugens Lw. Mortality caused by these parasitoids fluctuated around a mean level of 12%, but it is apparently not a key factor in the regulation of the puparia population. They are also not tsetse-specific. The k-values for this mortality showed a

significant inverse relationship with puparia density ($r = -0.50$, $P < 0.05$) with a delayed density dependent component. This is attributed to ineffective aggregative response or egg limitations. The monthly k-values varied very little from the mean that they can be used in a mathematical model as if they are constant.

26 Serological analysis of gut smears of potential predators for tsetse diet indicated that members of Gryllidae (Gryllus, Liogryllus, Phaeophillacris and Gryllulus species); Blatteria (Epilampra sp.); Coleoptera (Carabidae); Asiliidae, Araneae (Lycosa spp.); Sphecidae (Ammophila, Tachytes, Bembex, Sphex spp.); Vespidae (Belanogaster sp.); Eumenidae (Eumenes, Synagris spp.); Anisoptera and Zygoptera feed on tsetse.

27. Feeding responses of potential predators investigated are of two types, and are best described by Holling's Type II and sigmoid functional response curves. The former has feature with stabilizing effects on the interactions, while the latter has density dependent regulating feature implying inherently regulating possibilities as far as functional responses alone are concerned.

28. Levels of predation obtained in field puparia burying experiments were high, but predation did not show any clear density dependent relationship.

29. Percent predation by spiders of tethered adult flies of G. pallidipes was very low, and showed no relationship with tsetse density. Predation by ants was strongly density dependent, but that due to birds was density independent. However, the overall predation due to both ants and birds was curvilinearly density dependent, implying that these predators have regulating effect on the tsetse population.

30. Study on the relationships between predator abundance and tsetse numbers showed that most of the predators are not dependent on tsetse. Individually, the predators may not be important mortality agencies of tsetse, but cumulatively they may be effective in regulating tsetse population.

31. The implications of the findings of the present study are discussed. Integrated control approaches involving use of odour-baited traps, insecticide-impregnated targets and screens, releases of sterile insects, combined with restricted usage of non-residual chemicals, and importation and releases of natural enemies of tsetse or related species from other areas are advocated. The modification of the habitat to enhance the beneficial effects of the indigeneous natural enemies should also be considered. This could involve the provision of protected resting and breeding sites.

APPENDICES

Appendix 1 - Climatic data at Nguruman during the study period.

Year	Month	Temperature (°C) min.	max.	mean	Relative humidity (%)	Total Rainfall (mm)
1984	Oct.	21.9	36.9	29.4	26.4	23.3
	Nov.	21.8	35.8	28.8	35.0	90.1
	Dec.	20.7	35.7	28.2	28.7	59.0
1985	Jan.	21.8	40.6	31.2	20.6	0.0
	Feb.	21.0	36.2	28.0	34.6	88.0
	Mar.	21.6	37.9	29.8	25.0	110.5
	Apr.	21.2	32.1	26.7	42.9	182.9
	May	20.9	34.0	27.5	35.8	42.5
	June	18.0	34.9	26.5	30.9	5.8
	July	18.1	34.3	26.2	29.3	5.6
	Aug.	19.0	34.8	26.9	27.5	0.0
	Sept.	21.0	35.7	28.4	24.8	0.0
	Oct.	21.0	35.8	28.4	23.0	43.9
	Nov.	20.5	33.5	27.0	33.6	109.9
	Dec.	20.1	35.8	28.0	26.9	56.9
1986	Jan.	20.7	36.0	28.4	35.2	40.2
	Feb.	21.0	39.3	30.2	24.0	23.2
	Mar.	21.7	38.4	30.1	30.0	22.3
	April	22.1	34.8	28.5	47.0	107.2
	May	20.5	31.9	26.2	56.0	136.3
	June	16.9	31.7	24.3	40.0	0.2
	July	15.1	31.8	23.5	37.0	0.2

Appendix 2 - Climatic conditions (Mean ± S.E.) in selected larviposition sites of G. pallidipes at Nguruman, Kenya.

Year	Month	Temperature °C						Relative Humidity (%)		% Soil moisture content.
		Ambient		2cm deep in soil		4cm deep in soil				
		minimum	maximum	minimum	maximum	minimum	maximum	minimum	maximum	
1985	Feb.	27.5±0.9		26.0±0.2		25.5±0.2		44.7±4.1	61.3±0.9	35.4±2.0
	Mar.	22.1±0.7	27.0±0.9	20.4±0.3	24.8±0.3	21.4±0.2	24.1±0.3	25.9±0.4	61.3±1.6	33.8±2.3
	Apr.	21.7±0.7	29.4±0.7	22.8±0.3	26.4±0.9	22.8±0.2	25.4±0.7	42.7±4.0	63.0±1.4	32.7±1.6
	May	20.5±0.6	29.1±0.7	21.8±0.2	25.8±0.7	21.6±0.5	25.1±0.6	41.3±1.9	66.3±0.5	37.5±2.3
	June	19.3±0.8	30.0±0.4	20.4±0.3	25.3±0.3	20.0±0.3	25.0±0.6	35.8±1.7	65.3±0.4	35.5±1.1
	July	17.4±0.8	31.0±0.6	20.5±0.3	24.7±0.8	20.5±0.3	24.4±0.8	34.7±2.0	65.0±1.2	29.5±1.5
	Aug.	16.5±2.8	28.5±0.9	19.2±1.6	24.3±0.4	19.7±0.6	22.7±0.7	33.3±2.4	60.8±3.0	19.5±2.6
	Sep.	20.7±1.1	27.1±1.9	20.1±0.5	25.5±1.1	20.3±0.4	23.5±1.0	39.3±3.0	60.5±2.0	17.5±2.8
	Oct.	18.1±0.8	33.2±0.5	21.3±0.4	26.3±1.1	20.8±0.4	25.3±1.2	31.0±1.5	57.7±6.3	5.1±1.7
	Nov.	18.4±0.4	34.3±0.2	22.2±0.2	27.3±1.0	21.4±0.2	26.3±1.0	32.3±0.3	66.0±3.1	22.8±1.5
	Dec.	18.2±0.4	29.5±0.2	20.6±0.4	25.2±0.9	20.4±0.3	24.3±0.8	38.8±0.6	64.8±0.3	32.6±2.1
1986	Jan.	19.0±0.6	31.5±1.1	21.5±0.3	26.3±0.9	21.3±0.3	24.8±0.9	38.3±2.8	69.3±2.1	20.1±1.1
	Feb.	18.7±0.6	36.3±0.7	21.8±0.5	27.5±1.4	21.8±0.3	27.1±1.8	36.5±1.3	68.0±6.7	17.0±1.9
	Mar.	20.3±0.7	35.9±1.0	23.4±0.2	31.3±1.8	22.9±0.3	29.9±1.8	39.0±1.6	71.3±4.5	27.3±1.5
	Apr.	20.7±0.9	32.7±1.8	24.1±0.5	27.5±0.6	23.3±0.6	26.2±0.5	57.3±4.4	75.7±2.6	36.2±1.3
	May	19.7±0.5	28.6±1.0	22.4±0.2	26.2±0.8	21.9±0.1	25.0±0.6	48.0±2.0	74.8±0.5	49.8±1.4
	June	18.9±1.5	29.7±0.7	19.8±0.2	25.3±0.7	19.8±0.3	23.8±0.5	47.0±1.8	75.8±0.3	38.1±5.6
	July	14.2±0.7	31.3±0.7	19.4±0.5	25.5±1.4	19.4±1.1	24.3±1.4	38.3±0.6	71.5±1.3	23.7±0.8
	Aug.	15.1±0.1	31.4±1.2	19.6±0.3	25.9±1.0	19.3±0.3	24.5±1.2	45.3±1.7	74.3±3.8	20.5±1.5

Appendix 3 - LIST OF NATURAL ENEMIES KNOWN TO ATTACK *GLOSSINA PALLIDIPES* AND REFERENCES.

NATURAL ENEMY	COUNTRY	REFERENCE
ENEMIES OF PUPARIAL STAGE.		
DIPTERA		
Bombyliidae		
Exhyalanthrax abruptus (Lw)	Kenya	Minter, 1971.
E. abruptus	Kenya	Hursey, 1970.
E. abruptus	Zimbabwe	Heaversedge, 1969a.
E. beckerianus Bezzi	Kenya	Minter, 1971.
E. lugens (Loew.)	Zimbabwe	Heaversedge, 1969a.
E. salutaris Austen	Zimbabwe	Heaversedge, 1969a.
HYMENOPTERA		
Formicidae		
Pheidole spp.	Kenya	Minter, 1971.
Diapriidae		
Trichopria capensis	Kenya	Minter, 1971.
robustior Silv.	Uganda	Kangwagwe, 1971.
T. lewisi Nixon(P)	Kenya	Minter, 1971.
Eulophidae		
Syntomosphyrum albicans Kerrich	Zimbabwe	Heaversedge, 1969a.
Stomatocerus micans Waterston	Zimbabwe	Heaversedge, 1969a.
MUTILLIDAE		
Mutilla glossinae Turner	Zimbabwe	Heaversedge, 1969a

APPENDIX 3 (CONT'D)

NATURAL ENEMY	COUNTRY	REFERENCE
ENEMIES OF ADULT STAGE		
DIPTERA		
Asilidae	Kenya	Minter, 1971.
ARANEAE		
Hersilidae		
Hersilia setifrons Lawrence	Kenya	Minter, 1971.
SCORPIONIDAE		
Scorpions	Kenya	Minter, 1971.
BACTERIA		
Bacterium-like microbes	Uganda	Rogers, 1973.
NEMATODES		
Mermithid worm	Uganda	Moloo, 1972.
VIRUSES		
Virus-like particles	Kenya	Jaenson, 1978b
" "	Kenya	Odindo et al., 1981.

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