BIOLOGY AND ECOLOGY OF THE PREDATORY MOSQUITO, *CULEX* (*LUTZIA*) *TIGRIPES* GRANDPRÉ AND CHARMOY (DIPTERA:CULICIDAE) IN SOUTH-EASTERN GHANA.

by

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DECLARATION

This study was undertaken by Maxwell Alexander Appawu at the Department of Zoology and the Noguchi Memorial Institute for Medical Research, University of Ghana under the supervision of Dr.S.Q.Quartey

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DEDICATION

To my parents, Mark and Mante, my wife, Martha, and children, Kofi Kyenkyehene, Mame Mante and Mamaa Ampofoa.

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ABSTRACT

Culex (lutzia) tigripes Grandpré and Charmoy is a larvivorous mosquito with all instars of the larvae feeding primarily on the immature stages of other mosquito species found in their habitats. They breed in a wide range of water bodies but seem to prefer those already containing larvae of other mosquito species. The fluctuations in the population of the larval instars and pupae were studied by weekly sampling throughout the year. It breeds thoughout the year and the population peaks either coincide with or follow that of the preys; with both fluctuating with the rainfall. The larval densities of C.(L) tigripes were very small compared with those of other mosquito species; thus only 392-952 larvae of the predator were collected in the peak periods of May to July compared to 2786-8676 larvae of the prey mosquitoes.

No significant correlation was noted between variations in the numbers of C.(L) tigripes and the following physical and chemical properties of the breeding water: pH, Temperature, Chloride, Dissolved Oxygen and Total Alkalinity. Life-table studies showed the existence of high mortalities in the later stages of the predator. Starting from egg rafts collected from the field and providing C. quinquefasciatus larvae as the larval food and chicken as a source of blood, a colony of C.(L) tigripes was started but poor insemination appeared to be
the major obstacle to successful and permanent colonization.

Artificial insemination and copulation were also not successful. The optimum larval developmental temperature was 30°C, and 32°C for the pupae. Even though more prey larvae were consumed between 30-32°C than between 20-26°C, there was a reduction in weight of the final instar larvae and pupae at the higher temperatures. Depending on temperature each predator consumed between 160-229 larvae of C.quinquefasciatus during its entire larval development. With this rate of prey destruction, the predator can have big impact on the prey population despite the low proportion (1:7-9) of predator to prey. When larvae of C.(L) tigripes were reared on three non-living diets namely; Cerelac infant cereal, dog biscuit and milk casein, the developmental period of all instars was greatly prolonged and only one larva, reared on milk casein developed into adult mosquito. The weights of the final instar larvae reared on non-living diets were significantly lower than those reared on larvae of C. quinquefasciatus.

Culex (L) tigripes has well developed mandibles and serrated mouthbrushes for effective predation. The effect of the following factors on prey capture were studied: mobility, size, posture, the density and the extent to which prey and predator occur simultaneously in the same habitat. Ae.aegypti which moves more frequently was more preyed upon than An. gambiae and C. quinquefasciatus, and similarly, C.quinquefasciatus was selected more than chironomid. The strong integument of the pupae together with their large

sizes, spherical shape, posture in the water and ability to move quickly afforded them a better chance of escaping predation by C.(L) tigripes.

The effect of prey stage, predator stage and prey density on the predation rate was investigated using (C. quinquefasciatus) as prey. It was shown that the rate of predation increased with increase in the size of the predator and the density of the prey but decreased with increase in prey size. The functional response of the predator to changing prey densities followed Hollings type II model. The handling time of the predatory larvae on preys decreased as the length of time in which they were deprived of food was increased but the daily prey consumption was not affected.

Cannibalism occurred in all larval stages of the predator. The rate was higher among the early instars; was lower in the presence of mosquito prey and increased with crowding.

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CHAPTER 1.0 GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1 Scourge of mosquitoes

There are about 3,324 species and subspecies of mosquitoes belonging to 37 genera all contained in the family culicidae (Service 1990). The family contains three sub-families: Toxorhynchitinae, Anophelinae (anophelines) and Culicinae (culicines). The distribution of mosquitoes is world-wide but about 19% of all known species, have been recorded from the Afro- tropical region, which is defined as the subsaharan mainland Africa and offshore islands including Madagascar. Malaria, yellow fever, lymphatic filariasis and viral diseases are the major mosquito borne diseases. These diseases cause a high percentage of morbidity and mortality in the human populations in the tropics. The role of mosquitoes as vectors of these diseases has given them economic and medical importance in these parts of the world. In many temperate countries, mosquitoes may be of little or no importance as disease vectors but they can, nevertheless cause considerable annoyance because of their bites. In the Arctic Circle, for instance, the numbers of mosquitoes biting can be so great at certain times of the year as to make almost any outdoor activity impossible. In North America, more money is spent on killing culicine mosquitoes than is expended in most tropical countries where they are important vectors of disease (Gillett 1971).

Malaria

Sixty species out of the 400 known species of Anopheline mosquitoes throughout the world are important vectors of malaria under natural conditions. They are also known to be vectors of filariasis and viral diseases, but it is their role as the sole transmitters of malaria probably that makes the anopheline mosquito the most important vector of human disease in the world. The World Health Organization (WHO,1985) estimates that there are 110 million new cases of malaria a year, although about 270 million people may be carrying the malaria parasite. They further estimate that from one to two million people die each year from malaria and its complications and about 2.1 billion people (i.e. about half the World's population) in 103 countries are at risk of malaria. About eighty percent of the African population of 400 million people live in areas where little has been done to control malaria transmission and where the problem remains virtually unchanged or is worsening (WHO 1985). It is an incapacitating and debilitating disease and thus even without causing mortality, the economic losses are too great for us to be able to estimate. Malaria was ranked as the number one major disease in order of healthy days of life lost in Ghana (Morrow et. al. 1981). Malaria cases reported in Ghana rose gradually from 593,368 in 1985 to 1.56 million in 1989 (Ahmed, K. 1990 Personal communication).

Yellow fever

Yellow fever is an important mosquito borne viral disease which afflicts the people in Africa and tropical areas of America. It is a zoonosis, being essentially a disease of forest monkeys which under certain conditions can be transmitted to man. The arbovirus causing the disease is transmitted by mosquitoes. In Africa, the yellow fever virus occurs in certain cercopithecid monkeys inhabiting the forest and is transmitted amongst them mainly by Aedes africanus. Ae.africanus is a forest dwelling mosquito that breeds in tree holes and bites mainly in the forest canopy. This sylvatic or forest cycle maintains a reservoir in the monkey population (Lumsden 1951, 1952, Smithburn et al 1949). Aedes simpsoni which breeds in leaf axils of banana, plantains and other plants bites monkeys at the edges of forest and thus transmits the virus from monkey to man at the edges of forest. This is transmission cycle involving Ae simpsoni, men and monkeys is sometimes referred to as the rural cycle. Aedes aegypti breeds in domestic and peri-domestic water containers and transmits the virus among human populations in the urban cycle of transmission, which usually occurs during epidemics.

In tropical America, yellow fever is also a disease of forest monkeys, mainly cebid ones, but the most important vectors are Haemagogus and Sabethes species. Man becomes infected by disturbance of the tree top mosquitoes during tree-felling. The disease has occurred in Africa as sporadic

cases of jungle yellow fever, mainly in the forest areas or during outbreaks leading to high mortality. Between 1960 and 1962, a dramatic epidemic affected Southern Ethiopia where it was estimated that 100,000 cases and 30,000 deaths occurred in an area with a population of one million (Serie et al 1968). Estimates made on the basis of serological evidence produced the figure of approximately 40,000 infections and a death rate of about 10% during an urban yellow fever outbreak in Sudan in 1940 (Kirk 1941). Typical urban outbreaks occurred in Accra, Ghana, in 1926 and 1927, and again in 1937 (WHO 1986). Another outbreak in the Upper and Northern regions of Ghana in 1969-70 had 318 cases reported and 79 deaths. Five out of the then nine regions were affected with heavy mortalities recorded in Volta and Eastern regions during an outbreak in 1977-80 (Ministry of Health 1980). Yellow fever like malaria continues to be a major threat in endemic zones of Africa where the virus reappears even after long periods of quiescence.

Other Viral diseases

There are about 200 different viruses known to be transmitted by arthropods, over 100 of them are transmitted by mosquitoes. More than a 100 species of mosquitoes belonging to no less than 16 of the 37 genera have so far been implicated one way or another in the transmission of viruses; at least 40 of these belong to the genus Aedes, and some 20 each to Culex and Anopheles. Some of the arboviruses transmitted to man

by mosquitoes are Chikungunya in East Africa and India; O'nyongnyong, a non-fatal but painful disease found predominantly in Kenya and Uganda; Bunyamwera in Africa; West Nile in Africa, Europe, Asia, Trinidad and Panama; and Murray valley in Australia. Both the classical and haemorrhagic forms of dengue are transmitted principally by Ae aegypti. Various species of mosquitoes including, Mansonia, Aedes and Culex are known to transmit viral encephalitis, the most important are Eastern, Western, Venezuelan, St. Louis and Japanese encephalitis; all these involve a zoonoses with birds. The first three which are sometimes referred to as equine encephalitis are very virulent to horses and man.

Filariasis

The World Health Organization estimates that about 90 million people are infected with lymphatic filariasis, the cause of elephantiasis in the world (WHO 1990). It is transmitted by various species of Culex mosquitoes. Members of Culex pipiens complex, and in particular Culex quinquefasciatus which is a night biting mosquito, are the most important vectors of the nocturnally periodic form of Wuchereria bancrofti - the parasite which causes this disease. In addition to these mosquitoes, other species of Culex and some species of Aedes are considered to be of regional importance. The non- periodic form of W. bancrofti is transmitted mainly by Anopheles polynesiensis which has a wide

distribution in the Pacific region. The culicine transmitters of Brugia malayi, another parasite which causes filariasis, belong almost entirely to the genus Mansonia of which the most widespread appears to be Mansonia uniformis. Lymphatic filariasis is not as important in Africa as it is in the Far East. In Africa, Anopheline mosquitoes which transmit malaria have been implicated in the transmission of filariasis (Coker 1986). These scourges of mosquitoes cause tremendous pain and suffering ranging from internal organ damage, disabling anaemia and death. Beyond their toll of individual illness and death, these diseases have insidious effects on society. They impede national and individual development, impair intellectual and physical growth, and exact a huge cost in treatment and control programmes.

Control of Mosquitoes

With all the improvements in drugs and vaccines which have taken place, extensive reliance still has to be placed on reducing the population of vectors of these diseases. Measures for controlling the arthropod vectors of diseases including mosquitoes may be considered in two categories, the first comprising measures which may be employed to mechanically prevent the vector from coming in contact with the human host, and the second comprising measures of control such as chemical, biological,sanitary and cultural which are aimed at the destruction of the vector during some stage of its development. Mechanical barriers include the use of

repellent substances, mosquito proofing and bed nets. Insecticidal control methods are aimed at both the immature and the adult stages. Insecticides such as DDT, Dieldrin and HCH e.t.c., have been used extensively for mosquito control. The success achieved initially with insecticidal control of mosquitoes were so spectacular that for some time it was not only the control of the vectors but their total eradication was also considered. Chemical control has a number of advantages -

It is very effective and the results are quickly seen.

It is readily available and relatively simple to use.

It is the best method during epidemics.

Yet a number of problems have been found to be associated with this method of controlling vectors, some of which are:

(a) The need for repetitive application for control to be effective.

(b) Development of resistance to the chemicals by the mosquito populations

(c) Deleterious effects of the insecticides on populations of non- target organisms, including predators and parasitoids.

(d) Resurgence of treated populations, where the application of the chemical may destroy the natural enemies of the vector with the result that the vector or pest increases to a level even higher than that prior to pesticide application.

(e) Elevation of secondary vector or pest to a status of primary importance.

(f) General pollution of the environment and biomagnification of the pesticide in living organisms.

The growing awareness of the limitations and ecological hazards of insecticidal control, has stimulated the search for biological vector control agents. The natural enemies used as biological control agents are parasitoids, predators and pathogenic organisms. Biological control has a number of distinct advantages not offered by most other approaches to vector control. It is relatively permanent once it is established. The natural enemies on which it depends are self perpetuating, and they continually adjust to changes in the population density of the pest or vector they attack. Biological control has no side effects such as toxicity or environmental pollution, and they are not harzadous to the user.

Predation

Predation is one of the major causes of changes in numbers of composition of natural animal populations. This has been revealed by numerous field studies of various types,for example :

(1) Increased survival of prey in small parts of the environment from which predators had been excluded by screens (Connel 1961, Hancock and Urguhart 1965, Knight

1958, Smith 1966).

(2) Increased survival of prey during periods of artificially restricted numbers of predator (Elson 1962, Foerster and Ricker 1941).

(3) Decreased survival of prey after the introduction of a predator into a part of the environment that was formerly inaccessible to it (Macan 1965, Wijngaarden van and Morzer Bruyns 1961).

(4) Calculations from density of prey, and density and feeding rate of the predator (Connel 1961, Dempster 1960, Elson 1962, Horton 1961) and

(5) Direct measurements of predation percentages through counts of traces remaining of prey killed by predators in prey populations of known (or simultaneously estimated density) (Gibb 1958, Hiyama et al 1960, Maclellan 1959, Pearson 1966).

In all of these studies high percentages (usually above 50%) of the prey populations were destroyed by the action of predators of a single or a few species. Predators therefore have an important role to play as biological control agents. They can be very efficient in the field where they destroy large numbers of prey larvae; they are able to search for special breeding habitats used by their preys, and they can be colonized in large numbers for release in the field. Predation on mosquitoes by larvivorous predators is considered to be one of the most economic and lasting anti- mosquito

measures (Sailer and Lienk 1954, Reddy and Pondian 1974). From field and laboratory studies, aquatic insects like odonates (Hinman 1934, Hati and Gosh 1965), hemipterans (Ellis and Orden 1970), coleopterans (Christophers 1960,Bates 1965) and other invertebrates such as Planaria (Pal and Ramalingam 1981) have been found to play an important role in mosquito control. Among mosquito predators, the larvivorous fish Gambusia affinis has been studied most and it has been an agent of choice for controlling mosquitoes in many areas in the tropics. Matchavan (1976) however reported that insect predators like dragonfly numphs and hemipteran bugs devour larvae of Culex quinquefasciatus and Ae. aegypti in larger numbers than the well known larvivorous fishes, G. affinis and Poecillia reticulata. Mosquito larvae are mainly filter feeders, but a few species belonging to the subgenus Lutzia of Culex have been reported to be voracious predators (Rajasekaran and Chowdiah 1972, Surtee 1959). The larvae of all the species of subgenus Mucidus of Aedes and the genus Toxorhynchites have also been found to be predators (Service 1990, Trpis 1972). The genus Toxorhynchites contains about sixty-six species but only five species have been studied. These are Tx. brevipalpis (Brug), Tx. splendens (Wiedeman), Tx. rutilus rutilus (Coquillett), Tx. rutilus septentrionalis (Dyar and Knab) and Tx. amboinensis (Doleschall) (Pal and Ramalingam 1981). The subgenus Lutzia contains only about five species which are widely distributed in the tropics. Of

these only three have been studied to some extent, namely: Culex (Lutzia) fuscanus (Wiedemann), Culex (Lutzia) halifaxii (Theobald) and C. (Lutzia) tigripes. Recently, there has been a renewed interest in predatory mosquitoes. Because the larvae are predaceous on other mosquito larvae and they co-exist with the vectors in aquatic habitats, their potential usefulness for the biological control of certain vector mosquitoes in the tropics has been favourably discussed (NAS 1973). The aim of this study is to obtain information on the biology and ecology of the predatory mosquito, C. (Lutzia) tigripes, to identify the breeding habitats and to determine some of the factors that affect the breeding and the changes in the population of this species. The study is also to understand the predator - prey interaction such as the role played by various predator stages, prey stages and prey densities on the predation rate, and the factors that affect prey selection and the predatory efficiency of C.(Lutzia) tigripes. The information from these studies will hopefully form the basis for developing a biological control programme of mosquitoes of medical importance in an ecologically compatible and economically feasible vector management system. Considering the magnitude of the effect of malaria and other mosquito-borne diseases in Ghana and Africa as a whole, this work will increase our understanding of the biology and ecology of the predatory mosquito C.(L) tigripes, which will be a useful basis for designing vector programmes which when

coupled with chemotherapy may reduce the scourge of mosquito borne diseases in the country.

1.2 Literature Review

Morphology

The larvae of Culex (L) tigripes are whitish with a brown siphon and head and they are about 10 to 11mm long. The larvae have been described as unmistakable by Hopkins (1952) because of the distinct appearance of the mouthbrushes. The mouth-brushes have been modified for predation; they have been converted into stout bristles with sharp teeth (Hopkins 1952, MacGregor 1927). The portion of the head anterior to the clypeal spines projects strongly forward and it increases the area available for attachment of mouthbrushes. The antennae are extremely short (usually less than one-quarter the length of head). It is smooth with a tuft reduced to a minute seta near the base. The siphon is also very short with an index of about 2. The siphonal index is the length of the siphon divided by its basal width. The larvae normally lie nearly parallel with the surface of the water because of the shortness of the siphon. There are about 12 subventral tufts that are arranged in zigzag manner instead of being paired (Hopkins 1952). The anal segments have been described by MacGregor (1927) as chisel-shaped because the tip of the segment terminates obliquely. The saddle of the anal segment is much longer than wide with the surface covered with small spicules.

Normally, anal gills or papillae are used to take up salts (chloride) from water. So in general, larvae living in habitats such as tree holes in which the concentration of chloride is particularly low, are found to have exceptionally large anal papillae, whereas larvae from large swamps have exceptionally small ones, especially those from brackish waters. The predaceous larvae of C.(L) tigripes and Toxorhynchites which live in small containers form an exception: their anal gills are minute (Gibbons 1932, Wigglesworth 1933, Koch 1938), and it is presumed that these larvae obtain their salt supply indirectly from the larvae which they eat. There is very little information on the morphology of the eggs of African culicines and on their biology. MacGregor (1927) described the eggs of C.(L) tigripes as large and cigar-shaped and laid in rafts on water surface.

The adult C.(L) tigripes are large and dull brown in colour. The proboscis and palps are also dark but usually with some pale scales near the middle of underside. The thorax and abdomen are dark brown with variable markings. The legs are usually marked by pale spots (MacGregor 1927) and are equipped with unusually long and regularly arranged spines (Gillett 1972). The adults have been observed to rest in vegetation (Gillett, 1972). They are to a great extent a sylvan species but occasionally they are found elsewhere including human habitations (Horsfall 1955).

Distribution

Larvae belonging to the subgenus Lutzia have been known as predators of mosquito larvae for a long time (Ikeshoji 1966) and they are distributed widely over the world. Horsfall (1955) found them mostly in the tropical regions, South Africa, Mauritius and Aden. They occur in a variety of collections of water bodies; marshes with dense vegetation, pools without vegetation, concrete troughs and clear muddy water (Nieschulz et al 1934). They inhabit rock pools, ground pools and marshes in Mauritius (MacGregor 1927). Hopkins (1952) states that it is very uncommon in barrels and domestic water vessels and there is a single record from leaf axils (Kennan 1915). It has been recorded also from old banana leaves on the ground (Hancock 1930). It has been recorded as breeding in snail shells (Harris 1942) and even in " very saline water" (Someren Van 1943) even though he did not record the exact level of salinity. The breeding places seem to be limited more by the presence or absence of other larvae on which to prey than by any other factor (Hopkins 1952). Hopkins, however, states that it is much more commonly found in stagnant water such as swamps, pools of all kinds and ditches than in any other types of water. Gendre (1909) observed that they occur in the margins of streams with Anopheles species during dry seasons. The record of them in streams was by Bedford (1928) but there was no indication as to whether there was any appreciable current in the stream.

Macfie and Ingram (1916) recorded it among common species collected in thick forest of the Ashanti region but not in the Northern transitional zone, and Chinery (1969) also placed it among the less common mosquito species in Accra, being found in only 1.28% of the total sample of 25317.

Feeding and cannibalism

Information on the feeding activities of the larvae of C.(L) tigripes has also been scanty. MacGregor (1927) reported that the larvae will feed on chironomid larvae, small nematode worms, live insects trapped in the water and sometimes young minnows. Jackson (1953) observed that C.(L) tigripes showed some preferential feeding on mosquitoes offered to it. It preferred Aedes aegypti to Anopheles gambiae and Culex mosquitoes. She suggested that the preferential feeding behaviour could have been influenced by the amount of movement exhibited by the prey species. Gillett (1972) stated that adult C.(L) tigripes attack man at times by day, mainly outside houses. Most authors have reported that this species rarely or never bite man. C.(L) tigripes made up a major part (98.30% of 78 samples) of the catches in the bird baited traps and none in man-baited traps (Snow 1983). Precipitin tests done on blood meals of mosquitoes collected in the Gambia also showed that C.(L) tigripes fed almost exclusively on avian blood (Snow and Boreham 1973). MacGregor (1927) reported that examination of red blood cells in the stomach of this species were always found to be those of the goat.

Some workers have casually observed cannibalistic behaviour among C.(L) tigripes larvae. MacGregor (1927) stated that C.(L) tigripes larva retains its grip on or consumes another of the same species. Hopkins (1952), however, states that the larvae will eat each other, even in the presence of larvae of other species. This was confirmed by Haddow (1942) who observed that only the larger C.(L) tigripes larvae cannibalised the smaller ones.

Colonization

Limited attempts have been made to colonize the species of the subgenus lutzia in the laboratory and the few attempts at colonization have never been successful (Pal and Ramalingam 1981, Ikeshoji 1966). Nevertheless, the establishment of a lutzia colony and mass rearing in the laboratory is considered a prerequisite for its employment as a biological control agent. C.(Lutzia) fuscanus was partly colonized and maintained to the fourth generation but it died out apparently through poor insemination (Ikeshoji 1966). Prakash and Ponniah (1978) also colonized C. (Lutzia) halifaxii but the colony only survived a limited time. However, C.(L) tigripes has not been successfully colonized.

Natural enemies

A number of insects have been observed to attack and feed on immature stages of mosquito larvae (Sailer and Lienk 1954, Lee 1967). Mead (1980), observed that a predator, identified as hitherto unknown species of Mesostama (of the typhloplanoid

neorhabdocele group) killed most of the common mosquito species including C.(L) tigripes. Information on pathogenic organisms affecting this species are rare. The only informaticn of infection of C.(L) tigripes by entomopathogenic fungus was reported by Nnakumusana (1985). He tested the susceptibility of different species of culicid larvae exposed to zoospores of the entomopathogenic fungus Coelomomyces indicus for 72 hours. Infection rates of 85-100% occurred in C.(L) tigripes whilst in the predatory larvae of Tx brevipalpis, the infection rates were 0- 22%. Vyas-Patel (1988) found that C.(L) tigripes larvae were susceptible to Romanomermis culicivorax, when he evaluated the ability of this helminth, to infect, develop and emerge from Kenyan mosquito hosts.

Mosquitoes associated with C.(L) tigripes

Larvae of Lutzia species feed virtually on any species of mosquito larvae when they are kept together in a bowl. In the field, however, each species of lutzia is associated with a particular prey species because of similar preferences of habitats. For instance, Culex (Lutzia) vorax occurs with Culex pipiens pallens and sometimes with Aedes togoi in Japan (Sasa 1954), and with various Culicidae in Korea and Manchuria (Petriesceva and Cagien 1947). Culex (Lutzia) condor occurs with Anopheles stephensi in Calcutta (Iyengar 1920); C.lutzia halifaxii does so with Anopheles farauti in New Zealand (Laird 1946); Culex (Lutzia) bigoti with Aedes aegypti in Bazil

(Howard 1910) and C.(L) tigripes with An gambiae in Kenya (Haddow 1942). In South Africa it occurs with C. duttoni, Aedes caballus, Aedes lineatopennis and Aedes dentatus (Nieschulz et al 1934). Macfie and Ingram (1923) reported Ae aegypti as a close associate of C.(L) tigripes in tropical Africa and in Nigeria C.(L) tigripes occurs frequently with Ae. vittatus in rock holes (Boorman 1961).

1.3 Description of the Study Area

The study area is shown in Figure 1. It extends from Ho in the Volta Region in the East through Akosombo, Akuse, Ada, Accra, Aburi, Cape Coast to Takoradi in the West. Parts of the study area for example, Takoradi and Ho occur in the forest zone, while the bulk of the area falls within the coastal savanna. The two vegetational zones have two rainfall maxima with mean annual rainfall between 125 and 200 cm in the forest area and 74 and 89 cm in the coastal savanna area. The first rainy season is from May to June with heaviest rainfall around June and the second rainy season is from September to October. The coastal savanna area is the driest part in Ghana with the driest months occurring in December and January (Dickson and Benneh 1978). Accra is a typical station in the coastal savanna area. Average monthly relative

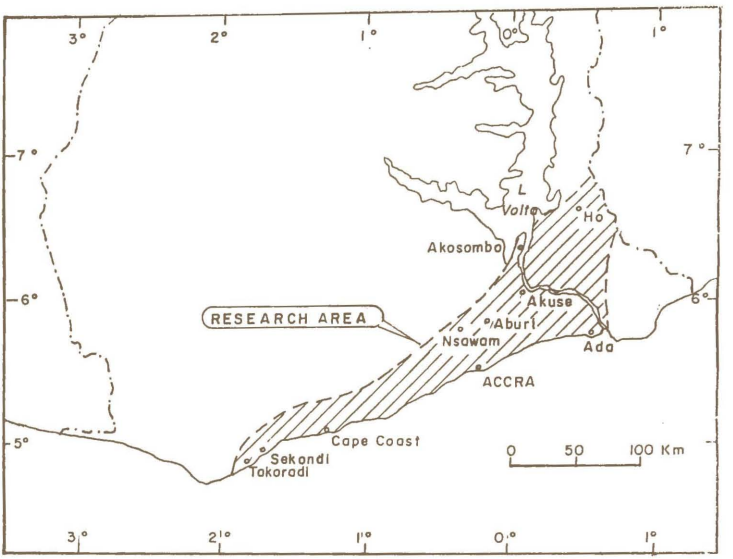


Fig. 1 LOCATION MAP OF RESEARCH AREA

humidities taken in Accra at 1500 hours are highest in May - September and the highest in the morning regimes taken at 0600 hours occur in June to September. The hottest month of the year falls in March to April just before the rainy season, while August is the coolest month (Fig.2). Putting all these climatic factors together, four seasons may be observed.

i. Hot-wet season, which runs from March to April and then October to November. Humidity is relatively low and rainfall is heavy but short.

ii. Cool-wet season, from May to June and then September which is characterised by showers of long duration with moderately strong winds.

iii. Cool-dry season which starts from late July through August with very little rainfall, and then

iv. Hot-dry season (harmattan season) which runs from December to February. It is the driest period of the year and temperatures are usually very high.

The vegetation in the forest region exhibits deciduous characteristics but destruction of forest by man has led to some parts of the forest region to be referred to as derived savannah. The vegetation in the rest of the study area is described as coastal shrub and grassland, which consists mainly of of grassland with coastal patches of shrub and occasional trees (Dickson and Benneh 1978).

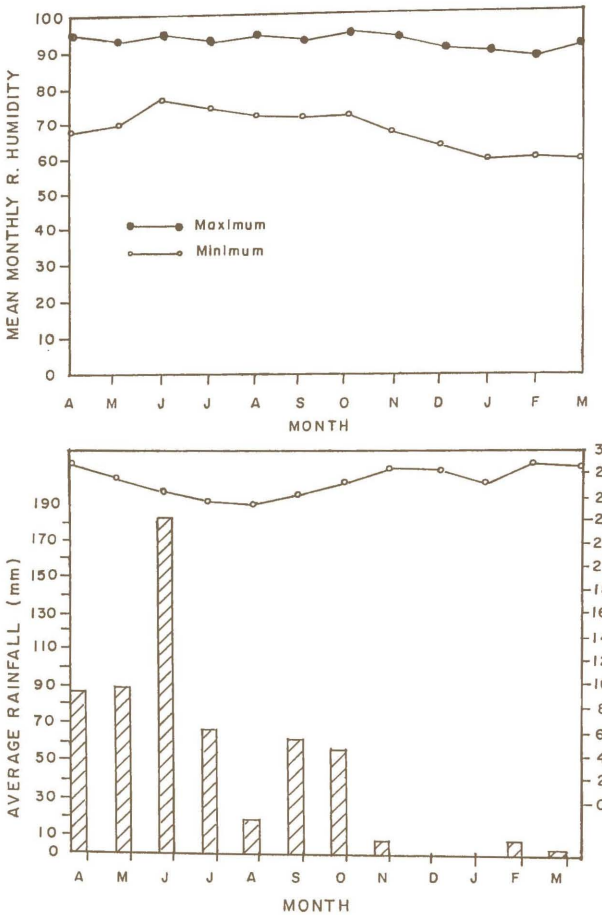


Fig. 2 MEAN MONTHLY RAINFALL, TEMPERATURE AND RELATIVE HUMIDITY OF ACCRA (April 1989–March 1990)

The primary occupation in the study area is sea fishing along the whole length of the coast and food farming and animal rearing towards the interior. Accra, the country's capital, is the largest urban settlement in the country. It is also the country's capital. It offers more opportunities for employment than any of the urban settlements. Tema, Takoradi and Ho are the other big cities in the study area. These towns are fast expanding and with this rate of urbanization, the problems of mosquito breeding becomes magnified. The striking features in these towns and cities are the lack of good sanitary facilities and poor drainage. The lack of good drainage system often results in many stagnant water bodies around the houses which provide suitable breeding sites for mosquitoes.

Chapter 2.0 BIONOMICS OF C. (LUTZIA) TIGRIPES

2.1 Introduction

Mosquito larvae and pupae are found in a variety of different habitats, ranging from large expanses of water such as swamps and cultivated fields to small collections of water as found in plant axils, snail shells etc. Some species exhibit considerable plasticity in their selection of breeding places and such larvae occur in several different types of habitats while others are more restricted in their choice. The mature stage of C.(L) tigripes have been reported to breed in a variety of habitats by various workers (Chapter 1). There are no reports on the preferred breeding habits, distribution and the population dynamics of this species. Thus the objectives of this study are to determine:

(1) the breeding habitats in which C.(L) tigripes are encountered.

(2) the characteristics of these breeding habitats.

(3) the frequency of association of this species with other mosquito species in its natural breeding habitats.

(4) the population distribution of C.(L) tigripes in the breeding places.

(5) the seasonal abundance and variations in the numbers of the immature stages of C.(L) tigripes and their mosquito preys.

(6) the relationship between the numbers of the immature stages of C.(L) tigripes and some physical and

chemical properties of the breeding places.

2.2. Materials and Methods

The great diversity of mosquito larval habitats, both the size and number of which can change overnight, are inherent difficulties and problems associated with sampling mosquito larval populations. Despite these problems a few sampling techniques have been developed to obtain quantitative estimates of either larval density or population size. The small size of many of the most important mosquito breeding habitats makes them impossible to sample by many of the normal limnological methods such as drag nets, dredges, cylinders and cages (Service 1971). The different sampling methods used by different authors to estimate relative densities of mosquitoes have been discussed by Service (1976). The choice of a particular method depends on the sampling accuracy desired, the physical characteristics of the area and the behaviour of the mosquitoes. The sampling technique used in this study was restricted to the larvae and pupae only, and all samples were collected with a dipper. The dipper is undoubtedly the most commonly used tool for collecting mosquito larvae and pupae that occur in large and small collections of ground water and various container - type habitats (Service 1976, Boyd 1949, Russell et al 1963).

2.2.1 Distribution of C.(L) tigripes and association with other mosquitoes

An extensive survey covering an area shown in figure 1 was carried out to determine the active breeding places of C.(L) tigripes and the types and frequency of other mosquito larvae which occur in the preferred habitats of C.(L) tigripes. The areas sampled in Accra and Tema were areas which are known for high mosquito populations (Chinery 1969, 1970). The survey was carried out from April 1989 to March 1990, a period which covered all the seasons encountered in a year. Water bodies which were accesible were selected and sampling was done once a week with a dipper which was 9.5 cm in diameter and 3.5 cm deep and could hold 250 ml of water. The inside was painted white to facilitate easy detection of larvae, and a long metal handle was attached to it so that it could reach relatively inaccessible water sources. The sampling procedure was standardized as sampling was carried out by one individual, the author, who without exception always employed the same techniques for taking the samples. That is in each sampling, the dipper was quickly dipped at an angle (about 45°C) at the water surface and removed before it overflowed. If the dipper was immersed too slowly, the larvae were disturbed and they dived to the bottom with the result that many escape collection. Also each sampling site was approached carefully to avoid the shadow of the sampler or dipper falling over the water surface to disturb the larvae. An interval of about

2 - 3 minutes was allowed between each dip to allow larvae and pupae which had moved down the water to return to the surface. Preliminary trials showed that most (about 80%) of the mosquito larvae which moved to the bottom of water after being disturbed returned to the surface within one to two minutes, and nearly all surfaced within three minutes. The principle of dipping relies on the fact that nearly all mosquito larvae sooner or later must come to the water surface for oxygen (Knight 1964). Individual artificial containers were examined for the presence or absence of C.(L) tigripes but larger water bodies like ponds, lagoons, swamps etc were recorded as not breeding C.(L) tigripes when all probable breeding sites yielded no C.(L) tigripes after examination, and they were recorded as breeding C.(L) tigripes if C.(L) tigripes was found in at least one dipping. A positive breeding place for C.(L) tigripes was any site in which either a larva, pupa or egg of C.(L) tigripes was found. Samples from all positive dips were collected into specimen bottles duly labelled with the pertinent data such as the date, the place of collection, time etc. (see Appendix Table 1) and sent to the laboratory for counting and identification. Culicine larvae were identified using characters described by Hopkins (1952), and anopheline larvae using De Meillon (1947). Only the fourth stage larvae were used for the identification of species, so when necessary younger larvae were reared to the fourth stage.

2.2.2. Characteristics of the breeding places

All breeding places as well as the positive collections were recorded on larval survey forms (Appendix Table 1) together with the following characteristics of the breeding places, which were examined visually:

(i) Permanence - as to whether the water will last during the dry season or will dry up.

(ii) Flow - as to whether the water is flowing or stagnant.

(iii) "Polluted" - as to whether the water contains sewerage pollutants or not (ie. by visual examination).

(iv) Vegetation - as to whether there are some emergent or floating vegetation in the water or not.

(v) Shade - as to whether the water is directly exposed to the sun or not during the day.

(vi) Other predators - as to whether there are other predators of mosquitoes in the water or not.

2.2.3. Seasonal population dynamics

Two semi-permanent water sources which were found to be breeding C.(L) tigripes and located on the campus of the University of Ghana, Legon were used for the population dynamics studies. The first breeding place, Site A, is a

manhole about 75x75x120 cm which is serving as a soakaway for septic tanks. It is constructed of concrete with the edges covered with green grass (Plate 1). The water has a foul smell and is polluted with urine and faecal matter. It is exposed directly to sunlight most of the time, except when the grasses at the edges grow tall and give some shade to the water during the day. The second breeding place, Site B, is a concrete drain about 40 cm wide and 1200 cm long, that had been blocked at one end with materials from a construction site (Plate 2). It contained fallen dry leaves and branches. Although the water in this site favoured the accumulation of leaf litters, it remained moderately clear throughout the study period. Tap water was sometimes added to this site whenever the water level fell very low.

The sampling period for the seasonal population dynamics was from April 1989 to March 1990. The same dipper as described previously was used except that in this case sampling was done three times a week (Monday,Wednesday and Friday) between 9.00 and 11.00 hours. During sampling from site A, a dip was taken near each of the four corners plus one from the middle. For site B, one dip was taken from five spots in the drain. The samples collected were taken to the laboratory and the number of eggs and the various immature stages per dip were recorded (Appendix Table 2). The mean number of larvae per dip and the degree of variability between samples (sample variance) was calculated to determine the

Plate 1. A man hole which serves as a soakaway for septic tanks (site A). It was breeding C. (L.) tigripes throughout the study period (April 1989-March 1990)

population distribution. Eggs of mosquitoes collected were identified after they had hatched.

2.2.4. Life Budget Studies

To understand the population dynamics of a particular insect, measurements of actual numbers of individuals in a generation passing through each stage of development is required. It therefore becomes necessary to construct ecological life tables of such insect. Ecological life tables can be described as the summary of the vital statistics of a population by a record of sequential measurements of individuals revealing population change of the insect throughout its life span in a natural environment. The purpose of a life table therefore is to summarize the survival and mortality rates of a population. Construction of life tables or budgets has been more extensively used in agriculture and forest entomology, but the technique has only recently been applied to mosquitoes because of lack of population data (Service 1976, WHO 1967). Life budget studies carried on mosquitoes include one on An. gambiae complex in Kenya (Service 1971, 1973), and on Ae. aegypti in Bangkok, Thailand (Southwood et al 1972). In all these studies, the data were obtained from continuous and intense studies on a single habitat. It has been emphasized by Varley and Gradwell (1970) that the most instructive life tables will usually be based on a continuous and intensive study of a population in

a single habitat, not by sampling different populations in a number of similar habitats in different years. Most methods of population analysis involving the construction of life budgets are designed to be used for species that have discrete generations, so that a cohort can be followed through its life. However, the majority of insects, particularly in the tropics, have overlapping generations or like mosquitoes, breed continuously (Southwood et al 1972). Time-specific or vertical life tables give a measure of the rate of an imaginary cohort by determining the age structure of the population at one given time. Both the age distribution of the population and deaths in the different age classes are recorded. This type of life-table is most useful with species having either overlapping generations or continual recruitment (Deevey 1947).

Instar Mortalities and Survivorship Curves

It has been recognized (Bates 1941) that if the duration of the different larval age classes is taken into consideration then there is a relationship between the numbers collected in the different age classes and their survivorship. The age distribution of the population should be assumed to give the same shape as the survivorship curve if the population is more or less stable (Service 1976).

One hundred samples were taken daily for ten consecutive days from breeding sites A and B with a 250ml dipper. The total numbers of each larval instar as well as pupae of C.(L)

tigripes collected on each sampling day were recorded. To obtain a histogram of the age distribution of the immature stages of C.(L) tigripes, the total numbers of different larval instars and pupae collected over the entire collecting period were divided by the appropriate instar durations. These values were plotted against age in days of the larvae and pupae, and the resultant graph represents the stage-specific age distribution. A curve drawn through the mid-points of each histogram represents the mid points in the life of each instar and give the age-specific distribution curve (Service 1976). This profile of age distribution will simulate the time-specific curve if the steady-state assumption holds. From the survivorship curve the numbers of larvae surviving to each age in days is read off to give the numbers (nx) surviving to age x. The life table is then constructed based on the percentages of the populations entering each stage on each sampling day corrected to 1000. The columns that make up the life budget are:

x - age in days

nx - No of larvae surviving to age x.

lx - No per 1000 surviving to age x.

dx - mortality between ages x and x+1

px - probability that a larva of age x would survive to age x+1

qx - probability that a larva of age x would die before reaching age x+1

ex - expectation of life

2.2.5. Physical and Chemical properties of breeding places of C.(L) tigripes

In order to obtain information on the physical and chemical properties of the breeding places in the study, the determination of the physico-chemical properties should be carried out at all such places during the extensive survey. However, since these properties do not remain the same in each breeding place but may change throughout the year, it would have been ideal to measure these factors throughout the seasons and at all sites. This could not be done because of logistic problems, so, two different semi-permanent habitats which breed C.(L) tigripes throughout the seasons were chosen for the water analysis. The surface temperature and the Hydrogen ion concentration (pH) were measured twice weekly in the field immediately after the larval sampling from breeding sites A and B, using a pocket pH meter with a thermometer attached, (Iuchi Model pH 51, manufactured by Yokogawa electric works, Tokyo, Japan). The probe of the meter containing the thermometer was immersed in the water to a depth of 6cm to measure the pH and the temperature. After taking the above measurements, the water for chemical analysis was also collected in 500ml bottles, with the mouths of the bottles immersed to a depth of about 5cm below the surface. For the Winkler test to measure dissolved oxygen, 125 ml

bottles were used, and the water was collected without air bubbles. The chemical properties analysed in the laboratory were chloride, dissolved oxygen and total alkalinity. The water was allowed to stand until the sediments settled at the bottom of the bottle. The supernatant water was then decanted off and analysed. Salinity or chloride content was measured by direct estimation of total chloride content by chemical reaction using a silver nitrate solution (WHO 1975). Dissolved oxygen and total alkalinity were measured by standard methods of American Public Health Association (APHA 1975).

2.3 Results and Discussion

2.3.1 Distribution and occurrence of C.(L) tigripes in the breeding places

Several arbitrary classifications have been proposed for the different types of mosquito breeding habitats (Bates 1949, Boyd 1930, Hopkins 1952, Mattingly 1969, Chinery 1969). The number of water bodies in which mosquitoes were breeding during the extensive survey were 1773, and they have been classified into six categories based on Chinery (1969). These are:

1. Water occurring in channels, which consisted mainly of concrete and earth drains, stagnant streams etc.

Table 1 Occurrence and Distribution of C. (L.) tigripes in breeding places

Category of breeding site	Type	No. of sites sampled	No. with C. (L.) tigripes	(%)	Total No. sampled in category	Total No. with C.(L.)tigripes	(%)
1. Water in channels	a) Concrete drains	283	40	(14.13)	400	50	(12.5)
	b) Earth drains	117	10	(8.55)			
2. Large artificial water containers	a) Hydrants	109	9	(8.26)	493	49	(9.94)
	b) Manholes	56	3	(5.36)			
	c) Septic tanks/ soakaways	120	16	(13.33)			
	d) Barrels	107	13	(12.15)			
	e) Water tanks	101	8	(7.92)			
3. Small artificial water containers	a) Lorry tyres	412	36	(8.74)	477	36	(7.55)
	b) Car parts	7	0	(0.00)			
	c) Tins/cans	52	0	(0.00)			
	d) Tree holes	6	0	(0.00)			
4. Standing water in large excavations	a) Ponds	82	4	(4.88)	119	6	(5.04)
	b) Lagoons	6	0	(0.00)			
	c) Borrow pits	31	2	(6.45)			
5. Marshy and swampy grounds	a) Marshes and b) Swamps	76	4	(5.26)	76	4	(5.26)
6. Standing shallow water on the ground	a) Ground pools	158	4	(2.53)	208	4	(1.92)
	b) Rain pools	30	0	(0.00)			
	c) Tyre print	13	0	(0.00)			
	d) Hoof prints	7	0	(0.00)			
Total		1773	151	(8.52)			

2. Large artificial water containers, such as hydrants, septic tanks and soakaways, barrels, drums, water tanks etc.
3. Small artificial water containers, consisting mainly of discarded lorry tyres and parts, tins, cans, tree holes etc.
4. Standing water in clearly defined excavations, such as ponds, lagoons, burrow pits etc.
5. Water in marshes and swampy grounds.
6. Standing shallow water on the ground, consisting mostly of ground and rain pools, pot holes, hoof prints, lorry tyre prints, broken pipes etc.

These can also be classified broadly into two main groups namely artificial or man-made and natural sources of water. Table 1 shows the occurrence and distribution of C.(L) tigripes in the breeding places. Water sources, both large and small, that were sampled and which were found to contain mosquito larvae were 1773 of which 151 (8.52%) of them were breeding C.(L) tigripes . They were encountered most often in water in channels (12.5% of breeding sites in category 1) and then in large artificial containers (9.94% in category 2), but they were found less in standing shallow water on the ground (1.92% in category 6). Concrete drains were the major source of breeding for C.(L) tigripes in category 1 while septic tanks and soakaways, then barrels and drums formed the

major breeding places in category 2. In Jos, Nigeria, C.(L) tigripes was among the two predominant species found present in septic tanks mainly in wet and early dry seasons (Irving-Bell et al 1987). Discarded lorry tyres formed the major source of breeding for C.(L) tigripes in category 3, but smaller water containers in category 3 such as tins and cans, car parts and tree holes were found not to be breeding C.(L) tigripes, so were the many standing shallow waters on the ground in category 6. These sites which were not breeding C.(L) tigripes were mostly temporary water sources which were much more likely to dry up in the absence of rains. Because they are liable to rapid desiccation, small and temporary collections of water are often free of predators (Gillies and De Meillon 1968). Ground pools which contained C.(L) tigripes were found only during the wet season when the water persisted for some days because of the frequent rains. Even though one would expect large water bodies to be favourite breeding places for C.(L)tigripes (Hopkins 1952), they were encountered less frequently in ponds, marshes and swamps and in stagnant streams. Hopkins (1952) reported that C.(L)tigripes were very uncommon in barrels and drums, but in this study they show a relatively high occurence and were encountered in 12.15% (13 out of 107) of all the barrels and drums breeding mosquitoes. The breeding preference of C.(L) tigripes with reference to location of domestic containers, i.e. whether outdoors or indoors is shown in Table 2. It indicates that C.(L) tigripes

are outdoor breeders because out of the total of 107 barrels which were breeding C.(L) tigripes (Table 1), 86 and 21 were placed outdoors and indoors respectively and 12 (13.95%) of those placed outdoors were found to be breeding C.(L) tigripes while only 1 (4.75%) of those placed indoors contained the predator.

Culex (L) tigripes constituted only 2.50% (612 out of 11240) of the larvae collected from the extensive survey. C. quinquefasciatus was the most predominant species collected throughout the study period and they formed 47.06% of all the larvae collected. It was followed in abundance by Ae. aegypti; An. gambiae; Ae. vittatus; C. univittatus; C. decens; C. thalassius and C. duttoni forming 22.61%, 12.53%, 6.99%, 3.86%, 2.54%, 1.24% and 0.78% respectively. The population of C.(L) tigripes seen here is very small compared to that of the other mosquitoes. Chinery (1969) found that only 1.23% of the total mosquito sample of 25317 collected in Accra were C.(L) tigripes. He also found C. quinquefasciatus, Ae. aegypti and An. gambiae to be the most predominant species and the rest of the mosquito species listed above as less common species.

The frequency of association of C.(L) tigripes with some of the other mosquito prey species is given in Table 3. It indicates that C. duttoni was the species most frequently associated with the predator in its preferred natural breeding places. It was followed by C. quinquefasciatusAe,Ae. aegypti,

able 2 Breeding of C. Lutzia tigripes in water containers (barrels) placed indoors and outdoors

No. of barrels sampled	Outdoor		Indoor	
	No. (%) outdoor	No. with C.(L). tigripes (%)	No. (%) indoor	No. with C.(L) tigripes (%)
107	86 (80.37)	12 (13.95)	21(19.63)	1(4.75)

ble 3 Frequency of association of C. (L). tigripes with some mosquito prey species in the breeding places

Mosquito species	Breeding places with pres species		% Association with C.(L)tigripes.
	with C.(L) tigripes	without C.(L) tigripes	
C. quinquefasciatus	63	611	9.35
C. univittatus	14	267	4.98
C. decens	12	169	6.63
C. duttoni	7	62	10.14
C. thalassius	3	53	5.36
Ae. aegypti	51	492	7.56
Ae. vittatus	24	181	6.83
An. gambiae	20	352	5.38

Ae. vittatus, C. decens, An. gambiae, C. thalassius , and C. univittatus.

The frequency of association of a particular mosquito species with C.(L) tigripes will depend on the extent to which their preferred natural habitats are similar. Most of the preferred breeding habitats of C.(L) tigripes are similar to those of C. duttoni because the predator also breeds in large and small, permanent and temporary, clean or foul and all sorts of artificial water containers (Table 1), and it does not breed in brackish water just like C. duttoni (Ikeshoji 1966). C.(L) tigripes occurred frequently with Ae. aegypti in breeding places such as discarded lorry tyres, barrels, water tanks, hydrants and in concrete and earth drains. C.(L) tigripes however, was not found in smaller water containers placed indoors, discarded tin cans, and tree holes which are also preferred breeding places for Ae. aegypti (Christophers 1960, Chinery 1969). It was observed that most of the occasions when An. gambiae concurred with C.(L) tigripes in the same habitat it occurred during the dry season, and this is due to the fact that in the dry season An. gambiae breeds mainly in habitats such as concrete and earth drains, stagnant streams and even in septic tanks (Irving-Bell et al 1987), when many of its preferred breeding places (cans and tins, discarded lorry tyres, tree holes etc) are dried out. Gendre (1909) observed that C.(L) tigripes occurred frequently with Anopheles species in the margins of streams during the dry

season. Even though the population of An. gambiae in the survey was higher than that of Ae. vittatus there was not much difference between the frequency at which they occurred with C.(L) tigripes in its preferred natural habitats (Table 3). This may be because the preferred natural habitats of Ae. vittatus and that of the predator are much more similar than those of An. gambiae. Ae. vittatus breeds in a wide variety of places, particularly in concrete drains, water hydrants, manholes and water tanks. A study of the habitats of Ae. vittatus in the Plateau Province of Northern Nigeria by Boorman (1961), showed that Ae. vittatus occurred most frequently with C.(L) tigripes in rock holes which were the preferred natural breeding places for Ae. vittatus. Similarly, C. duttoni was found with C.(L) tigripes in their breeding habitats more frequently than C. thalassius (Table 3), but C. duttoni formed only 0.78% of the total number of mosquitoes collected, whilst C. thalassius formed 1.24% of the total population. C. thalassius breeds mostly in brackish water besides the sea and lagoons which do not support breeding of C.(L) tigripes, whilst C. duttoni breeds mostly in a variety of places including ponds, marshes and swamps and also in septic tanks and soakaways, which are also preferred by C.(L) tigripes. These observations confirm the assertion that the frequency of concurrence of mosquito species with the predator will depend on the extent of similarity of their natural breeding habitats. The frequency of concurrence of

the various species with the predator will also influence the type of species which will be preyed upon by the predator.

2.3.2 Characteristics of the breeding places

Table 4 shows the characteristics of the breeding places of C.(L) tigripes. 20.53% (31 out of 151) of the sites breeding C.(L) tigripes were found to be "polluted". These sites that contained sewerage pollutants sometimes had foul- smelling water. Septic tanks and soakaways formed the major part of the sites with "polluted" water which were also breeding C.(L) tigripes. Concrete drains and septic tanks are particularly abundant in the towns and cities and they are usually badly kept and so contained water containing sewerage pollutants. These, although allowing some mosquitoes such as C.(L) tigripes and C. quinquefasciatus to develop, remain unfavourable to species like An. gambiae to develop. This may also explain the low frequency of occurrence of An. gambiae in the preferred breeding habitats of C.(L) tigripes. 9.27% (14 out of 151) of the sites breeding C.(L) tigripes had some type of vegetation either floating or submerged in the water. Vegetation was found in all the marshes and swamps as well as the ponds which were breeding the predator; these were breeding sites with relatively large water bodies and are usually permanent. The concrete drains which had vegetations (5%) were those in which soil had accumulated to allow the vegetation to grow. 13.91% of the sites had the water surface shaded from direct sunlight during the day, and 11.26%

Table 4 Characteristics of the breeding places of *L.* (*Ae.*) *tigripes*

Category of breeding places	Type	No. with *L. tigripes*	"Polluted"		Vegetation		Shade		Other Predators	
			No.	%	No.	%	No.	%	No.	%
1	Concrete drain	40	6	15.0	2	5.0	0	0	4	10
	Earth drain	10	0	0	4	40.0	0	0	5	50
2	Hydrant	9	2	22.22	0	0	0	0	0	0
	Manholes	3	0	0	0	0	0	0	0	0
	Septic tanks/soakaways	16	16	100.0	0	0	13	81.25	0	0
	Barrels	13	0	0	0	0	0	0	0	0
	Water tanks	8	0	0	0	0	0	0	0	0
3	Lorry tyres	36	0	0	0	0	8	22.22	0	0
	car parts	0	0	0	0	0	0	0	0	0
	tins and cans	0	0	0	0	0	0	0	0	0
	tree holes	0	0	0	0	0	0	0	0	0
4	Ponds	4	4	100	2	50	0	0	4	100
	lagoons	0	0	0	0	0	0	0	0	0
	Burrow pits	2	2	100	0	0	0	0	2	100
5	Marshes and swamps	4	0	0	4	100	0	0	2	50.0
6	Ground pools	4	1	50	0	0	0	0	0	0
	Rain pools	0	0	0	0	0	0	0	0	0
	Hoof prints	0	0	0	0	0	0	0	0	0
	Lorry tyre print	0	0	0	0	0	0	0	0	0
Total		151	31	20.53	14	9.27	21	13.91	17	11.26

"Polluted" - sewerage pollutants

contained other known mosquito predators such as odonates, dytiscids, notonectids and tadpoles. These results suggest that C.(L) tigripes breeds mostly in sunlight and relatively clean water, with little vegetation and other predators of mosquitoes.

2.3.3 Seasonal population dynamics

Monthly variations in the breeding of the pre-adult stages of C.(L) tigripes in the two semi- permanent sites - a manhole serving as a soakaway for septic tanks (Site A) and a concrete drain blocked at one end (Site B), and also the mean monthly rainfall are given in Figure 3. There are fluctuations in the numbers but two obvious peaks can be seen in the population of C.(L) tigripes in both sites A and B. The major peaks seems to coincide with the major rainy seasons, which occur in May to July and then around October. Precipitation during the major rainy seasons is usually very heavy and sometimes cause flooding of many mosquito breeding sites, washing away many of the pre-adult stages. Flooding occurred during the course of this study and affected both sites. Sites B and A were flooded in June and July respectively. These might explain the sudden decline in the numbers of the larvae at those times in both sites. The seasonal abundance of C.(L) tigripes and mosquito prey from both sites A and B are shown in Figures 4 and 5 respectively. The fluctuations in the populations of the predators followed the pattern of the mosquito preys; the seasonal peaks in the prey abundance

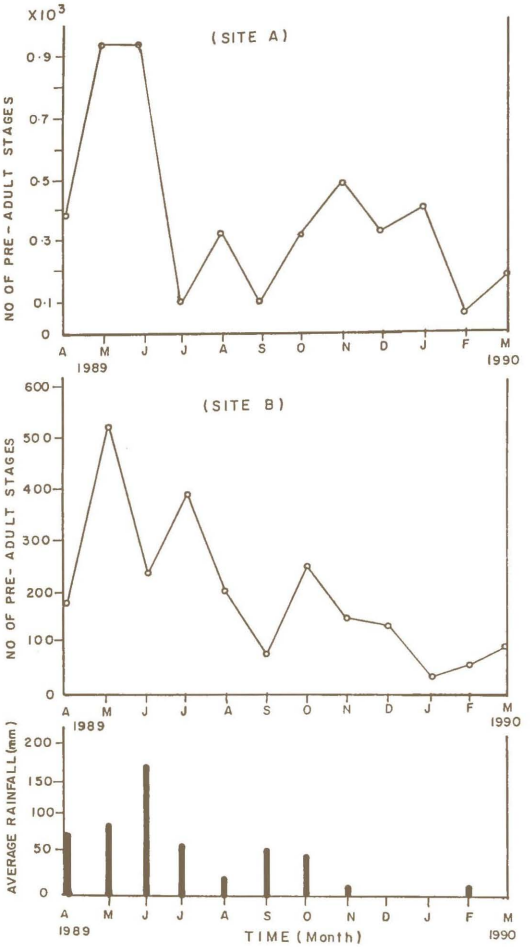


Fig.3 SEASONAL VARIATIONS IN THE NUMBERS OF C.(L) TIGRIPES FROM TWO BREEDING SITES, A MANHOLE (SITE A) AND A CONCRETE DRAIN. (SITE B)

either preceded or coincided with the peaks in C.(L) tigripes at both sites A and B.

The oscillations in the population of C.(L) tigripes and the preys show a time lapse between the emergence of the predator and active predation. Abundance of prey will influence the predator population in the following generation after the predator larvae have metamorphosed into adults. The time lapse therefore includes the pupal stage, the time until the females are able to lay eggs, and the duration of embryonic development until the hatching of new larvae. The numbers of C.(L) tigripes collected during the period of study were relatively small compared to that of the other mosquitoes (Appendix Tables 4 and 5). The highest numbers collected from site A were 952 in May, compared to 8676 in May for the mosquito prey species. The numbers for site B were 533 for the predator in May and 7081 for the mosquito prey species in the same months. The ratio of the predator density to the preys were about 1:10.18 and 1:7.75 for sites A and B respectively. Even though the C.(L) tigripes was not present in large numbers, its population never fell to zero during the long dry season of December to March (Figure 3). The question is with such a low population in nature, will it be able to cause sufficient impact on the population of the prey species in these habitats ? Later studies showed that each predator

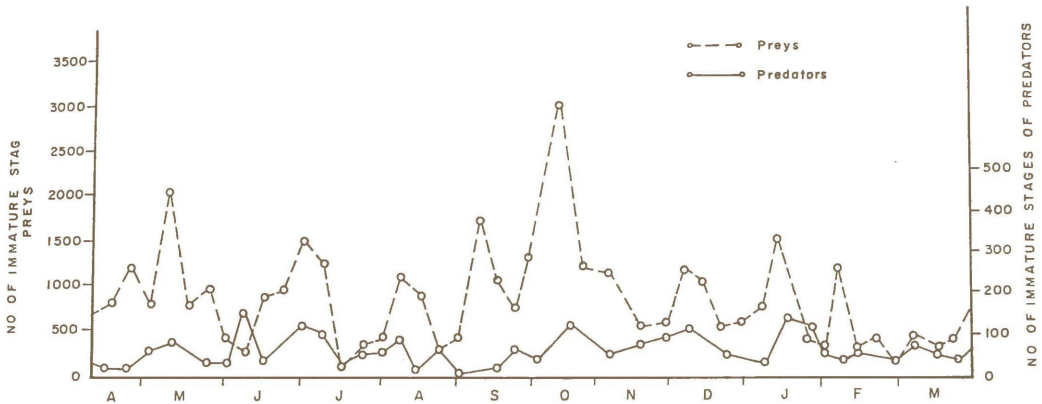


Fig. 4 SEASONAL ABUNDANCE OF C.(L) TIGRIPES AND MOSQUITO PREYS IN A MAN HOLE SHOWING OSCILLATIONS OF PREDATORS AND PREYS (SITE A)

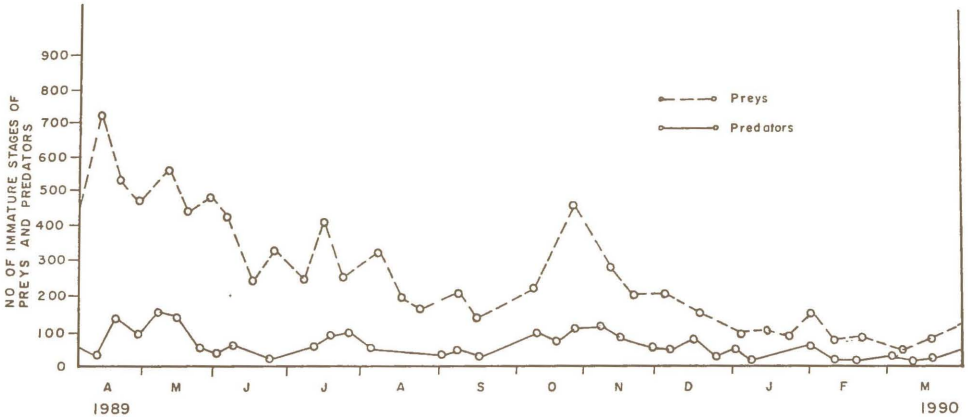


Fig. 5 SEASONAL ABUNDANCE OF C. (L) TIGRIPES AND MOSQUITO PREYS IN A CONCRETE DRAIN SHOWING OSCILLATIONS OF PREDATORS AND PREYS (SITE B)

larva could consume about 140 to 220 prey larvae of identical stages during development, depending on the water temperature (see section 3.4.3.), which suggests that the predator could be effective in reducing the population of the preys.

The population distribution of C.(L) tigripes in sites A and B was determined by compiling the frequency distribution of the numbers of the larvae in the breeding places (Appendix Table 4). The ratio of variance (S^2) to mean (X), for both sites were greater than one indicating a contagious or clumped type of larval distribution. This sort of larval distribution is not uncommon for mosquito larvae (Service 1971). Many factors may affect the distribution of mosquitoes in a habitat, particularly, the temperature of the water. For example if temperatures of some parts of a pool are too low or too high, larvae will avoid such places (Haufe 1957) and thus escape the deleterious effects of short periods of extreme temperatures. The shallow edges of water bodies may occasionally experience extreme temperatures.

2.3.4 Life budget studies

The numbers of immature stages of C.(L) tigripes collected each day in 100 samples from larval breeding sites A and B, are given in Appendix Tables 7 and 8 respectively. It seemed reasonable to assume that, during the limited period for which collections were made from any one habitat, the population size of C.(L) tigripes was approximately stable. If the steady state assumption holds, then the age distribution of

the population should give the same shape as the survivorship curve (Figs.6 and 7). The age distribution and survivorship curves for the immature stages collected from the two habitats (sites A and B) are similar despite possible sampling errors. Since populations of the various developmental stages are expressed as numbers per median day, a knowledge of the average time and time range occupied by each developmental stage is fundamental to the construction and analysis of a life budget. Developmental durations in the laboratory were used in this study (see section 3.4.1) although Southwood (1972) suggested that it would be preferable to use developmental durations in the field. Time-specific life budgets calculated from the survivorship curves are given in Appendix Tables 9 and 10, but Service (1971) observed that because of the limited data collected from the field in such experiments the construction of time-specific life tables may be highly ambitious. A more simplified method would be to estimate daily mortalities of the various instars assuming that in any given instar the mortality is constant but not necessarily between instars and in this way only mortalities are considered (Tables 5 and 6). The k-values are killing power of a mortality factor expressed as the difference between the logarithms of the populations under consideration (Varley and Gradwell 1960, Southwood 1966).

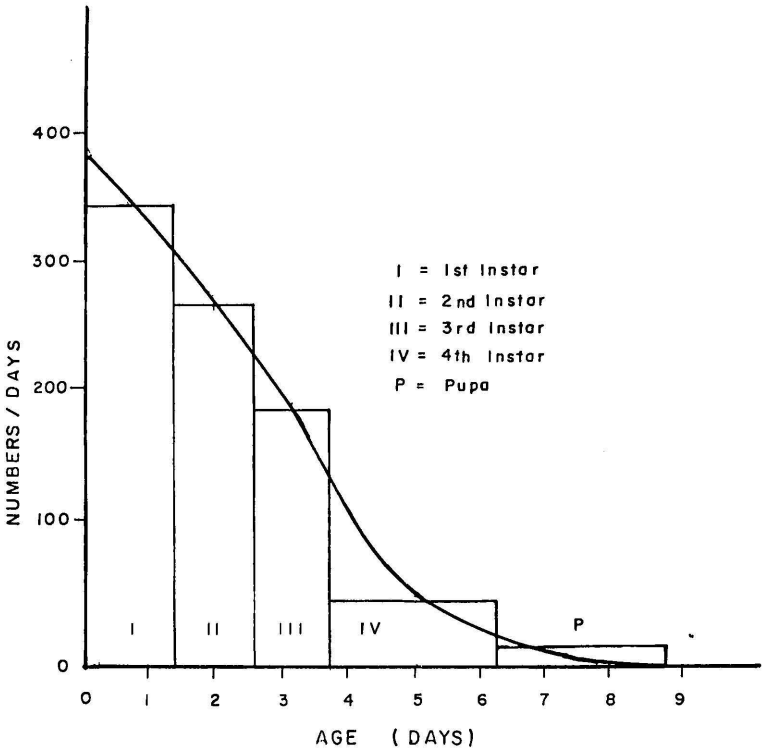


Fig. 6 AGE DISTRIBUTION AND SURVIVORSHIP CURVE OF THE IMMATURE STAGES OF C.(L) TIGRIPES FROM A MANHOLE (SITE A)

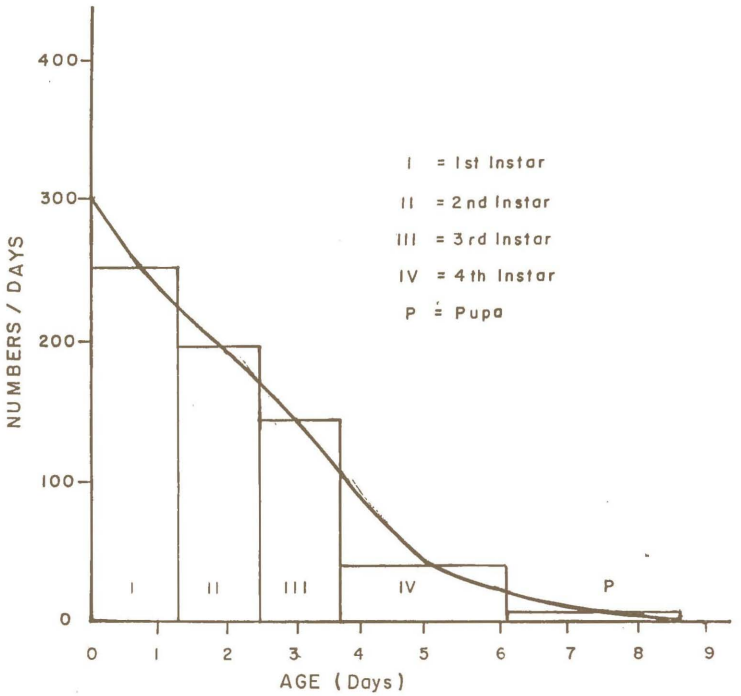


Fig. 7 AGE DISTRIBUTION AND SURVIVORSHIP CURVE OF THE IMMATURE STAGES OF C (L) TIGRIPES FROM A CONCRETE DRAIN (Site B)

mortalities of C. (L) tigripes from a man hole (site A)

in days eginning nstar :1	No. entering instar (S_{ti-1})	Death in instar (Di)	Relative proportion dying in instar $\left(\frac{Di}{S_{ti-1}}\right)$	Proportion dying daily in instars $1-\left(\frac{S}{S_{ti-1}}\right)^{1/d}$*	k**
	379	69	0.1821	0.1402	0.0873
.33	310	80	0.2581	0.2186	0.1296
..54	230	90	0.3913	0.3458	0.2156
.71	140	118	0.8429	0.5052	0.8037
5.34	22	20	0.9091	0.6913	1.0410
3.38					K = 2.2776

duration in days
ce between successive values of log of number entering instar

Instar mortalities of C. (L) tigripes from a concrete drain (site B)

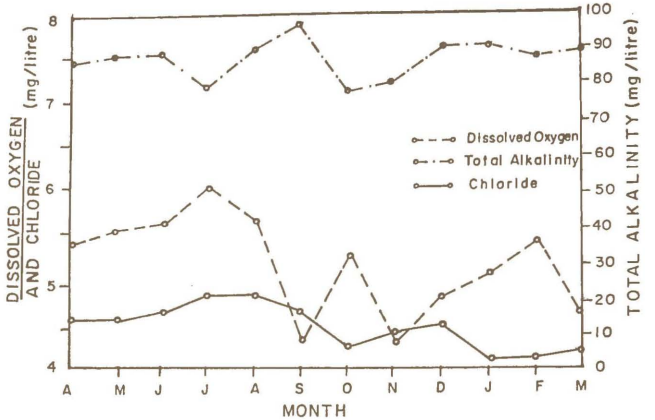
n days ginning istar	No. entering instar	Death in instar	Relative proportion dying in instar	Proportion dying daily in instar	k**
-1	$(S_{\ell i-1})$	(Di)	$\left(\frac{Di}{S_{\ell i-1}}\right)$	$1-\left(\frac{S}{S_{\ell i-1}}\right)^{1/d}$ *	
0	300	71	0.2367	0.1838	0.1173
1.33	229	59	0.2576	0.2182	0.1294
2.54	170	65	0.3824	0.3376	0.2828
3.71	105	90	0.8571	0.5228	0.8451
6.34	15	14	0.9333	0.7349	1.1761
8.38					K = 2.5507

duration in days
ce between successive values of log of number entering instar

A high survival expectation is shown in the early stages than in the later ones (Appendix Tables 9 and 10) and this point is further demonstrated by the k-values (Tables 5 and 6) where the highest mortality occurred among the later stages (4th and pupae). The results suggest that mortality of the later stages is high and therefore the survival of these stages (4th and pupae) would probably determine the adult populations of C.(L) tigripes emerging from those habitats.

2.3.5 Physico-chemical properties of the breeding water

The results of the analysis of water from the two C.(L) tigripes breeding sites (A and B) are shown graphically in Figures 8 and 9 (Appendix Table 11). There was very little fluctuations in the Hydrogen ion concentration (pH) of the water from both breeding places (site A and B). The pH value ranged from 7.1 to 8.0. Similarly, the water surface temperature measured at a depth of 6 cm. varied only slightly throughout the seasons at both breeding places: it varied from 24.3 to 28.9°C and from 25.1 to 31.1°C in sites A and B respectively. The water in site B (concrete drain) was much shallower than the water in site A, so the temperature of water in site B increased more during the hot dry season from December to March (Figures 8 and 9). Chloride content which also gives the measure of salinity of the water did not fluctuate much. The total alkalinity which is a measure of the amount of carbonates and bicarbonates in the water ranged from



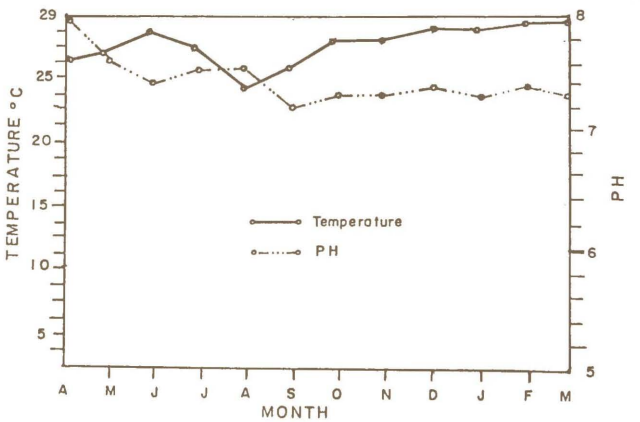
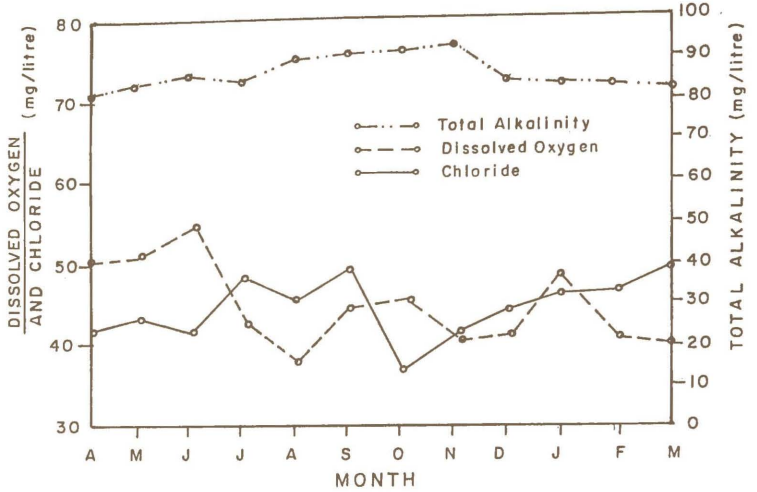


Fig. 8 FLUCTUATIONS IN THE PHYSICAL AND CHEMICAL COMPONENTS OF A MAN HOLE (SITE A) BREEDING C. (L) TIGRIPES



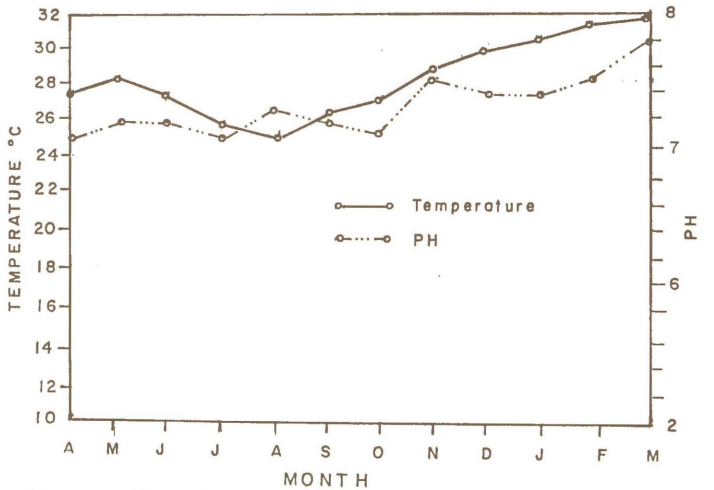


Fig. 9 FLUCTUATIONS IN THE PHYSICAL AND CHEMICAL COMPONENTS OF A CONCRETE DRAIN (Site B) BREEDING C.(L) TIGRIPES

78.65 to 98.33mg/litre in site A and 82.6 to 91.2mg/litre in site B. Dissolved oxygen from both breeding sites fluctuated between 3.43 and 5.53 mg/litre. Table 7 gives the statistical analysis to determine the relationship between the mean values of the physical and chemical parameters and the numbers of both preys and predators from the two breeding sites. It indicates that there was no measurable correlation between the hydrogen ion concentration of the water and the population of the immature stages of C.(L) tigripes from both breeding sites A and B. There is, however. a significant correlation between the pH of the water and the population of the immature stages of the mosquito preys from the concrete drain (site B). The correlation coefficient (r) was - 0.6926 which suggests that the population of the mosquito prey increases with decrease in the pH. The coefficient of determination (r^2) indicated that the pH accounts for only 47.97% of the variations in the numbers of mosquito preys. Hydrogen ion concentration (pH) of waters is considered to have very little influence on the larvae themselves, but has an indirect influence by controlling other factors such as the micro-organisms serving either as food or producing diseases upon which larval development depends (Senior-White 1926). None of the other parameters measured had any correlation with the numbers of both predator and the preys from the two breeding sites. C.(L) tigripes was not found breeding in brackish water which has relatively high chloride content, but they

Table 7 Analysis of physico-chemical parameters and the larval incidence from a man hole and a concrete drain (sites A and B)

a = correlation coefficient
b = coefficient of determination

Parameter		C. (L.) tigripes		Preys	
		SITE		SITE	
		A	B	A	B
pH	a	-0.3053	-0.5185	-0.0228	-0.6926**
	b	0.0932	0.2688	0.0050	0.4797
Temp °C	a	-0.0049	-0.4328	0.1858	-0.6244
	b	0.0000	0.1873	0.0345	0.3899
Chloride	a	0.1252	-0.2455	-0.4592	-0.2776
	b	0.0157	0.0603	0.2109	0.0771
Total Alkalinity	a	-0.0070	-0.0553	-0.2754	0.2811
	b	0.0000	0.0031	0.0759	0.0790
Dissolved oxygen	a	-0.2059	0.2647	-0.1331	0.3808
	b	0.0424	0.1330	0.0177	0.01450

** Significant $P < 0.05$

were found in "polluted" water such as septic tanks where the dissolved oxygen would be expected to be very low. Dissolved oxygen of 3-5mg/litre was obtained between 09.00 - 11.00 hours in breeding site A which contained polluted water from septic tanks, and 4-5 mg/litre was obtained in site B which contained relatively clean water. Very little information is available on dissolved oxygen in mosquito larval habitats, probably because all mosquito larval instars frequently come to the surface of water to breath atmospheric oxygen through spiracular openings, and so dissolved oxygen is not considered very important. But the survival of mosquito larvae when submerged in water depends on their ability to absorb oxygen through the cuticle (Wigglesworth 1933). Reiter (1978) reported that the critical oxygen concentration above which cutaneous respiration adequately compensates for the absence of siphonal respiration was higher for species like C. quinquefasciatus than for An. gambiae, which indicates that the cuticle may be less permeable to oxygen. A less permeable cuticle would reduce the rate at which oxygen diffuses out from the mosquito into the water; it would therefore be a useful adaptation in a mosquito which often breeds in highly polluted (low oxygen) water. The breeding habitats of C.(L) tigripes were generally not "polluted" because only 20.53% of 151 breeding places were considered " polluted " to some extent. Thus cuticular respiration in C.(L) tigripes may not be that important. Even though some physical and chemical

parameters such as pH and Calcium (Smorodinzew and Adowa 1930) and ammonia nitrogen (Beattie 1932) have been observed to show positive or negative correlation with the breeding incidence of some mosquito species, all the parameters determined from both site A and B in this study did not show any correlation with the larval incidence of C.(L) tigripes. The successful development of mosquito larvae under natural conditions is dependent not upon one, but upon many factors which constitute a complicated equilibrium of physico-chemical and biological interactions, so the existence of correlation between some physical or chemical factor and the population of a particular species may be due also to the presence or absence of another factor (Senior - White 1926).

3.0 DEVELOPMENTAL BIOLOGY OF C. (LUTZIA) TIGRIPES

3.1 Introduction

To establish the life cycle of C.(L) tigripes, the developmental biology should be studied. The duration of development from egg to adult is dependent on several factors such as availability of food, sexual differences and water temperature. The most important among these is water temperature and under natural breeding conditions, it is probably the main factor (Nielsen and Haeger 1954).

The objectives of this study are to:

(1) determine the duration of development of C.(L) tigripes under laboratory conditions.

(2) determine the number of mosquito prey larvae that the predator requires to complete development.

(3) determine the effect of different constant temperatures on its developmental duration.

(4) determine the relationship between constant temperatures and prey consumption by the predator.

(5) determine the effect of temperature on the size (weight and length) of the final instar predator larvae and the weight of pupae.

(6) determine the ability of the larvae and pupae of the predator to withstand high temperatures.

(7) determine the development on non-living diets.

(8) colonize C.(L) tigripes in the laboratory.

3.2. Materials and methods

3.2.1 Development under laboratory conditions

Eggs of C.(L) tigripes were collected from the field and brought to the laboratory. Some of the eggs were separated and put individually in round plastic bowls (6.2 x 3cm) containing 30ml of water. Tap water which had been left standing for at least 24 hours to remove some of the chlorine was used. The first instar larvae which emerged from the eggs were each provided with 40 1st-instar larvae of C. quinquefasciatus. Preliminary experiments had shown that one 4th-instar C.(L) tigripes larva could not consume more than 40 mosquito prey larvae of identical stage in 24 hours when reared in the laboratory. The number of prey larvae alive after 24 hours of exposure to a predator was counted and the number of prey larvae consumed was calculated by subtracting the number alive from the initial number offered. The water in each bowl was examined every 24 hours for larval exuviae for evidence of moulting. The head widths of the larvae were measured at the greatest width, ie across the eyes, using a micrometer eye piece in a dissecting microscope. Each bowl was then cleared and refilled with water of the same volume and 40 prey larvae were provided. Thus each C.(L) tigripes larva was provided with 40 prey larvae of the same instar as the predator. This feeding procedure was followed as 1st and 2nd instar predator larvae were found not able to devour

enough 3rd or 4th-instar prey larvae. Each specimen was observed until it moulted into a pupa and then into the adult. Since the pupal stages do not feed, no food was provided. The period of pupation, the time of adult emergence and the sexes of the adults were also recorded. The temperature of the water in the rearing bowls was measured twice daily at 8am and 6pm.

3.2.2. Effect of different constant temperatures on development

Plastic bowls (6.2 x 3.2cm) containing 30ml of water were placed in water baths set to obtain constant temperatures of 20, 26, 30, 32, and 34°C. The bowls holding the larvae to be reared at 12°C were kept in the cold room in order to maintain that temperature. Eggs collected from the field were placed individually into the rearing bowls to prevent any larval cannibalism after emergence. Freshly emerged predator larvae were each provided with 40 1st-instar *Culex* larvae, and thereafter, each predator was offered prey larvae of the same stage as the predator. The bowls were examined every 24 hours and the number of prey larvae alive and the number consumed daily were recorded. Head-widths of each instar of the predator larvae were measured every 24 hours to assign instars, and the bowls were examined for discarded exuviae. The temperature of the rearing water were monitored regularly with glass thermometers for any fluctuations. Whenever the temperature fluctuated greatly, due mostly to power failures, the experiment was stopped and then started afresh. Each

specimen was observed till it pupated and emerged into adult. Fourth-stage larvae and pupae of the predator were weighed immediately they emerged with a Mettler H-10 balance, with an accuracy of 10^{-5} gm. The live larvae and pupae were placed on blotting paper to remove all water from the body surface and then transferred onto wax paper and weighed. The larvae or pupae were returned to their rearing bowls after weighing. Means and standard deviations of the developmental times were calculated for each temperature. One way analysis of variance was used to check if constant temperature had an effect on the response variables.

3.2.2.1 Ability of larvae and pupae to withstand high temperatures

Fourth instar larvae and pupae were collected from the wild, washed in clean water and placed separately for defined periods in plastic bowls (6.2 x 3cm) containing water which had been equilibrated in water bath to the desired temperature. The bowls containing pupae were covered with fine gauze held in place with a rubber band. At the end of the exposure period, the larvae and pupae were transfered into water at room temperature. The numbers surviving after 24 hours were noted. Controls were performed in the same manner but the hot water bath was omitted.

3.2.3 Development on non-living diets

One of the methods of applying biological control using natural enemies is by inundation, which involves mass rearing and periodic release of large numbers of natural enemies of proven value, usually over a small area. The objectives of this method is to raise the abundance of the natural enemies to a high level at a time when the pest or vector is most vulnerable to them. Inundative release of adults of predatory mosquitoes, particularly Toxorhynchites has been proposed to upset the predator - prey relationship in favour of the predator, thus effecting control (Musprat 1951). In determining the practical utility of C.(L) tigripes as a biological control agent, the ability to rear it could be as important a parameter as the biological aspects of the mosquito that makes it a candidate as a biocontrol agent. Studies on the developmental biology of C.(L) tigripes show that one C.(L) tigripes may require at least a minimum of 145 Culex mosquito larvae as food, thus a rather large colony of prey mosquito would be required for mass production of the C.(L) tigripes in the laboratory. In view of the expense and time involved in maintaining a large colony of prey mosquitoes, it is essential to look at the use of alternate food sources for C.(L) tigripes.

The objectives of this study therefore are to determine:

(1) the duration of development of C.(L) tigripes when reared on different non-living diets.

(2) the effect of non-living diets on the 4th-stage larval and pupal weights.

(3) to compare these results with the developmental biology of those larvae reared solely on mosquito prey larvae.

The three non-living diets selected were the ones which are normally available in the market and are used to rear other mosquitoes in the laboratory (Coluzzi 1964). These are Cerelac, Dog biscuits and Milk casein. Cerelac is an infant milk cereal, manufactured in Ghana by Food Specialities Ghana Ltd. It is a powdered material made from whole maize, partially skimmed milk, sucrose, vegetable oil, $CaCO_3$, Iron pyrophosphate and vitamins. The average composition by weight per 100gm as stated by the manufacturer is given in Appendix Table 16. The dog biscuits are weaning biscuits for puppies (manufactured in Japan by Nippon Pet Food Co. Ltd.) They are rectangular shaped biscuits but are grounded into powder before use. They are made from wheat powder, meat powder, bone powder, skimmed milk and animal and plant oil. The nutrient composition is given in Appendix Table 17a. The milk casein comes as a fine granular material manufactured in Japan by Wako Pure Chemicals Industries Ltd. The average composition by weight as given by the manufacturers is given in Appendix Table 17b. These three diets were chosen for this study because of the diversity of their composition especially the high protein content which was considered to be very essential

for the predatory diet. They do not promote as much scum formation on the water as is found with other materials used as food for rearing mosquito larvae (eg. dried yeast and malt). They are also commercially available and only moderately expensive, so the cost of using them for rearing C.(L) tigripes would not be prohibitive.

Eggs of C.(L) tigripes were collected in the field and were individually put in 30ml of water in plastic bowls of 80ml capacity at the laboratory temperature of 24°-27°C. Newly emerged larvae were fed by sprinkling very small amounts of the food on top of the water. Each bowl was labelled as to which type of food was added. Controls were set with a group of individual predatory larvae which were fed under similar conditions but with 40 Culex mosquito larvae of identical stages as the predator. Each container was examined every 24 hours for discarded larval exuviae and also each larval head width was measured with an eye piece micrometer to determine the stage of the larvae. The water and food in the rearing bowls were changed daily. Records were kept of the developmental periods of each predator instar. The weights of the 4th-stage larvae reared on living and non-living diets were recorded. Each rearing bowl was observed until the predator larvae pupated and emerged as adult or died.

3.3 Colonization in the laboratory

To evaluate the importance of C.(L) tigripes as a potential biological agent for controlling mosquito vectors, they should be reared in large numbers and maintained in the laboratory. The objectives of this study is to establish a colony of C.(L) tigripes in the laboratory and to provide enough material for further studies.

3.3.1 Rearing of the immature stages

The insectary used in this study was a room (324cm x 290xm x 267cm), with metal shelves and wooden benches to carry larval rearing trays and cages. There were no windows so artificial light was provided.

Eggs were collected from the field, separated into batches of 20 and were put into 3 litre white enamel trays (35cm x 25cm x 6cm) filled to a depth of 4cm with tap water. All stages of predatory larvae were fed with prey larvae of equivalent stages. The number of larvae which died during development were recorded. Prey-predator ratio of about 30:1 was provided in each rearing tray. Adults of C.(L) tigripes which emerged were collected with a dropping pipette and put into 350ml bowls (9.5cm x 5.5cm) filled with 3cm of water, and placed in the cages. Two different sizes of cages (46 x 46 x 46cm and 32 x 32 x 32cm) were used to accommodate the adults (Plate 3). They were constructed of 2 x 2cm fixed wooden frames covered on top and on all sides except the front with mosquito netting (18 x 22 mesh). The front of the cages were

Plate 3. Cages used for the breeding and maintenance of adult C. (L.) tigripes in the laboratory

fitted with 30cm long cylindrical sleeves of cloth attached to 14-16cm diameter openings (Plate 3). The four corners of the wooden frames at the bottom of the cages were fitted with nails, so that the nails rested in small containers containing motor oil to support the cages off the wooden benches and to prevent ants from entering the cages.

3.3.2 Feeding of Adults

Both adult males and females were initially provided with cotton wool pads soaked with 10% sugar solution. The bottles were stoppered with cotton wool pads and placed on the floor of the cages. They were renewed every other day to prevent fungal growth. Adult female mosquitoes were offered animals from the third day after emergence and thereafter twice weekly. The animals offered were guinea pigs, rabbits, mice, and chicken. Before feeding, the feathers on the abdomen or sides of the chicken were removed while the fur on the abdomen or sides of the other animals were shaved off. The wings and legs of the chicken were tied with a rope to immobilize them, and the mice werw restrained in a small wire gauze. The other animals were immobilized by intraperitoneal injection of a veterinary nembutal (pentobarbitone sodium). 2ml per kilogram of body weight was used for the rabbit and 1ml per 2.3kg of body weight for the guinea pig (WHO, 1975). In these cases the anaesthesia was complete in 10-15 minutes and lasted for about 1-2 hours. The animals were then placed sideways on top of the cages for the adult mosquitoes to feed on them. The

hand of a human was also offered to the adults C.(L) tigripes by attaching a 125ml paper cup containing 10 to 20 female adults to the hand of either the author or some volunteers. The paper cups were covered with mosquito netting or gauze and tied with rubber bands, to facilitate feeding on the human arm and prevent the adults from flying away. Water in 350ml bowls were provided in the cages for ovposition. Eggs laid were removed and counted under a binocular microscope. They were returned to the bowls and observed for hatching. Sunlight which penetrated into the room did not reach the breeding cages so artificial lights were provided by two 40-watt fluorescent tubes from 6am to 6pm daily. The temperature of the insectary was recorded daily with a maximum and minimum thermometer, and the relative humidity by a dry and wet thermometer.

3.3.3 Artificial insemination

When natural insemination did not occur, induced mating was attempted in order to obtain fertilized eggs. Methods similar to those of Trimble and Corbett (1975) and WHO (1975) were employed with some modifications. Four to five day old males of C.(L) tigripes were anaesthesized with either ether or chloroform. A minute pin attached to a wooden applicator stick was passed laterally through the thorax of each male, and the heads and legs were removed. Females were similarly anaesthetized and were put on white filter paper with their ventral surfaces uppermost. The males were manipulated so

that their terminalia touched the female terminalia at an angle of about 45°. When a male was firmly attached to the female, the couple were transferred into a paper cup leaving the females to recover inside. Individual males were used to mate a maximum of 2 to 3 females.

3.3.4 Longevity of adults in the laboratory

A known number (120) of pupae reared from eggs were placed in a cage, and the number which emerged into adults were recorded. The adults were fed on sugar and those which died were removed sexed and counted. This was done until all individuals in the cage died.

3.4 Results and Discussion

3.4.1 Development under laboratory conditions

The results of the study of larval and pupal developmental duration and the number of prey larvae required as food by the larval stages of C.(L) tigripes are presented in Table 8. Larval development took 6.34 ± 1.92 days from the 1st instar to the emergence of pupa and the pupal stage took 2.04 ± 0.46 days. The total number of days taken by the immature stages to complete development to adult stage was 8.38 ± 2.38. The mean developmental durations for the first three instars were between 1 to 2 days, but that of the 4th-stage predator larvae was consistently higher than those of the other larval stages and also the pupae. The temperature of the rearing water was between 24° and 27°C. As stated in the method, each larval stage was offered prey larvae of identical stage. Observations show that the mean number of prey consumed increased as the larvae matured. The developmental duration of male and female larvae and pupae is given in Table 9. Since it was not possible to differentiate the sexes of the larvae, the sexes were determined after the emergence of the adults. There was no significant difference ($P > 0.05$) between the sexes in the developmental duration of both larvae and pupae and in the mean number of prey consumed. The ratio of males to females in this study was 1:1.18. Figure 10 shows the changes in the width of the head capsule of the larval stages during

elopment of C. (L). tigripes in the laboratory

LARVAL STAGES				Pupa	Total
st	2nd	3rd	4th		
± 0.48 = 24)	1.21 ± 0.48 (n = 24)	1.17 ± 0.38 (n = 24)	2.63 ± 0.58 (n = 24)	2.04 ± 0.46 (n = 24)	8.38 ± 2.38 (n = 24)
9 ± 15.29 n = 24)	27.50 ± 13.83 (n = 24)	30.29 ± 13.48 (n = 24)	62.25 ± 10.12 (n = 24)	-	145.67±17.33

as provided with prey of the same stage

al differences in developmental duration of L. tigripes and in prey consumed during
lopments in the laboratory

	Pupal days	Total larval & pupal days	T-test	Total No. of prey consumed	T-test
..70	2.00 ± 0.45 (n=22)	8.27 ± 0.90 (n=22)	T=0.72*	145.73±14.44 (n=22)	0.05*
1.02)	2.08 ± 0.49 (n=26)	8.46 ± 1.13 (n=26)		145.46±19.86 (n=26)	0.05

ificant)

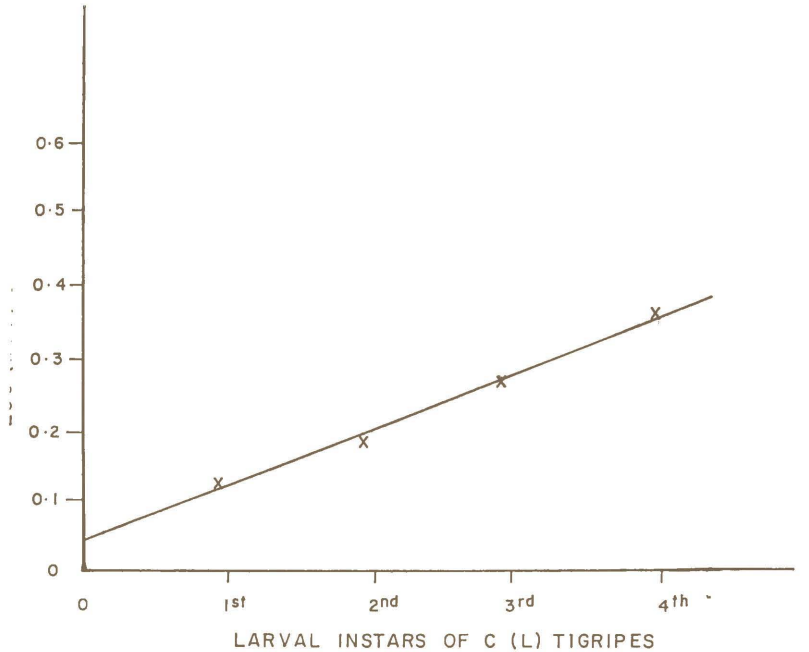


Fig. 10 MEASUREMENT OF HEAD WIDTH OF LARVAL INSTARS OF C. (L) TIGRIPES

development.

The means of the head widths followed Dyar's rule, i.e. it increased geometrically by a ratio of 1.5.

3.4.2 Effect of temperature on the duration of development of the immature stages

The results of rearing larvae and pupae of C.(L) tigripes at different constant temperatures are presented in Figure 11 and Table 10. The first instar larvae reared at 12°C survived for 2-3 days and died without moulting. At 34°C the first instar larvae were lethargic. At this temperature, the larvae remained at the top of the water and moved only after they had been disturbed. The above results suggest that 12°C is close to or below the lower developmental threshold for the immature stages and 34°C is also close to the upper developmental threshold. Further work needs to be done to establish the lower and upper developmental thresholds. The total duration of larval and pupal development at 20°C was 20.93 ± 1.62 days The development for these same stages was much faster at 26° and 30°C. The total pre-adult (larva + pupa) days were 10.65 ± 0.92 and 8.0 ± 0.82 respectively. Development at 32°C (11.32 ± 1.06) was faster than that at 20°C but it was slower than those reared at 26°C and 30°C (Fig 13). The development of the immature stages at 26°C was about half the time required for complete development at 20°C and all the larvae completed development to adults.

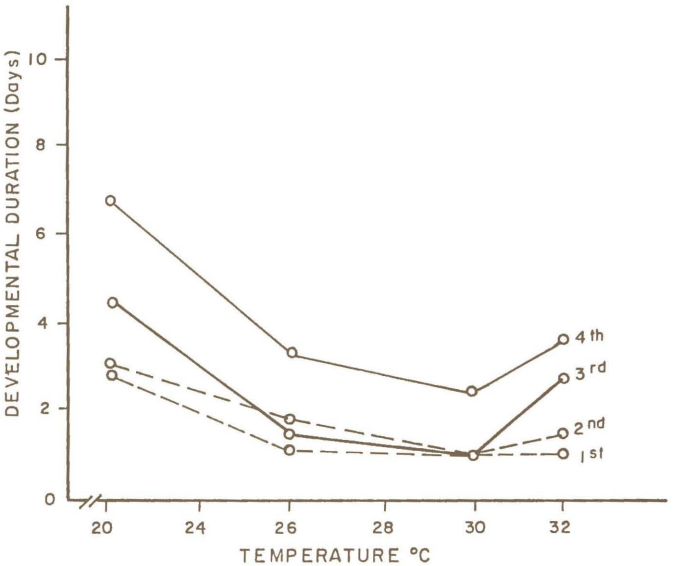


Fig. 11 DURATION OF LARVAL DEVELOPMENT OF C. (L) TIGRIPES AT DIFFERENT CONSTANT TEMPERATURES

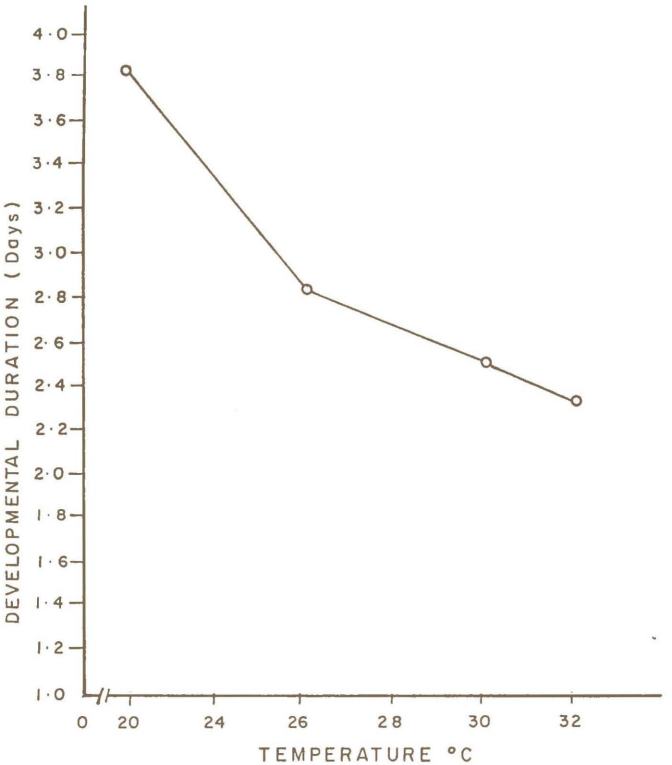


Fig. 12 DURATION OF PUPAL DEVELOPMENT OF C.(L) TIGRIPES AT DIFFERENT CONSTANT TEMPERATURES

At 30°C, the larval and pupal development was completed two days earlier than at 26°C, and all the larvae completed their development. Survival of larvae reared at 32°C was 81.25% and lower than those reared at 26° and 30°C but it was higher than those reared at 20°C (Table 11). The duration of development of the immature stages was significantly ($P< 0.05$) longer at 20°C and at 32°C than at 20°C, 30°C and 32°C. Further, there were no significant differences between the developmental durations of the larvae reared at 26°C, 30°C and 32°C. The duration of the pupal stage was shortened from 3.83 ± 0.15 days to 2.33 ± 0.52 days when temperature was increased from 20°C to 32°C (Fig 12). The decrease was significant ($P<0.05$). Pupal developmental duration is thus different from that of the larvae, since the the shortest developmental time was recorded at 30°C, whereas that of the larvae was at 32°C. This difference may be attributed to the hard exoskeleton of the pupae which enables them withstand relatively higher temperatures than the larvae (Appendix Table 12).

Blunck (1924) has defined the most suitable developmental temperature as the "optimum", and the optimum in turn as the temperature at which the greatest percentage of individuals accomplish their development within the shortest period of time. Others have used the highest survival to the adult stage in the shortest time to determine the optimum temperature (Brust 1967, Trpis and Shemanchuk 1969, 1970). The optimum developmental temperature for C.(L) tigripes in this study is

30°C since it gave the shortest developmental time with the highest survival of the immature stages to the adult stage (Fig 13, Tables 10 and 11).

3.4.3 Effect of temperature on prey consumption

Temperature has a significant effect ($P < 0.05$) on the daily consumption of mosquito larvae by C.(L) tigripes. Considering the fact that predator larvae were fed with prey larvae of the same stage, more individual prey were consumed daily at 30°C than at lower or higher temperatures (Fig. 14 and Table 12). The fact that the rearing temperature of 32°C slowed down the duration of larval development (Fig 11) suggests that the larvae were uncomfortable at that temperature and less active and therefore could not consume large numbers of prey larvae.

ion in days of larval and pupal development of C. (L). tigripes
fferent constant temperatures

20°C	26°C	30°C	32°C
2.83 ± 0.75 (n = 16)	1.16 ± 0.41 (n = 16)	1.00 ± 0.00 (n = 16)	1.00 ± 0.00 (n = 16)
3.0 ± 0.00 (n = 12)	1.83 ± 0.75 (n = 16)	1.00 ± 0.00 (n = 16)	1.50 ± 0.51 (n = 13)
4.5 ± 0.00 (n = 10)	1.50 ± 0.52 (n = 16)	1.00 ± 0.00 (n = 16)	2.83 ± 0.75 (n = 13)
6.83 ± 0.76 (n = 10)	3.33 ± 0.34 (n = 16)	2.50 ± 0.58 (n = 16)	8.99 ± 1.82 (n = 13)
17.16 ± 2.06	7.82 ± 2.23	5.50 ± 0.52	8.99 ± 1.82
3.83 ± 0.15 (n = 10)	2.83 ± 0.98 (n = 16)	2.50 ± 0.52 (n = 16)	2.33 ± 0.52 (n = 13)
20.93 ± 2.11	10.65 ± 3.21a	8.0 ± 1.21a	11.32 ± 2.34a

by the same letters are not significantly different (P > 0.05)

The mean number of prey consumed per stadium by C.(L) tigripes was however different from the number consumed in 24 hours at the various temperatures. At 20°C and 32°C, the mean numbers of individual prey larvae consumed per stadium were 229.33 ± 25.30 and 184.00 ± 23.81 respectively (Table 13). The daily prey consumption was less at 20°C and 32°C than at 26°C and 30°C and the larval development was most rapid at 30°C (Tables 10 and 12). This suggests that at temperatures above and below the optimum, development was slower and since it took a longer period, the predator consumed more prey. This suggests that the impact of predation could be greater at the lower and higher temperatures. Similar observations were made by Trpis (1972) with Tx. brevipalpis (Theobald).

3.4.4. Effect of temperature on the size of the immature stages

The relationship between the size (weight and length) of the final instar (4th-stage) larvae and the weight of pupae of C.(L) tigripes reared at different constant temperatures are presented in Figure 15 and Table 14. As temperature was increased from 20°C to 32°C, the 4th-stage predator larvae and pupae became smaller (Fig. 15) although larvae reared at 32°C consumed more prey larvae than those reared at 26°C and 30°C (Table 13). As temperature increased the rate of daily prey consumption also increases while the duration of development

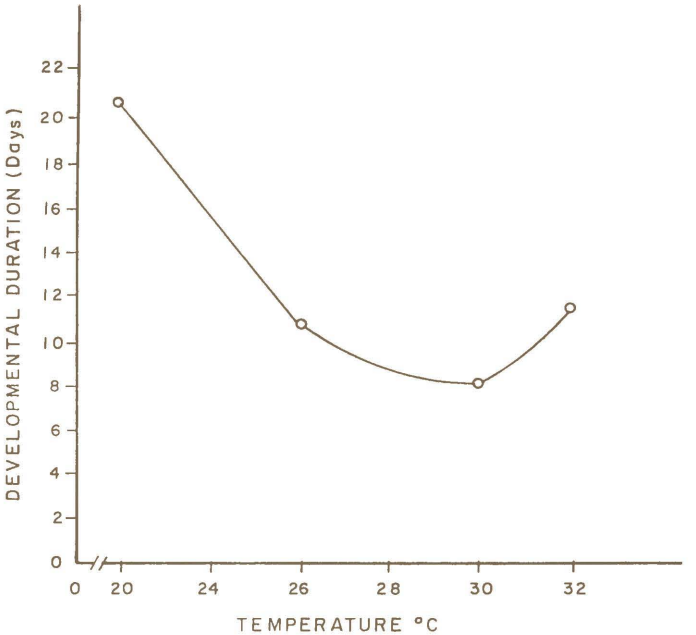


Fig. 13 TOTAL DURATION OF PRE-ADULT (Larva + pupa) DEVELOPMENT OF C.(L) TIGRIPES AT DIFFERENT CONSTANT TEMPERATURES

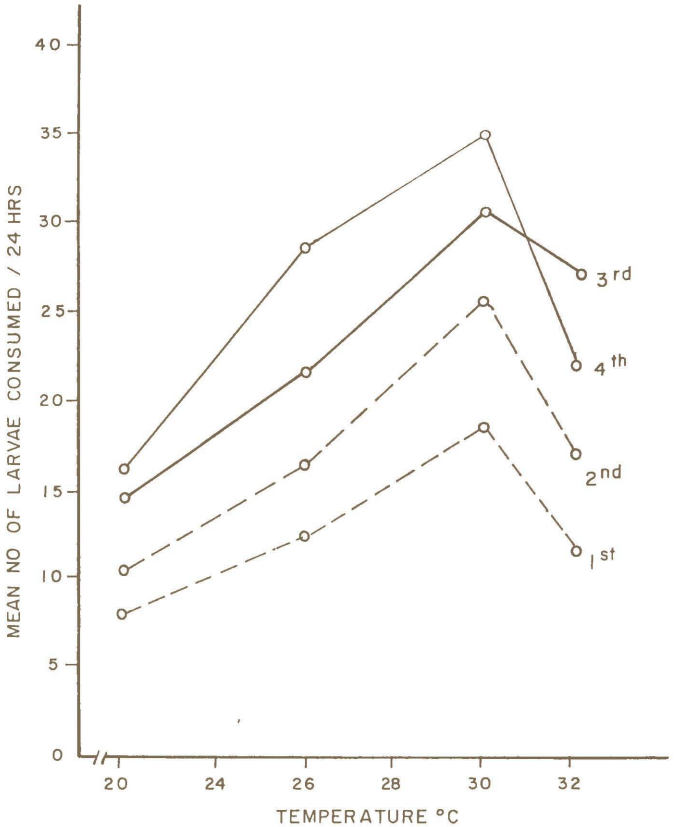


Fig. 14 EFFECT OF TEMPERATURE ON THE DAILY PREY CONSUMPTION OF C.(L) TIGRIPES

ble 11 Survival of the immature stages of C. (L.) tigripes reared at different temperatures

	12°C	20°C	26°C	30°C	32°C	34°C
No. of larvae	16	16	16	16	16	16
No. developed to adults	0	10	16	16	13	0
% Survival	0	62.5	100	100	81.25	0

Table 12 Effect of temperature on number of prey consumed in 24 hours by C. (L.) tigripes

Larval stages	20°C	26°C	30°C	32°C
1st	8.00 ± 0.63 (n = 16	12.33 ± 0.82 (n = 16)	18.33 ± 1.75 (n = 16)	10.50 ± 0.84 (n =16)
2nd	10.33 ± 1.51 (n = 12)	16.37 ± 0.82 (n = 16)	25.50 ± 0.83 (n = 16)	14.36 ± 1.21 (n = 13)
3rd	14.66 ± 0.82 (n = 10)	21.50 ± 1.05 (n = 16)	30.33 ± 1.03 (n = 16)	27.00 ± 1.41 (n = 13)
4th	16.16 ± 1.60 (n = 10)	28.33 ± 1.86 (n = 16)	34.50 ± 2.17 (n = 16)	22.00 ± 1.41 (n = 13)
Total No. consumed	49.15 ± 4.56	78.53 ± 4.55	108.66 ± 5.78	73.86 ± 4.87

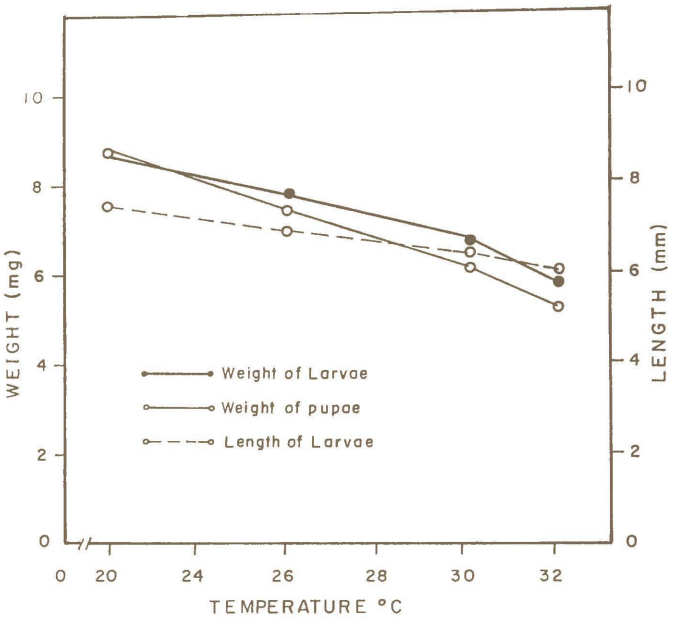


Fig. 15 EFFECT OF DIFFERENT CONSTANT TEMPERATURES ON THE SIZE (LENGTH AND WEIGHT) OF 4th-STAGE LARVA AND WEIGHT OF PUPA OF C.(L) TIGRIPES

temperature on total prey consumed during each stadium
tigripes

	26°C	30°C	32°C
.31 5)	14.33 ± 4.80 (n = 16)	18.36 ± 1.73 (n = 16)	10.50 ± 0.84 (n = 16)
52)	29.50 ± 10.82 (n = 16)	25.00 ± 0.83 (n = 16)	21.50 ± 8.04 (n = 13)
11)	32.50 ± 12.68 (n = 16)	30.37 ± 1.03 (n = 16)	71.50 ± 19.63 (n = 13)
.18 1	94.50 ± 16.63 (n = 16)	86.50 ± 21.03 (n = 16)	80.50 ± 11.17 (n = 13)
30	170.83 ± 37.27	160.17 ± 21.61	184.00 ± 23.81

of temperature on weight and length of larvae
ght of pupae of C (L) tigripes

0°C	26°C	30°C	32°C
0.59 10)	7.82 ± 0.43 (n = 16)	6.83 ± 0.68 (n = 16)	5.82 ± 0.60 (n = 13)
0.36	7.10 ± 0.37	6.73 ± 0.28	6.42 ± 0.32
0.36 10)	7.48 ± 0.40 (n = 16)	6.28 ± 0.41 (n = 16)	5.30 ± 0.14 (n = 13)

decreases. This suggests that more energy will be utilized to hasten development, and the rate of metabolism will also be expected to increase with temperature. All these factors may explain the reduction in the size of the larvae and the weight of the pupae with increasing rearing temperature.

3.4.5 Colonization in the laboratory

Information on the breeding of large numbers of C.(L) tigripes in the insectary is summarized in Appendix Table 13. Eggs brought from the field hatched within 24 hours and the percentage hatchability was 81.95% (n=703). Out of 568 adults which emerged, 265 were males and 303 were females (a ratio of 1:1.14). Out of the 303 females, 102 (33.66%) took some blood meal and 13 (12.75%) were able to lay eggs, with a pre-oviposition period of 8.08 days (range 6-12 days) to lay the first batch of eggs (Appendix Table 14). The average number of eggs laid per females was 60.92 $\pm$ 32.55 (range 20-128) and a total of 792 eggs were obtained but none of them hatched into larvae.

Figure 16 and Appendix Table 15 show the longevity curves of C.(L) tigripes under laboratory conditions expressed as percentages surviving. 3.70% of the males were alive 56 days after emergence while 15.0% of the females were alive during the same period. All the males died by age 63 days while the females died 70 days after emergence. These results show that the females lived slightly longer than the males. All the mosquitoes were fed on 10% sugar solution. Comparison

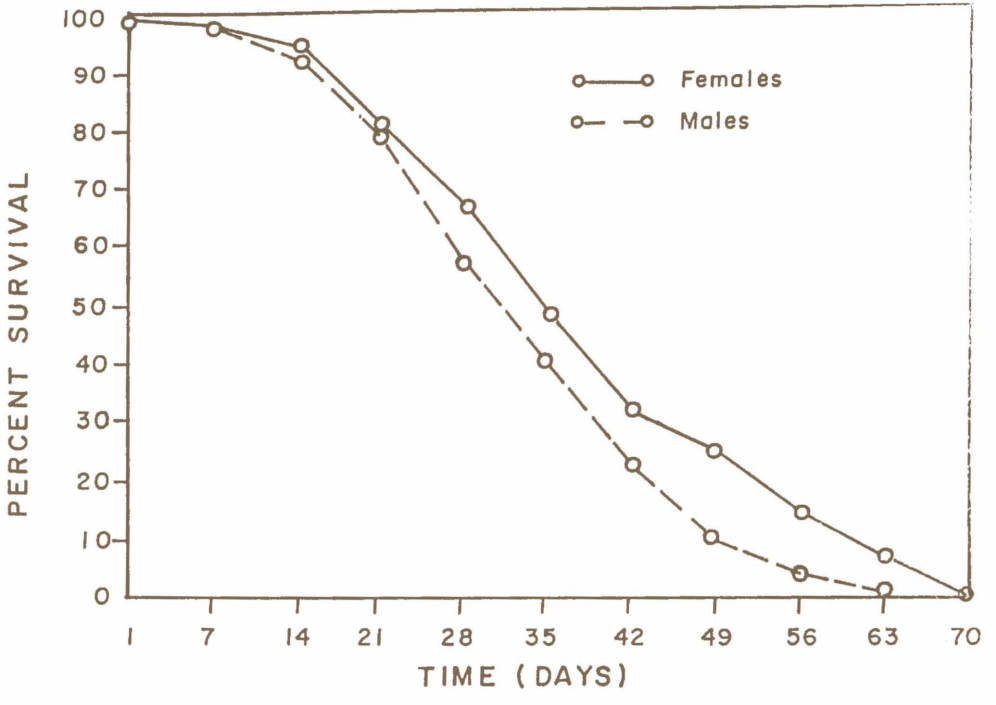


Fig. 16 SURVIVAL OF ADULT C. (L) TIGRIPES IN LABORATORY

could not be made with females fed solely on blood because the females usually took some sugar before taking blood meal. However the maximum survival time of females after blood meal intake was 41 days.

3.4.5.1 Rearing of the immature Stages

The eggs were whitish in colour when first laid but changed to yellowish - brown a few hours later. They were broadly oval in outline, but more pointed blunte at one end. The average lenght was 1.08 ± 0.13mm and 0.23 ± 0.46mm at the greatest breadth (n = 250). They were larger than the normal eggs of Culex species encountered which averaged about 0.73mm x 0.15mm (Christophers 1945). The surface of the eggs appeared uniformly smooth except at the anterior and posterior poles, where they were stippled brown while the rest of the eggs looked yellowish-brown; this colour was quite distinct from those of other Culex eggs encountered in the field, which were greyish-brown.

Cannibalism was one of the sources of loss during larval development and this occurred mostly during the first three days of development. This however, was reduced when the number of C.(L) tigripes larvae per tray was reduced to 10 and the number of prey larvae was increased. There was no pupal loss due to cannibalism. Pupal mortality was only 0.52% and a further 1.90% loss occured due mostly to failure of the adults to emerge (Appendix Table 13).

With the exception of the chicken, the adult female C.(L)

tigripes did not feed on any of the animals offered including human arms. This feeding behaviour confirms the observations made by some authors (Lewis 1947, Snow 1983, Snow and Boreham 1973) that C.(L) tigripes rarely feeds on man but rather prefers avian blood. No mating of the adults was observed in both the small and large cages. Lack of insemination was therefore thought to be the cause of the production of sterile eggs. A female is considered successfully inseminated only if her spermotheca contained spermatozoa (Lea and Evans 1972). Spermothecae of thirty females were therefore dissected out in saline and crushed under cover slips and examined for living spermatozoa. None of the three spermothecae in each of the 30 females examined contained spermatozoa thus confirms the observation that the production of sterile eggs was due to the fact that the females were not inseminated. Adults of many Culex species of mosquitoes have failed to copulate in laboratory cultures (Horsfall and Taylor 1967, Christensen and Rowley 1978, Thompson 1948). The three favourable factors required for the development of the ovary in mosquitoes are full blood meal, fertilization and temperature (Gillett 1971, WHO 1975). The low number of blood fed females that laid eggs (12.75%) and the small number of eggs laid per female (20-128) may be due to insufficient intake of blood by the females. The number of eggs produced by mosquitoes have been found to be related to the size of blood meal taken by the female (Woke et al 1956, Colless and

Chellapah 1960). The temperature and the relative humidity of the insectary ranged from 24°-28° and 68-75% respectively. These two factors can also affect the reproductive biology of the predator.

3.4.5.2 Artificial insemination

The induced insemination of C.(L) tigripes carried out in this study was not successful. Observation of the behaviour of females when presented to males under the binocular microscope, showed that the females retracted their 8th abdominal segments thereby preventing union of the genitalia and thus, insemination. Observation of females of An. gambiae which were successfully inseminated using the same technique revealed that the receptive females responded to the males by extending their 8th abdominal segments thus facilitating union and transfer of spermatozoa. Firm union was never established between the sexes of C.(L) tigripes in any of the 62 attempts made. Several factors have been reported to affect the efficiency of copulation and the rate of insemination of mosquito. Other than the requirement for a vigorous mosquito stock, age of the mosquitoes (Lea and Edman 1972, Horsfall and Taylor 1967) and the type of anaesthesia used to immobilize females before induction of copulation (Fowler 1972) could influence them. All males and females used for the artificial copulation were at least 4 to 5 days old. The rate of both receptivity and the rate of insemination increases as the age of female C. quinquefasciatus increases

(Lea and Evans 1972). Fowler (1972) reported that the rates of insemination of Aedes vexans (Meigen) were consistently high for females anaesthetized with nitrogen, intermediate for those anaesthetized with carbon dioxide and low for females anaesthetized with chloroform. He indicated that the efficiency of insemination during induced copulation is enhanced by the use of anaesthetic which allows rapid recovery of adults such as nitrogen. It is possible that the anaesthesia which were available and used in this study, chloroform and ether might have contributed to the unsuccessful insemination of the adult C.(L) tigripes.

3.4.6 Development on non-living diets

The results of the study of the developmental periods for C.(L) tigripes larvae reared on the three different non-living diets, namely, Cerelac infant cereal, Dog biscuits and Milk casein are given in Table 15. Larvae maintained on diets of Cerelac, Dog biscuits and milk casein took an average of 18.47 ± 1.22, 17.71 ± 3.31 and 19.05 ± 1.80 days respectively to complete larval development, while those reared on living mosquito prey larvae, took a shorter period of 6.63 ± 0.50 days. The difference in the developmental duration of larvae reared on mosquito prey and those reared on the non-living diets is significant ($P < 0.01$). The mean weight of the 4th-instar larvae reared on mosquito prey larvae was 7.19 ± 0.96mg, and was much heavier than those reared on non-living diets which were 1.66. ± 0.20, 1.82 ± 0.27 and 2.78 ± 0.58mg

for Cerelac, Dog biscuits and milk casein respectively. Duncan's multiple range test showed that there was no significant difference between the weights of the 4th-instar larvae reared on Cerelac and Dog biscuits, but all the other mean weights were significantly different from each other. Only one C.(L) tigripes larva which was reared on milk casein was able to pupate and emerge as adult (Table 15) after spending 17 and 3 days in the larval and pupal stages respectively. This pupa looked smaller and paler and weighed 5.33mg compared with those reared on mosquito preys. The male adult which emerged from it also looked smaller than normal and it died immediately after emergence. The minimum weight of the 4th-instar larvae which pupated when reared on mosquito prey larvae was 5.80mg, compared to the weight of the larva (2.78mg) which pupated upon feeding on the casein diet. The critical weight threshold necessary for pupation has been calculated for certain non-predatory insects, such as Manduca sexta (Nijhout 1975) and it has also been observed that prey availability may influence the weight at which predatory insects moult to the next instar (Beddington et al 1976). Based on these observations it may be suggested that failure of the 4th-instar C.(L) tigripes larvae to pupate was probably due to their low weights (Table 15). The 4th-instar larvae reared on the non-living diets looked paler in colour and the typical blackish-brown contents of the thorax and gut found in those reared on mosquito prey larvae were absent.

Table 16 gives the survival of the predator larvae in the different instars when reared on different diets. The data indicates that in all cases, the percentage of survival of the larvae decreased as the larvae developed from the 1st-instar to the 4th-instar. This may be due to deficiencies in the diet or insufficient intake of food during their development. Mortality was highest in larvae reared on Cerelac followed by Dog biscuit and it was least in larvae reared on Milk casein. The mouthparts of C.(L) tigripes become more sclerotized as the larva grows and it would be expected that the larger larvae would find it difficult to filter feed effectively. The early instars may be able to filter feed to some extent because the mouthbrushes which are used for such feeding are not heavily sclerotized, also no movements of the mouthbrushes of the predators were observed even in the early instars as found in other mosquitoes which feed by filtering.

C. (lutzia) fuscanus larvae failed to grow and survive on either dog biscuits with vitamin complex, meat, dried fish or live Daphnia (Ikeshoji 1966). Jackson (1953) could not rear C.(L) tigripes on dog biscuit, but she obtained two pupae, one of which took 7 days and the ensuing adult appeared normal. She did not rear the larvae from the 1st-instar as was done in this study. They were reared from the 2nd-instar collected from the field and it is not clear whether the larvae consumed some living preys before they were brought into the laboratory. Predatory larvae of Tx. rutilus rutilus,

were successfully reared to adult stage on non-living diets of Tetramin, a tropical fish meal (Focks et al 1978). Development was, however, very slow and took 107.5 ± 19.8 days to complete development compared to 15.6 ± 1.40 days when reared on Ae. aegypti larvae. The weights of the 4th-instars larvae and pupae were much smaller when they were reared on the non-living diet than on living mosquito prey. He observed that the extremely long developmental periods and the reduced size and weight of the 4th-instar larvae are undesirable aspects of using non-living diets to mass rear the larvae of Tx. rutilus rutilus, even though larval and adult survival and fecundity of that predator fed on non-living diet were not significantly different from those fed on the prey diet.

The results from this study indicates that non-living diets tested are not suitable for rearing C.(L) tigripes, nevertheless, a wider range of non-living diets should be tried for rearing this species until an appropriate diet is found. The results also gives an indication of the ability of the C.(L) tigripes larvae to survive over relatively long periods without preys. This may be important when the predator larvae are the first to appear in a small water body without preys.

elopmental period (days) of larvae and larval weights of
. (L) tigripes reared on different diets

	1st instar	2nd instar	3rd instar	4th instar	Total (larvae)	Pupa	Larval weight (mg)
.c	2.72 ± 0.08 (n = 29)	3.41 ± 0.98 (n = 29)	5.61 ± 2.92 (n = 28)	7.74 ± 1.15 (n = 19)	18.47 ± 1.22ab (n = 19)	0	1.66 ± 0.20d (n = 19)
t	2.71 ± 0.72 (n = 22)	3.95 ± 1.50 (n = 21)	5.15 ± 1.90 (n = 17)	6.24 ± 1.56 (n = 17)	17.71 ± 3.31a (n = 17)	0	1.82 ± 0.27d (n = 17)
n	2.69 ± 0.47 (n = 25)	3.36 ± 0.76 (n = 25)	4.08 ± 0.86 (n = 25)	8.86 ± 1.80 (n = 21)	19.05 ± 1.80b (n = 21)	3.0 (n = 1)	2.78 ± 0.58 (n = 21)
Mosquito prey	1.32 ± 0.48 (n = 10)	1.21 ± 0.42 (n = 19)	1.15 ± 0.37 (n = 19)	2.95 ± 0.40 (n = 19)	6.63 ± 0.50 (n = 19)	2.16 ± 0.37 (n = 19)	7.19 ± 0.96 (n = 19)

Mean developmental days and mean larval weights followed by the same letter are not significantly different based on Duncans Multiple range test ($P<0.05$)

Table 16 Survival of C. (L). tigripes larvae reared on different diets

Diet		1st instar		2nd instar		3rd instar		4th instar		pupae	
	No. of Larvae	No.	%	No.	%	No.	%	No.	%		
Cerelac	29	29	100	29	100	27	93.1	19	65.52	0	0
Dog biscuit	22	22	100	22	100	21	95.45	17	77.27	0	0
Milk casein	26	26	100	25	95.15	25	96.15	21	80.77	1	4.76
Mosquito prey	19	19	100	19	100	19	100	19	100	19	100

Chapter 4.0 PREDATORY BEHAVIOUR

4.1 Introduction

A study of the predatory behaviour would help to understand the part it plays in the control of mosquitoes in their natural habitats. The first attempts to analyse the mechanism of predation in the field (eg. Tinbergen 1960) showed the natural situation to be exceedingly complex. It proved to be extremely difficult to get a satisfactory quantitative answer to such fundamental questions like: which factors determine how many individuals of each of the various prey types present are destroyed, and how these factors operate. In this study, the approach followed was done with the idea that the intricate processes which occur under natural conditions are composed of simple elements; that these elements can be identified, and their interactions studied in the laboratory; and that the results of such laboratory work will give us useful information which may be applicable to field situation. The laboratory situation however well simulated, is not the same as what actually goes on in the field. Thus in the laboratory, it is possible to restrict the number of interacting predators and prey, and the number of environmental variables that may affect the predation process, so that precise hypotheses can be tested.

4.2. Materials and Methods

4.2.1. Prey Capture and Feeding Habits

The typical mode of feeding employed by culicine mosquito larvae is to filter out of the surrounding medium, food particles brought in by currents set up by their pre-oral mouthbrushes. The mouth- parts of culicine mosquito larvae are of the generalized type, having mouthbrushes with fine lamellae, well developed mandibles and maxillae and a central mentum composed of the fused segments of a degenerate labium (Surtees 1959). Throughout the various genera, specializations have taken place so that the basic filter-feeding method has given way to browsing and predation, with changes in the mandibles and maxillae. The former has become larger and more important whilst the latter become smaller. Concurrent with these changes, the mouthbrushes have become shorter, stronger and usually serrated.

The objectives of the present investigation are

(1) to elucidate the methods of attack, prey capture and the feeding habits of C.(L) tigripes.

(2) to study the morphological modifications associated with these activities.

The methods of attack, prey capture and feeding were first observed with the naked eyes and then under a bionocular microscope, after the larvae of C.(L) tigripes and other mosquito larvae (An. gambiae, C. quinquefasciatus and Ae. aegypti) were placed together in a transparent bowl. C.(L)

tigripes larvae which had captured prey were transferred into petri-dishes containing water to examine the feeding closely under the high power of the binocular microscope. The part of prey larvae (ie neck, thorax, abdomen, tail and siphon) seized during attack by the predator was also recorded. For the detailed examination of the morphology of the mouth parts, some of the C.(L) tigripes larvae were quickly pipetted into hot water to be killed, and were mounted in Berlese's fluid on glass slides.

4.2.2. Effect of predator stage, prey stage and prey density on the predation rate

Many aquatic predator species have been qualitatively evaluated for their possible use in mosquito control programmes (Sailer and Lienk 1954, Prakash and Ponniah 1978, Muspratt 1951, Haddow 1942, Jackson 1953, Rajasekaran and Chowdiah 1972). However, none of these workers studied the effectiveness of the predators at different stages of predator-prey development and densities.

The objective of this investigation is to determine the effect of predator stage, prey stage and prey density on the rate of predation of C.(L) tigripes. The four larval stages of C.(L) tigripes were tested against C.quinquefasciatus larvae of identical stages at three different densities. One predator larva was exposed to 10, 20, and 40 Culex prey larvae in 30ml of water in an 80ml capacity plastic bowl (6.2 x 3cm) for a period of 24 hours. These were designated densities D1,

D2, and D3 respectively. Prey larvae which were consumed were replaced with larvae of the same developmental stage. The total number of combination of predator stage (4), prey stage (4) and prey density (3) was 48. All observations on the rate of predation were conducted at room temperature (25 ± 2.0°C).

4.2.3. Effect of water volume on predation rate

Water volume and container size are known to influence the activities of some predators. The larvivorous fish Gambusia affinis kills more C. quinquefasciatus larvae with increasing volume of water in the aquarium up to 1500ml (Reddy and Pandian 1973). The predatory activity of the final or fourth instar of Tx. rutilus rutilus was significantly affected by the container size. The rate of prey consumption varied inversely with container size (Padgett and Focks 1980), but the predatory capacity of Culex (lutzia) raptor was not influenced by differences in the volume of aquarium water ranging from 150 to 700mls (Prakash and Ponniah 1978).

The objective of this study is to determine the effect of different water volumes on the predation rate of C.(L) tigripes. Round plastic bowls (9.5 x 5.5cm) were filled with 30, 60, 90, 120, 150mls of water. Into each of these bowls, one 4th-stage C.(L) tigripes larva which had previously been deprived of food for 24 hours was also introduced. The predator was deprived of food for 24 hours to minimize differences in individual hunger levels (Nakamura 1977). The number of Culex larvae killed or consumed in 24 hours was

recorded for each volume of water.

4.2.4. Feeding Preference of C.(L) tigripes

The feeding preference of a mosquito predator such as C.(L) tigripes may be affected by several factors, including the prey size, mobility, defense or avoidance behaviour, palatability, abundance and the extent to which the predator and prey habitats overlap (Ellis and Borden 1970). Some of the characteristics of a prey which will elicit an attack response of a predator, and presumably, those preys possessing those characteristics which tend to elicit an attack would be most vulnerable to predation. The preferred prey will therefore be determined by the degree to which the predator responds to some of the factors mentioned above. The objectives of this study are:

(1) to determine the effect of prey mobility on the feeding preference of C.(L) tigripes.

(2) to determine the common species of mosquito preys preferred by C.(L) tigripes.

(3) to determine the feeding preference of C.(L) tigripes with respect to prey stages.

4.2.4.1 Spontaneous and Induced Movements of C.(L) tigripes and mosquito preys

Healthy 4th-stage larvae of C.(L) tigripes, An.gambiae, C.quinquefasciatus and Ae. aegypti were selected and put individually into plastic bowls (6.2 x 3cm) filled with 30ml of water. These bowls were watched in rotation and the total

time in seconds in which each larva moved spontaneously in one minute was recorded. Fifty replications were made for each species. Fifty healthy 4th stage larvae of the four species were again selected for induced movement studies. Individual larvae were put in separate bowls with the same design as above. Larvae were individually stimulated by tapping the edge of each bowl once with a glass rod, and the time in seconds during which movement of the larva occurred after the stimulation was recorded. Twenty five larvae of each of the four species were subjected to this type of stimulation. The other twenty larvae were stimulated individually by touching the abdomen of the larvae once with a glass rod, and the time in seconds during which the larvae continued to move was recorded. Stop watches were used to time the movements of the larvae within the tested period. In all these trials the larvae were allowed to settle down and remain motionless before any stimulation was given. All external stimulation such as vibrations were eliminated by making sure that no movement occurred during the trials.

4.2.4.2 Feeding Preference by Prey Species

Fixed numbers of 4th-stage larvae (10 and 20) of An. gambiae, C. quinquefasciatus and Ae. aegypti were selected and put in individual plastic bowls (6.2 x 3cm) filled with 30ml of water. One 4th-stage larva of C.(L) tigripes was introduced into each of the bowls. In all cases, the C.(L) tigripes larvae had previously been starved for 24 hours. The number

of each species of larva killed or consumed in 24 hours were recorded.

In another experiment, three of the same bowls were set up, each containing one 4th-stage larva of An. gambiae, C. quinquefasciatus and Ae. aegypti. One 4th-stage C.(L) tigripes was introduced into each bowl and the bowls were examined every 30 minutes. The order in which the prey were consumed was recorded. Forty-two replicates of this experiment were performed. Similar feeding preference tests were carried out on chironomid and C. quinquefasciatus larvae because chironomid larvae were observed to be consumed by C.(L) tigripes in its natural habitats. One 4th-stage C.(L) tigripes larva treated as above was exposed to 10 and 20 each of chironomid and 4th stage C. quinquefasciatus larvae. The sizes of chironomid larvae were about the same as the Culex. Trials were made using tap and field water because chironomid larvae were observed to form tubes around themselves in their natural habitats. The numbers of each species consumed or killed in 24 hours were recorded.

4.2.4.3 Feeding Preference by Mosquito Prey Stages

One 4th-stage larva of C.(L) tigripes was exposed to equal numbers (10 and 20) of 4th-stage larvae and pupae of C. quinquefasciatus in a bowl (6.2 x 3cm) containing 30ml of water. The number of larvae and pupae consumed or killed in 24 hours was recorded. Similar experiments were conducted by introducing one 4th-stage C.(L) tigripes larva into bowls

containing 1st and 3rd stage Culex larvae, and 2nd and 4th-stage Culex larvae. The number of each larval stage consumed or killed in 24 hours was recorded.

4.2.5 Wasteful Killing

It has been observed by many authors that some predatory organisms killed more prey than they could possibly consume. This behaviour is not uncommon among larvivorous predators; for instance the larvivorous mosquito Tx. brevipalpis kills 26% more larvae than it can consume (Trpis 1972) and a similar behaviour has been found in other species of Toxorhynchites (Muspratt 1951, Corbet 1963, Corbet and Griffiths 1963). Notonecta undulata (Say) is also known for its characteristic overkilling of Culex larvae (Toth and Chew 1972, Ellis and Borden 1970). C. (lutzia) raptor was also found to exhibit this killing behaviour (Prakash and Ponniah 1978). C.(L) tigripes has not been studied with regard to this killing behaviour. This phenomenon has been referred to as wasteful killing or compulsive killing behaviour. The former usually refers to cases of partial consumption of prey leaving parts of the prey uneaten (Johnson et al 1975) while the latter is killing without consuming any part of the prey (Trimble and Smith 1978). This behaviour is similar to the normal predatory behaviour except the dead larva is not consumed (Crans and Slaff 1977), and factors which affect this behaviour have been found to be similar to those which affect normal predation. High temperature was found to increase the

daily number of prey killed but not consumed by both Tx. brevipalpis (Trpis 1972) and Tx. rutilus spetentrionalis from two geographical regions in North America (Trimble and Smith 1978). Both the number of prey killed but not eaten and the length of the killing phase in Tx. brevipalpis increased and were linearly correlated with increase in prey density (Lounibos 1979). Russo (1985) reported that surplus killing of five species of Toxorhynchites never began before the species achieved the minimal larval weight required for pupation. However, Lounibos (1979) confirmed (and it was also suggested by Corbet and Griffiths 1963) that the killing behaviour was not a necessary prerequisite for metamorphosis, and that the weight threshold of Tx. brevipalpis for pupation was substantially lower than that for killing behaviour. Compulsive killing behaviour was reported to be displayed by all larval instars of Tx. splendens both before and after each moult, but it was most pronounced just before pupation (Chan 1968). It was generally found to be most intense after the pre-pupa has formed and feeding is no longer possible (Crans and Slaff 1977, Muspratt 1951, Corbet 1963, Corbet and Griffiths 1963, Furumizo and Rudnick 1978). The ecological significance of this behaviour is unclear but it has been suggested that pre-pupal killing is a significant intraspecific interference mechanism with the potential for stabilizing the predatory-prey interaction (Hassell and May 1973). The most generally accepted theory to explain this

phenomenon is that this habit of pre-pupal killing is probably a protective mechanism to ensure the continuance of the species, since the pupae are more vulnerable to attack and injury by other predaceous larvae, and also because they cannot defend themselves when attacked.

The objectives of this study therefore are

(1) to determine if C.(L) tigripes exhibits wasteful killing behaviour.

(2) and the conditions that may affect this behaviour. Third-stage C.(L) tigripes larvae were reared individually until they reached the 4th-stage. Each 4th-stage larva was provided daily with either 40, 60, or 100 Culex larvae of equivalent stage as the predator. This feeding procedure was followed until the larvae pupated. The larvae were monitored for the onset of killing behaviour by checking daily, the number of prey larvae consumed and for the presence of prey larvae killed but not eaten. Normally a C.(L) tigripes larva will take in the entire prey larva captured and will discard the head capsule and sometimes the siphon in larger preys. In this study, a prey larva that was more than half eaten was regarded as eaten whilst the one that was less than half eaten was recorded as not eaten (ie it died as a result of wasteful killing). Dead prey larvae which showed signs of injuries on the body presumably caused by the mandibles of the predator, were also recorded as killed but not eaten.

4.2.6. Functional response of C.(L) tigripes to prey density

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. Information on functional response is essential for a clear understanding of the predator-prey interaction. The total number of prey destroyed by predators is the product of the number killed per predator and the number of predators that are present (Holling 1966). Solomon (1949) first proposed the terms to describe this two-fold nature of the predation process - the response of a predator to changes in prey density. He applied the term functional response to changes in the number of prey consumed by individual predators, and the term numerical response to changes in the density of predators. Functional response of predators has been classified into three categories by Holling (1959a) as follows: type 1 - where there is a linear rise to a maximum in the number of prey eaten per predator as prey density increases; type 11 - where the response rises at a decreasing rate towards a maximum value, and type III - where the response is sigmoid with an initially increasing slope and again approaching an upper asymptote. Type III responses are thought to be more characteristic of vertebrate predators that can learn to concentrate on a prey as it becomes abundant (Holling 1965). Type II responses are generally associated

with invertebrate predators, and has attracted the most theoretical attention. The best known description being the disc equation of Holling (1959b);

$$\frac{Na}{P} = \frac{aNT}{1 + a\ Th.N.}$$

Where Na = the number of prey killed (attacked)

p = the number of predators

N = the density of prey

a = a constant, the attack rate of the predators or the predators rate of successful search

Th = a constant, the handling time, including the time spent pursuing, subduing and digesting each prey

T = total time predator and prey are exposed to each other.

A number of factors determine the characteristics of these functional response curves. The most important ones have been identified to be:

(a) the time predator and prey are exposed to each other

(b) the rate of searching of the predator (which influences the magnitude and character of the functional response), and

(c) the time spent in handling prey (which affects the response by decreasing the time available for active search.

All these are basic factors incorporated in the disc equation to obtain the basic functional response equation. Other subsidiary factors such as hunger and characteristics of the environment of the predator and of the prey may affect the basic responses by changing their magnitude rather than their form.

The aim of the present study is to determine the predation rate of C.(L) tigripes larvae in response to changing mosquito prey larvae densities. Fourth stage larvae of C.(L) tigripes which have been deprived of food for 24 hours were exposed to various numbers of C.quinquefasciatus larvae in plastic bowls (6.2 x 3cm) filled with 30mls of water. The prey densities were 10, 20, 40, 60, 80, 100 and 120 larvae per bowl of 30 ml of water. These densities were kept constant by replacing larvae which have been destroyed by the predator, and the number of prey larvae destroyed in 24 hours was recorded.

4.2.6.1 Effect of Handling time on Predatory Activity

One of the basic factors affecting functional response of predator to prey density is the handling time. It has subcomponents which include

(1) the time spent orientating to, pursuing and subduing prey.

(2) the time spent eating prey and

(3) the time spent in a digestive pause during which the predator is not hungry enough to eat further prey.

They are all time consuming activities and once initiated they preclude further search (Holling 1966). The objectives of this investigation are:

(1) to determine the changes in handling time between different stages of C.(L) tigripes larvae attacking the same stage of prey larvae.

(2) to determine the changes in handling time within the same stage of C.(L) tigripes larvae attacking different stages of prey.

(3) to determine changes in handling time of the predator with successive feeding on the same size of prey larvae.

Freshly moulted first to fourth instar larvae of C.(L) tigripes were each provided with 20 of 2nd stage Culex larvae. Handling time was recorded with a stop watch starting from the time a C.(L) tigripes larva seized a prey in its mouth -parts to the time it disposes of the unwanted part (ie the head capsule) from the mouth. In another experiment individual 4th-stage larvae of the predator were provided with 20 of either 1st, 2nd, 3rd or 4th stage C. quinquefasciatus larvae in a bowl, and the handling time on each prey consumed was recorded. Lastly, individual 4th-stage larvae of the predator were provided with 20 of 2nd stage larvae of Culex. Handling times were recorded as before for the first five prey larvae consumed.

All C.(L) tigripes larvae used in these tests were starved for 24 hours prior to each test.

4.2.6.2 Effect of food deprivation on predation rate

The length of time the predator goes without food may exert an influence on its subsequent food intake. It is assumed that food deprivation time influences behaviour because of increasing hunger (Holling 1966). Hunger has been defined as the emptiness of the gut and it is the internal drive motivating all components of feeding behaviour in Hollings predation model (Holling 1966). A number of workers (Beukema 1968, Miner 1955, Ware 1972) have used the amount of food consumed by fish in relation to deprivation as an assessment of hunger. With a view to study the effect of hunger on the predatory behaviour of C.(L) tigripes, the length of time of food deprivation is used as the criterion for assessing hunger.

The objectives of the present study are to

(1) determine the effect of different lengths of food deprivation on predation rate.

(2) to determine the effect of different lengths of food deprivation time on the handling duration of prey.

Fourth stage larvae were initially exposed to abundant supply of 4th stage Culex mosquito larvae, and thereafter were deprived of food for 6, 12, 24, 36, and 48 hours, and subsequently exposed to a constant number

of 40 4th-stage C. quinquefasciatus larvae for 24 hours. The number of prey consumed in 24 hours was recorded.

In another series of experiments 4th-stage C.(L) tigripes larvae which had been deprived of food for various hours as above were exposed individually to 40 C. quinquefasciatus larvae and the time taken to consume the first five preys was recorded.

4.2.7. Cannibalism

4.2.7.1 Effect of predator stages on cannibalism

Two experiments were conducted, the first was to determine the degree of cannibalism among the larval stages of the predator. Twenty each of 1st, 2nd, 3rd, and 4th-stage larvae of C.(L) tigripes were put into separate plastic bowls (6.2 x 3cm) containing 30ml of water. The number of larvae killed or consumed in 24 hours from each bowl was recorded. The second experiment was to determine the effect of different stages of the predator on cannibalism. One 4th-stage of the predatory larva was introduced into separate bowls containing 20 of either 1st, 2nd, 3rd, 4th stage predatory larvae or pupae. The number of various stages of the C.(L) tigripes killed or consumed in 24 hours was recorded.

4.2.7.2. Effect of crowding on cannibalism

Four plastic bowls (6.2 x 3cm) were filled with 15ml, 30ml, 60ml and 120mls water, and then 15 of 4th-stage larvae of the predator were introduced into each of the bowls. The number of larvae killed or consumed in 24 hours from each bowl was

recorded. The different larval densities (ie 1, 0.5, 0.25 and 0.125 larvae per millilitre of water) were supposed to simulate different levels of crowding.

4.2.7.3 Effect of presence of prey on cannibalism

One 4th stage C.(L) tigripes larva was exposed to 10 larvae each of 2nd stage larvae of C.(L) tigripes and C. quinquefasciatus in a bowl. In another set-up one 4th-stage predatory larva was also exposed to 10 each of 2nd stage larvae of the predator and 4th-stage larvae of C. quinquefasciatus. The number of larvae of different stages of the two species consumed in 24 hours was recorded. These results were to be compared with the results obtained after ten of 2nd-stage larvae of the predator have been exposed to one 4th-stage larva of the predator in a bowl for 24 hours.

4.3 Results and Discussion

4.3.1. Prey capture and feeding habits

The larvae of C.(L) tigripes are generally bigger than the larvae of an equivalent stage of almost all the mosquito larvae on which they prey. The mandibles are very large with strongly sclerotized and pointed claws (Plate 4). Associated with the claws are large stiff spines which also aid in grasping the prey, particularly those posterior to the main claws. The mouth-brushes are thick and consist of several lamellae which are also sclerotized with the apical portions containing numerous sharp teeth arranged in rows (Plate 5). The mouth-brushes of C.(L) tigripes have been described as hairs cemented together to form prehensile fangs with which the prey is seized and held while it is consumed (MacGregor 1927). The mentum is well developed with only nine large and pointed teeth. The maxillae are reduced in size but have strong setae attached to them. The antennae and the other spines on the head are also greatly reduced in size.

The larva of C.(L) tigripes usually stays motionless at the surface of water and waits until a prey comes within a striking distance, and then with a very rapid darting movement, the prey larva is captured. This sudden dart made by C.(L) tigripes has been described by Hopkins (1936) as reminiscent of a snake and as resembling the ferocity of a crocodile by MacGregor (1927). Hopkins (1936) reported that

prey larvae were seized only when they came into contact with the mouth-brushes of C.(L) tigripes. This certainly occurs but observation in this study showed that more often, prey larvae are seized when they are within a striking distance of the predator, without necessarily coming into contact first with the mouth-parts. Sometimes C.(L) tigripes larva can even bend its body round to seize a prey larva moving almost behind it. The sight of the predator, especially the 4th-instars may play a role in its predatory activity. For instance, when the predator is either resting or obtaining its air supply at the surface, and there is a prey larva also resting near by, the predator will move its head towards it and sometimes align itself in that direction, but prey capture only occurs if the prey movement carries it towards the predator. Haddow (1942) stated that C.(L) tigripes larvae almost always seize large or small anopheline or culicine larvae by the tail. Observations made in this study showed that C.(L) tigripes often seizes prey by the tail although it can seize its prey by any part of the body depending on the orientation of the prey larva at the time of attack. The observations on this show that 8% of the prey were seized by the thorax 2% by the siphon, 20% by the abdomen, 26% by the neck region and 44% by the tail. Careful observation showed that most of the prey larvae normally swam backwards and this frequently brought them either in contact or within striking distance of the predator with the tail end first.

Plate 4. Ventral side of the head of 4th-stage larva of C.(L.) tigripes showing mouth brushes and a well developed mandible with a sharp claw (arrowed) (magnification X 250)

Plate 5. Part of the mouth brushes of C.(L.) tigripes showing numerous fine teeth on the lamellae

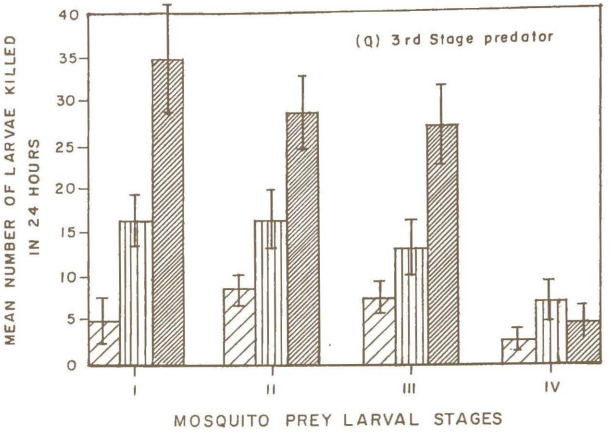
C.(L) tigripes always seized and devoured pupae of mosquitoes from the tail because it is softer compared to the heavily sclerotized cuticle of the cephalothorax. In general however, C.(L) tigripes seizes its prey from the lateral side. Haddow (1942) reported that the specialized mouth-brushes of C.(L) tigripes appear to penetrate the soft abdominal integument of the prey almost immediately. In this study, it was rather observed that in all instances the predator used only the mandibles and not the mouth-brushes to seize and hold prey. The sharp teeth of the mandibles penetrate the body of the prey and become pointed downwards with the tips directed towards the oral cavity while the mouth-brushes are still extended outwards from the head. The mandibles are therefore the main prehensile organs in C.(L) tigripes. Surtees (1959) has, however, suggested that both the mouth-brushes and the stiff spines at the posterior end of the mandibles aid in grasping prey as reported earlier in this section. Observations on another predatory mosquito, Megarhinus septentrionalis now called Tx. septentrionalis by Breland (1949), revealed that the proper functioning of the mandibles was dependent in some way upon the mouth-brushes. The methods by which C.(L) tigripes catches prey depends primarily on the location of the prey in the water i.e. at the water surface or at the bottom of the container. C.(L) tigripes larva normally stay at the water surface but when it moves to the bottom after it has been disturbed, it stays there for

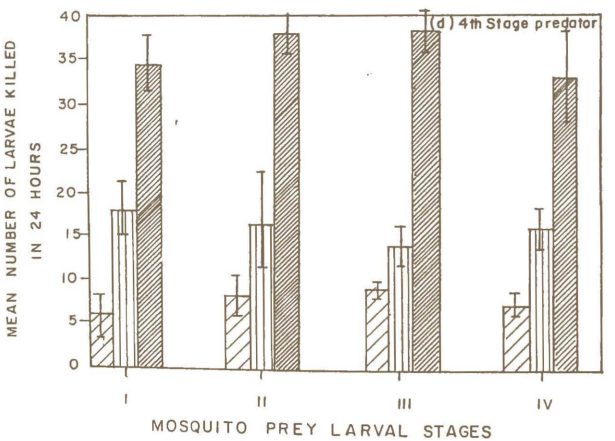
sometime before it surfaces again. Thus in addition to catching prey at the surface catches prey larvae which dive to the bottom after disturbance at the water surface and also browse on submerged food particularly Aedes species. C.(L) tigripes was not observed to attack or seize a prey within the water column. After capturing a prey C.(L) tigripes often changes its normal posture of lying almost parallel to the water surface i.e. anopheline-like, and assumes the normal Culex posture, that is it slants at about 45° to the water surface. This may be due to the extra weight added to the anterior end of the predator by the captured prey. However, in this posture, the prey larva or pupa which is held firmly in the mouth parts, will become fully submerged in the water and is denied contact with the water surface leading to accelerated death by suffocation. The seized prey is often held firmly in the mandibles and the predator either stays at one place or it drifts along in the water if the prey is large and struggles to free itself. Mosquito larvae caught by C.(L) tigripes cannot usually free themselves but captured mosquito pupae frequently struggle and break free but they may suffer physical damage caused by the mandibles of the predator. C.(L) tigripes larvae do not usually wait for their victims to die before they consume them. Slow movements of the victims often continue after feeding has began; sometimes till almost the entire abdomen has been consumed. MacGregor (1927) observed that larvae captured by C.(L) tigripes, usually

struggles violently for a few seconds, and are slowly consumed alive until the devouring mandibles finally crush the large nerve ganglia in the thorax. C.(L) tigripes usually feed on its prey in such a way that the thorax is eaten last while the head capsule is either partially eaten or completely discarded depending on the size of the prey relative to the predator. First instars whose head capsules are not fully sclerotized are usually consumed whole, without discarding the head capsule. It was observed in the present study that most 4th-stage C.(L) tigripes larvae usually defaecate when they start consuming captured prey. This behaviour was probably to empty the gut to make way for the new food. This behaviour is not peculiar to C.(L) tigripes because a fully satiated dragonfly nymph (Mesogomphus lineatus) exposed to a constant supply of mosquito larvae did not attack until such time that the nymph defaecated. Apparently in the dragonfly, the defaecation facilitated the transfer of a part of chyme from the stomach to the intestine, so the stomach or intestine evacuation appeared to control the return of appetite (Mathavan 1976). Stomach or intestinal evacuation has also been shown to play a major role in returning appetite in fishes (Windell 1967, Brett and Higgs 1970, Pandian 1967).

4.3.2 Effect of predator stage, prey stage and prey density on predation rate

The results of the mean predation rates of the various combinations of predator stage, prey stage and prey density are given in Appendix Table 18 and illustrated in Figures 17 and 18. The first and second stages of the predator consumed more prey larvae of their own stage and the mean numbers consumed daily increased as the prey density also increased. The mean number of prey consumed at prey density D3 when 2nd-stage C.(L) tigripes fed on 3rd-stage prey was an exception; less prey larvae were consumed at density D3 than D2 (Fig.17). Both the 1st and 2nd-stage C.(L) tigripes were not very effective at feeding on larger stages (3rd and 4th) of the prey. The predation rate decreased at almost all densities as the prey-stage increased. The 3rd-stage C.(L) tigripes is capable of consuming large numbers of prey of all stages except the 4th-stage prey larvae (Fig.18). The 4th-stage larvae of C.(L) tigripes consumed relatively large numbers of the prey of all stages, including prey of its own stage (4th). The trend of predation rates shown by the various stages of the predator is as expected because more prey larvae





would be required to satiate a bigger predator. The 4th-stage larva of C.(L) tigripes is the most voracious of all the stages because its rate of predation on the different stages of the prey larvae at different densities were consistently higher than those of the other three instars. This suggests that the final (4th) stage larva is better adapted for catching and consuming mosquito larvae of all stages and at all densities. A general picture of the effect of the three factors (predator stage, prey stage and prey density) on the numbers of C. quinquefasciatus consumed by C.(L) tigripes larvae have been shown graphically in Figures 19-21. The mean values for each of the factors were derived by blocking out the interactions of the other factors and each line graph summarizes the relationship of each factor to predation rate. It is observed that the older predators consumed more prey larvae than did the younger predators (Fig.19) and the younger mosquito prey larvae were more susceptible to predation than the older preys (Fig.20). The predation rate became higher as the prey density increased (Fig.21) but was not directly proportional to prey density, since the magnitude of the predation rate started to diminishe with increasing prey density D3. Higher prey densities would be needed to be tested to show the declining gradient clearly. The results of this study may have some implications on the potential importance of C.(L) tigripes in the natural control of mosquitoes. They indicate that the individual predators

became increasingly efficient as they developed from 1st to 4th-instar with regards to the number of mosquito prey larvae they killed in a given period of time. Furthermore, the early stages (1st and 2nd) of the prey larvae were found to be more susceptible to predation than the older larvae. This suggests that fewer mosquitoes would be allowed to reach reproductive maturity if the high rate of predation on the early stages is either maintained or increased by the predator. They may therefore have a more detrimental effect on adult mosquito population levels, however, because the effect of increasing prey density on the predator's rate of predation diminishes in magnitude from low to high density (Fig.21), the predator may not be able to repress a rapid increase in larval numbers in nature.

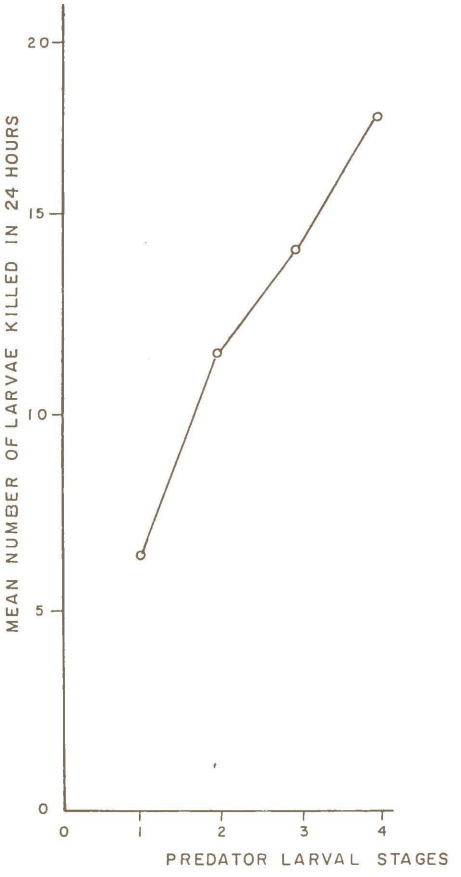


Fig. 19 THE NUMBERS OF C. FATIGANS CONSUMED BY DIFFERENT STAGES OF C.(L) TIGRIPES

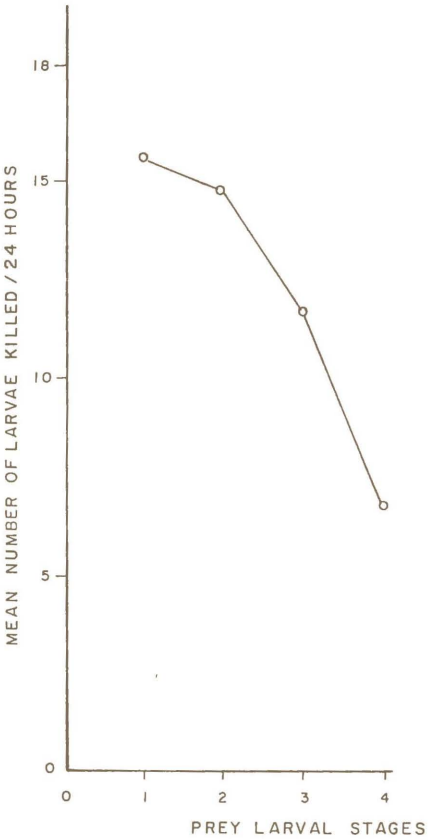


Fig. 20 THE NUMBERS OF DIFFERENT STAGES OF C. FATIGANS CONSUMED BY C. (L) TIGRIPES

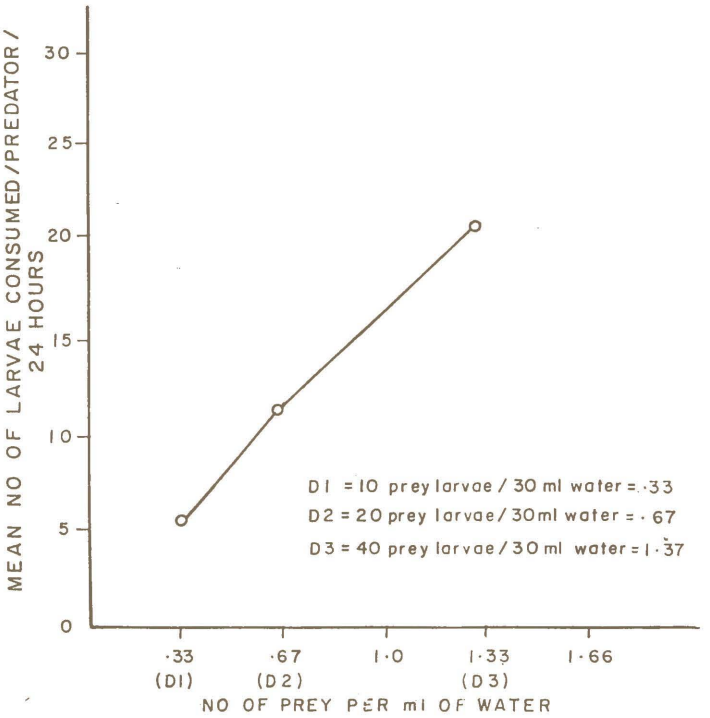


Fig. 21 THE NUMBER OF C. QUINQUEFASCIATUS CONSUMED AT DIFFERENT DENSITIES BY C.(L) TIGRIPES

4.3.3. Effect of water volume on predation rate

The results of the effect of changing water volume on the predation rate of C.(L) tigripes are presented in Table 17. The rate of predation in different volumes of water decreased significantly ($P<0.01$) as the volume was increased. The difference in the daily rate of predation was not significant ($P>0.05$) as the water volume was increased from 30 through 60mls, to 90mls but beyond this the difference became significant. This result is not surprising because it is expected that as water volume increases, the density of the preys will decrease so the chances of prey larvae coming into contact or moving closer to the predator will be decreased and therefore the number captured will be expected to decrease. Padgett and Focks (1980) found that the size of water container affected the rate of predation of Tx. rutilus rutilus. The rate of predation varied inversely with container size and directly with prey density, and they suggested that the difference may be from the variable ratios of container surface area to predator. Water volume affected the predation rate of C.(L) tigripes in the same way as container sizes in Tx. rutilus rutilus ; it varied inversely with predation rate.

Table 17 Effect of water volume on predation rate of C. (L). tigripes

Water volume (mls)	No. of prey offered per predator	No. Consumed or killed in 24hrs	No. of trials	F ratio
30	40	37.2 ± 3.01b	20	18.33 P< 0.01
60	40	35.0 ± 3.74 ab	20	
90	40	31.1 ± 3.25 a	20	
120	40	26.8 ± 4.94	20	
150	40	22.4 ± 6.38	20	

Means followed by the same letter are not significantly different (Duncans Multiple range P > 0.05)

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4.3.4. Effect of food deprivation on predation rate

The results of the rate of predation of C.(L) tigripes after different periods of food deprivation are shown in Figure 22 and the results of the time taken to consume a fixed number of five prey larvae after different periods of food deprivation are shown in Figure 23. The predation rate increased as the length of food deprivation increased and reached a peak after 24 hours of food deprivation, then started to decline gradually with further increase in the length of food deprivation (Figure 22). The difference in the mean values were, however, not significantly different ($P>0.05$). The time taken by C.(L) tigripes to consume five prey larvae decreased as the length of food deprivation was increased (Fig.23), and the difference was highly significant ($P<0.001$). The mean handling durations shown in Table 18, would give us 64.8, 60, 33.6, 31.6 and 27.6 seconds as handling times per prey respectively for the various lengths of food deprivation, indicating that less time was spent on individual preys as the deprivation time increased. It was therefore expected that the daily prey consumption would have continued to increase as the length of deprivation was increased from 6 hours to 48 hours, but it did not (Fig.22). Moreover, there was no significant difference between the rate of daily prey consumption after various lengths of deprivation. These suggest that maximum appetite of the predator might have returned after 24 hours of food deprivation, and after that both the handling duration

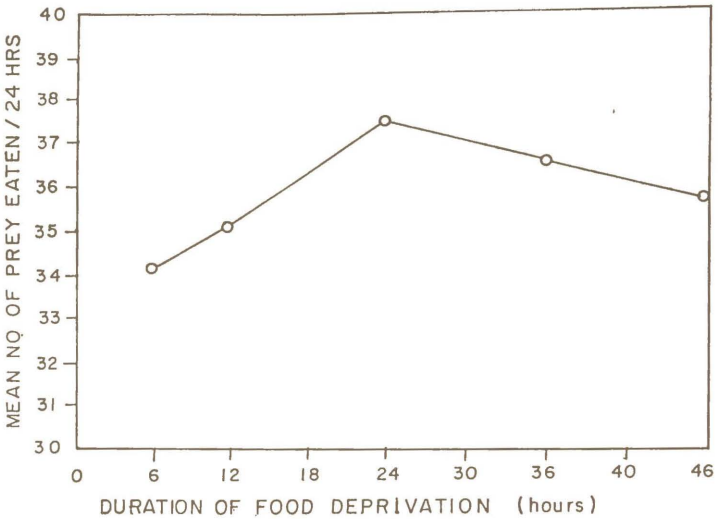

Fig. 22 THE INFLUENCE OF THE DURATION OF FOOD DEPRIVATION ON THE PREDATION RATES OF C. (L) TIGRIPES

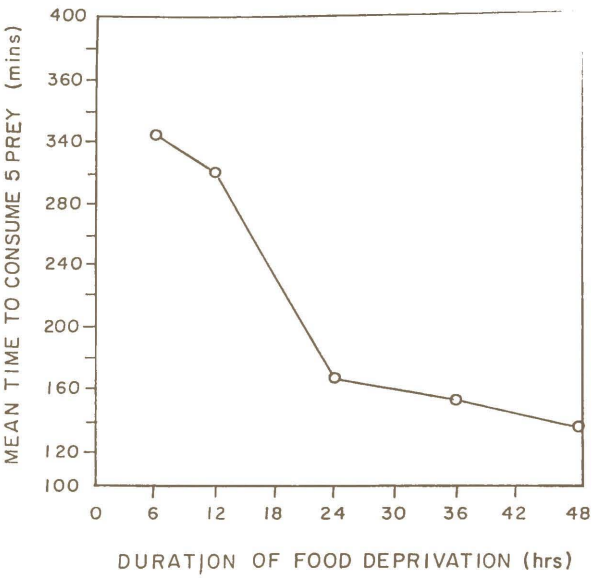

Fig. 23 EFFECT OF THE DURATION OF FOOD DEPRIVATION OF C.(L.) TIGRIPES ON THE PREDATORY ACTIVITY

and the average daily prey consumption almost levelled off indicating stability in hunger. The pattern of prey consumption therefore did not have any significant effect on the total prey larvae consumed in a day, after the return of maximum appetite. The length of food deprivation (which gives an indication of the hunger level) affects the predatory activities of some predators such as N.undulata (Ellis and Borden 1970). The predator searches more actively for its prey after different lengths of food deprivation and when preys are captured, less time is used to handle individual prey with the resultant increase in daily numbers of prey destroyed as the length of deprivation increases.

Table 18 Effect of varying periods of starvation of C. (L) tigripes on time it takes to consume prey (handling time) and on number of prey consumed per day

Hours of starvation	Handling Time (mins)	No. of prey consumed
6	324 ± 55.82a (n = 20)	34.2 ± 2.78 (n = 20)
12	300 ± 54.37a (n = 20)	35.2 ± 3.68 (n = 20)
24	168 ± 25.00b (n = 20)	37.6 ± 1.26 (n = 20)
36	158 ± 23.94b (n = 20)	36.6 ± 2.46 (n = 20)
48	138 ± 19.89b (n = 20)	35.8 ± 2.25 (n = 20)
F ratio	49.68 P<0.001	2.49 P>0.05 NS)

NS = not significant (P > 0.05)
Mean followed by the same letter are not significantly different (P > 0.05 Duncan's multiple test)

4.3.5. Feeding preference

4.3.5.1. Feeding preference by prey species

The results of the prey species preference tests of C.(L) tigripes are presented in Table 19. Mosquitoes which are the most common species associated with the predator in its natural breeding places were used against the most voracious predator stage (4th). The results indicate that C.(L) tigripes larvae showed a strong preference for Ae. aegypti as compared to An. gambiae and C. quinquefasciatus particularly at the higher prey density of 20 larvae per bowl ($p<.001$). At the lower prey density of 10 larvae/bowl, more Ae. aegypti larvae were again consumed daily than either C. quinquefasciatus or An. gambiae ($p<0.01$). Another test carried out by offering to the predator, one larva each of the three mosquito prey species, also showed that C.(L) tigripes exhibited a definite preference for Ae. aegypti larvae (Fig.24). The results indicate that in 64.3% of the trials ($n = 42$), Ae. aegypti larvae were killed first, and C. quinquefasciatus and An. gambiae were killed first in 42.9% and 16.7% of the trials respectively. However, in comparing the feeding preference of C.(L) tigripes for An. gambiae or C. quinquefasciatus no significant difference was observed ($p>0.05$) (Table 19). Larvae of chironomid were commonly observed to be consumed by C.(L) tigripes in the field and preference tests carried out indicated that C.quinquefasciatus

Table 19 Feeding preference of C.(L) tigripes for prey larval species

Predator instar	No. and species of prey bowl	No. of trials	Mean No. of prey species consumed/24hrs X ± SD	Test
4th	10 An. gambiae 10 C. quinquefasciatus 10 Ae. aegypti	30	8.0 ± 2.08 a 7.3 ± 2.71 a 9.4 ± 0.86	F =8.58 P<0.01
4th	20 An. gambiae 20 C. quinquefasciatus 20 Ae. aegypti	20	11.7 ± 1.45 b 12.2 ± 1.58 b 15.2 ± 1.62	F = 29.91 P< 0.001
4th	10 C. quinquefasciatus 10 Chironomid	21	6.0 ± 1.25 5.05 ± 0.15	t = 2.25 P<0.05
4th	20 C. quinquefasciatus 20 Chironomid	20	16.5 ± 1.05 10.5 ± 1.40	t = 15.36 P< 0.001
4th	10 C. quinquefasciatus 10 Chironomid	15*	7.89 ± 1.55 2.40 ± 1.65	t = 9.65 P<0.001

*field water was used for the test

Means followed by the same letters are
not significantly different (Duncan's multiple range test)
P < 0.05

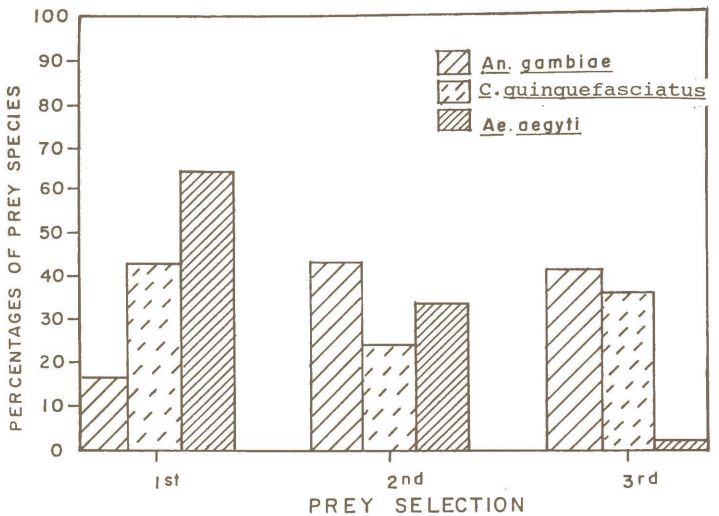

Fig. 24 FEEDING PREFERENCE OF C. (Lutzia) TIGRIPES, WHEN OFFERED A CHOICE OF 3 PREY SPECIES. (Percent killed refers to the frequency with which a prey species was killed 1st, 2nd or 3rd.)

larvae were preferred to chironomid at both prey densities tested (Table19). Results of a similar preference test performed using water collected from the field instead of tap water, again showed a highly significant preference for C. quinquefasciatus ($P<0.001$). The mean number of chironomid larvae killed from tests with water from the field were much lower than was previously observed for tap water. This difference was due to the fact that when the field water was used, many of the chironomid larvae formed tubes around themselves at the bottom of the containers using particles in the water from the field. The results thus suggest that characteristics of the chironomid larva which enables it to avoid capture by C.(L) tigripes will make it less of a prey particularly in the preference of other mosquito prey.

4.3.5.2. Spontaneous and Induced movements of mosquito larvae.

The results of the duration of spontaneous movements of the three mosquito prey species: Ae. aegypti, C.quinquefasciatus and An. gambiae, and C.(Ll) tigripes are given in Table 20 (Appendix Table 20). The results indicate that Ae. aegypti larvae were more active and moved more frequently than the other mosquito larvae including the predator. The difference between the mean values of duration of spontaneous movement is highly significant ($P<0.001$), however, the duration of spontaneous movements of C. quinquefasciatus and An. gambiae are not significantly different ($P>0.05$). The total duration

of movements by all the fifty C.(L) tigripes larvae was 83.0 seconds compared to 726, 311, and 205 seconds moved by Ae. aegypti, C. quinquefasciatus and An. gambiae respectively. The longer duration of spontaneous movement of Ae. aegypti means it will increase the chances of its coming within the striking distance of the predator compared to C. quinquefasciatus and An. gambiae. In fact the lack of difference in the preference by C.(L) tigripes for either of these two species is butressed by the lack of difference in their spontaneous movement. Thus only 6.29% of all the spontaneous larval movements were shown by C.(L) tigripes compared to 54.79%, 23.47% and 15.47% for Ae. aegypti, C. quinquefasciatus and An. gambiae respectively. The results indicate that C.(L) tigripes larvae seldom moves spontaneously in comparison to the three prey species.

The results of induced movement of the larvae of the four mosquito species caused by two different methods of stimulation are given in Table 21 (Appendix Tables 21 and 22). Ae. aegypti larvae continued to move for a longer time than all the other larvae after stimulation by tapping the edge of the container as well as by tapping the larvae. The durations of movement of C.(L) tigripes after both methods of stimulation were longer than the durations shown by C. quinquefasciatus and An. gambiae. No significant difference ($P>0.05$) was observed between the two methods of stimulation. These results may explain what has been observed both in the

field and in the laboratory with C.(L) tigripes. It usually stays at one place in the water and seldom moves around by itself. Prey larvae which come into contact with it or close to it are captured and consumed. Thus prey larvae, like Ae. aegypti which move more frequently in the water habitat are more likely to either get into contact with the predator or move into the predator's striking distance to be captured. Considering the posture that the mosquitoes assume, Anopheles larvae lie horizontal to the water surface, whereas Culex and Aedes larvae hang at about 45° to the surface. Ae. aegypti larvae normally rest at the surface or at the bottom of the water. While at the bottom, they usually browse for particulate food but they must surface every few minutes for air thus exposing themselves to the predator more often than the other two species. Also,it was often observed that Ae. aegypti larvae were also captured at the bottom by C.(L) tigripes. It appears that the angle at which the prey larvae and the predator come to rest at the surface did not affect the feeding preference of the predator. C.(L) tigripes, particularly the early instars rest at the surface almost in the same posture as Anopheles species, but this posture did not seem to enhance the predator's chances of capturing this prey. Though C. quinquefasciatus and An. gambiae showed different postures at the surface of the water, the difference in the predation rate on the two species was not significant ($p>0.05$)(Table 19) even though more An. gambiae were taken

than C. quinquefasciatus.

Factors such as prey mobility and avoidance behaviour have been observed in these studies as some of the characteristics that influence the type of prey selected by C.(L) tigripes. The tendency to remain motionless more often when not stimulated seem to be a good attribute for the predator such as C.(L) tigripes which does not actively search for its prey but lays in ambush for it.It will be advantageous to stay motionless in order not to attract the attention of any potential prey moving towards it. Turnball (1960) observed a somewhat similar situation in the selection of prey by the spider Linyphia triagularis (Clerck), and stated that an ideal prey was one which, among other things, was highly mobile, as this attribute increased its chances of becoming ensnarled in the spiders web. However, when C.(L) tigripes is stimulated it moves for a relatively longer period than Culex and Anopheles. Usually the movement of a prey may cause some ripples or movements in the water or cause body contact with the predator, so it may consider such a stimulus as indicating the presence of a prey. The increase in the duration of movement of C.(L) tigripes after stimulation may therefore be a follow up to capture a potential prey.

The factors which may affect prey selection by a predator include prey size, mobility, palatability, avoidance behaviour or defense, abundance and the extent to which the predator and prey concur in the same habitats, (See Section 4.2.3). Young

(1967) and Turnball (1960) pointed out that, each of these factors is part of a complex and the degree to which the predator responds to this complex will determine the preferred prey. For selecting a prey in nature, an even more important factor may perhaps be the degree to which the predator and prey share the same microhabitat. C.(L) tigripes larva spends much time at the surface film but often moves to the bottom of water container and remains there for a long time before surfacing again. Because it spends much of its time at the surface film it comes into contact most often with prey which are regularly found at that level in the water column such as mosquito larvae, and this may explain why more Culex larvae were taken than chironomid larvae. Larvae of Culex were used instead of Aedes, which is the preferred species, because the former occurs more frequently with the predator in the same breeding habitats. Preys such as Aedes larvae which in nature spend a long time crawling at the bottom of containers browsing for food may again be more vulnerable to predation by C.(L) tigripes particularly when the latter is at the bottom of the water. C.(L) tigripes larvae did not feed on other organisms such as psychodidae larvae and pupae and nematodes when offered these organisms even though they occurred in the same habitat as C.(L) tigripes. Similarly, adult insects which fell into the water were not preyed upon by C.(L) tigripes. This is in contrast to the observation made by MacGregor (1927) that C.(L) tigripes will eat almost

anything including some of the organisms mentioned above.

4.3.5.3. Feeding preference by prey stages

The results of the predation rates obtained when 4th-stage Culex larvae and pupae were offered simultaneously to C.(L) tigripes indicate that C.(L) tigripes selectively preyed on the larvae (Table 22) and that the mean numbers of larvae and pupae consumed in 24 hours at the two densities (10 and 20 per container) are significantly different ($P<0.001$). The difference may be attributed to the hard exo-skeleton of the thorax of the pupae in contrast to the soft integument of the thorax and abdomen of the larvae, which makes it difficult for the predator to consume more of the pupae. Since the pupae do not feed, they often tend to hang at the surface of the water and move only when they are disturbed, thus reducing the probability of encounter.

Table 20 Duration of spontaneous movements of mosquito larvae

Movement	An. gambiae	C.quinquefasciatus	Ae. aegypti	C.(L)tigripes	F
Time (sec) moved/ larva (X ± SD)	4.30 ± 4.44a (n = 50)	6.22 ± 5.68a (n = 50)	14.52 ± 10.30 (n = 50)	1.66 ± 0.77 (n = 50)	38.9 P<0. 01
Total time moved/ larval species	205	311	726	83	
% of movement/ larval species	15.47	23.47	54.79	6.29	

Table 21 Duration of Induced movements of mosquito larvae after

(i) Stimulation by tapping edge of bowl
(ii) Stimulation by tapping larvae

Movement	An. gambiae	C. quinquefasciatus	Ae. aegypti	C.(L)tigripes	F
(i) Time (sec) moved/ larva (X ± SD)	2.4 ± 1.38a (n = 25)	2.6 ± 1.38a (n = 25)	9.4 ± 7.03 (n = 25)	4.4 ± 1.76a (n = 25)	18.86 P<0.001
Total time moved/ larval species	60	65	235	110	
% of movement/ larval species	14.63	15.85	57.32	26.83	
(ii) Time (sec) moved/ larva (X ± SD)	2.0 ± 0.87b (n = 25)	2.84 ± 1.21b (n = 25)	9.88 ± 6.24 (n = 25)	3.24 ± 1.42b (n = 25)	30.57 P<0.001
Total time moved/ larval species	50	71	247	81	
% of movement/ larval species	11.13	15.81	55.01	18.04	

The pupae are relatively larger than the larvae and move very quickly and more powerfully than larvae. It has been suggested by Young (1967) that the susceptibility of aquatic prey to the larvae of Dystiscus marginalis involve factors such as the width of the prey in relation to the distance between the mandibles of the predator. This may also explain the preference of C.(L) tigripes for the larvae over the pupae. The few pupae which were consumed were captured from the tail end only, which suggests that the shape and size of the pupae contributed to the inability of the predator to hold and subdue them. A similar situation has been observed with C. (Lutzia) raptor which could not prey on normal pupae of C. quinquefasciatus (Rajasekaran and Chowdiah, 1972). It was suggested that because the pupae are spherical, they could not be held and subdued by the predator. Prakash and Ponniah (1978) however, found that 'mini' pupae of C. quinquefasciatus which emerged from starved 4th-instar larvae, were easily preyed on by C. (Lutzia) raptor, suggesting that the size of the prey also contributed greatly to its selection. Mathavan (1976) found that the dragonfly nymph (Mesogomphus lineatus) also selectively preyed on the larvae of C.quinquefasciatus, when offered the larvae and pupae and attributed the difference to the fact that pupae usually hang to the surface of the water, whereas the larvae move freely in the water, perhaps for feeding purposes.

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Table 22 Feeding preference of C (L) tigripes for mosquito prey stages

Predator stage	No. and stage of prey/bowl	Mean No. prey consumed in 24 hrs X ± SD	No. of trials	T test	
4th	10 C.quinquefasciatus pupae 10 C.quinquefasciatus larvae	2.68 ± 2.48 8.00 ± 2.05	31	8.12	P<0.001
4th	20 C.quinquefasciatus pupae 20 C.quinquefasciatus larvae	3.4 ± 1.35 15.55 ± 1.61	20	25.88	P<0.001
4th	10 C.quinquefasciatus larvae (2nd-stage) 10 C.quinquefasciatus larvae (4th-stage)	8.77 ± 1.07 6.37 ± 1.80	30	6.30	P<0.001
4th	10 C.quinquefasciatus larvae (1st-stage) 10 C.quinquefasciatus larvae (3rd-stage)	9.87 ± 0.34 7.33 ± 1.69	30	2.04	P<0.05

He therefore suggested that predators generally appear not to be efficient in capturing floating and hanging prey organisms. Chiszar and Windell (1973) also found that predators like the fish Lepomis machrochirus are more efficient in seizing and grasping sinking preys than floating ones. The strong integument of the pupae together with their large sizes, spherical shape, posture in the water and ability to move quickly are the characteristics which probably afforded the pupae better chance of escaping predation by C.(L) tigripes in this study.

Results of preference tests carried out with different prey larval stages show that C.(L) tigripes selectively preyed on the smaller stages when offered a choice of two larval stages. The mobility of the different prey larval stages were not determined, but if it is assumed to be the same for a species, then the size of the prey larvae might be the major factor determining the preferential feeding of the predator on the different larval stages. The smaller larval stages would be easier to capture and subdue than the larger ones. Even though more energy will be expended in capturing and consuming more of the smaller prey stages before satiation of C.(L) tigripes, this may be compensated for by the decrease in handling duration per prey. Swift and Fedorenko (1975) have observed that the strike and contact efficiencies of 4th-instar predator larvae of Chaoborus americanus and C. trivittatus increased as the size of the prey decreased.

Lounibos (1979), however found that the 4th-instar of Tx. brevipalpis preferred 4th rather than 2nd-stage Ae. aegypti prey larvae and he explained it on the grounds of optimal foraging strategy: the presumed decrease in attack rate resulting from selecting large prey may outweigh the added energy expenditure in increased handling time per prey item.

4.3.6 Wasteful killing

The results of the final (4th) instar of C.(L) tigripes larvae monitored for wasteful killing behaviour are shown in Figure 26 (Appendix Table 22). The results indicate that predation rate decreased as the final instar grows, with the highest rates occurring during the first two days and then decreasing until pupation (Figure 25a). The predator started killing the prey without eating them from prey density of 60 per container of 30mls of water upwards, and the mean number of prey larvae killed but not consumed also increased as the prey density increased (Figure 25b).

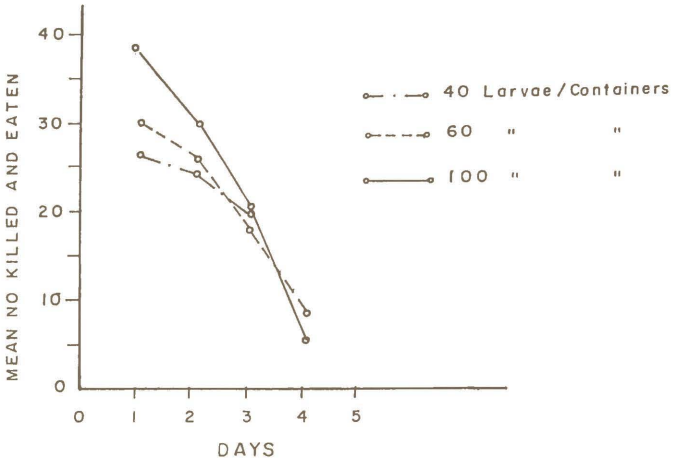

Fig. 25 a RATE OF PREY CONSUMPTION BY FINAL (4th) INSTAR LARVAE OF C. (L) TIGRIPES

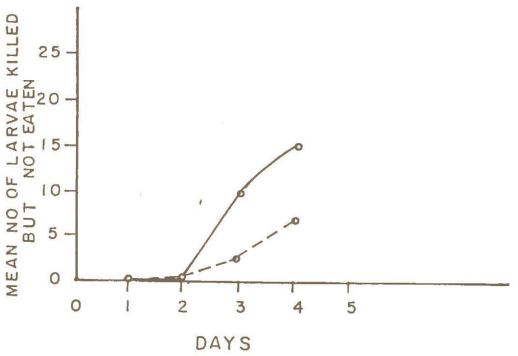

Fig. 25b RATE OF PREY KILLING BY FINAL (4th) INSTAR LARVAE OF C. (L) TIGRIPES

This behaviour started from the 3rd day and the switchover from feeding to killing without eating appears to be abrupt. It may represent a transition from larval to pre-pupal development. At prey density of 40 per container, all the larvae pupated on the 3rd day and all the larvae killed were consumed. The means of prey larvae killed but not eaten on day 3 were 2.0 ± 1.21 and 10.35 ± 2.99 at prey densities of 60 and 100 larvae per container respectively. Four and six larvae pupated on day 4 from prey densities 60 and 100 respectively and they killed a mean of 6.5 ± 1.07 and 14.36 ± 2.76 prey larvae but did not consume them before pupation. The results show that C.(L) tigripes kills prey in excess of food requirements but it leaves behind a large number of prey larvae alive in the container. Thus if the rationale behind this killing behaviour is solely for achieving survival during the relatively helpless pupal stage as postulated by some authors (see section 4.2.5) then one would expect that, either all or most of the prey larvae in the container should have been killed. Corbett and Griffiths (1963) reported that the final (4th) instar of Tx. brevipalpis usually kills all the preys in the same container before pupating and also it does not ingest prey once the killing phase has begun. This behaviour would definitely ensure the survival of the pupa. The increased number of prey larvae killed but not eaten by C.(L) tigripes may probably be explained by the fact that the predator might have eaten enough, and stopped eating but

killed larvae which came within its striking distance due to its innate killing behaviour.

4.3.7 Functional response of predator to prey density

The results of the response of C.(L) tigripes larvae to changing prey densities are shown in Figure 26 (Appendix Table 23). The response of the predator indicated that in the presence of increasing levels of prey density in the laboratory, the predators at first increase their rate of food consumption in proportion to prey density, but at higher prey densities, their feeding rate eventually levels off (Fig. 26). This experiment should probably have been continued for 2 or 3 more prey densities to really confirm the levelling off of the rate of prey consumption. The response curve is curvilinear and is similar to the Hollings Type II functional response curve in which predation rate decreases as predator satiation sets an upper limit to food consumption. It can therefore be represented by the disc equation (Holling 1959b). The disc equation has been described by Thompson (1975) as an instantaneous equation and as such makes no allowance for a reduction in prey numbers during the course of the predation. A single predator reduces the density of the prey whenever it eats one (i.e. prey exploitation). Consequently it should only be used when an experiment is run for a very short time or when a prey item is replaced as soon as one is eaten. With the procedure described for this experiment (section 4.2.6), it was impracticable to replace immediately all the

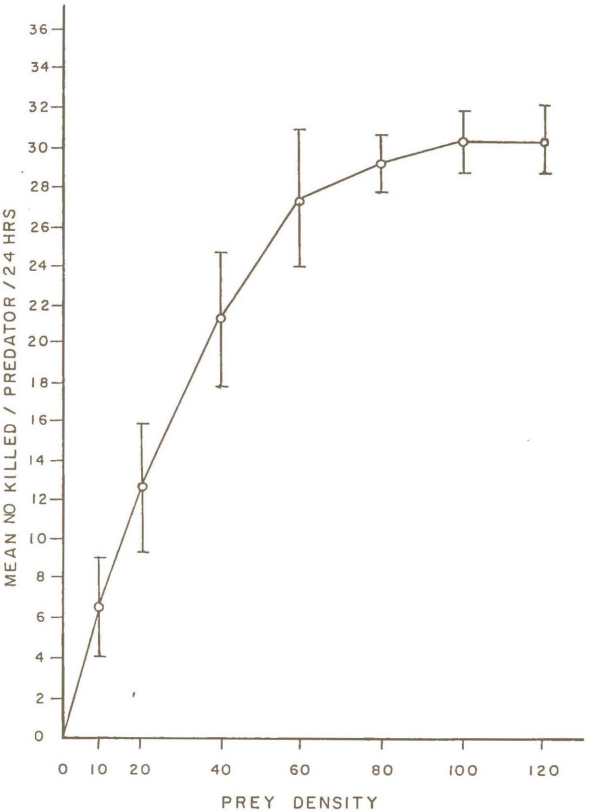

Fig. 26 FUNCTIONAL RESPONSE OF C. (L) TIGRIPES TO PREY DENSITY

preys that were eaten during the course of the experiment, so that the results are affected to some extent by prey exploitation. This problem may be circumvented by a more robust equation by Rogers (1972) $Na = N(1-e^{-a(T - Na\,Th)})$ where Na, N, T, a and Th are as defined for the disc equation which allows prey exploitation and assumes random search for prey. The inclusion of this equation in simple population models has shown that the type II functional response cannot contribute to the stability of a predator-prey interaction (Hassell and May 1973, Murdoch and Oaten 1975). It therefore follows that if a predator (such as C.(L) tigripes) has a type II functional response, stability results from other components affecting predators or prey. A review of some of these has been presented by Lawton et. al. (1975), Murdoch and Oaten (1975), Beddington et al.(1976) and Hassell et al.(1976).

4.3.7.1 Effect of handling time on predation rate

The handling times of different stages of C.(L) tigripes feeding on 2nd-stage C. quinquefasciatus are shown in Figure 27. It shcws that the handling time decreased considerably as the predator stage increased. The decrease in the mean handling times which ranged from

105 $\pm$ 6.24 minutes for the 1st-stage C.(L) tigripes larvae to 79.27 $\pm$ 10.48, 27.87 $\pm$ 4.83 and 14.07 $\pm$ 5.50 minutes for 2nd, 3rd and 4th-stage respectively is highly significant ($P<0.001$). Figure 28 shows the handling times of one stage

(4th) of C.(L) tigripes larva attacking different stages of prey larvae. The mean handling times which increased from 1.67 ± 0.52, 11.23 ± 2.14, 22.97 ± 4.31 and 53.0 ± 6.90 minutes for the 1st, 2nd, 3rd and 4th-stage prey larvae respectively, was highly significant ($P<0.001$). These variations in handling times with predator and prey stages may be interpreted in terms of the probable changes in the subcomponents of the handling time (See section 4.2.6.1). Thus, as the predator becomes larger relative to the size of the prey, it is expected that handling time should decrease, since smaller prey will, in general, be easier to subdue, consume, and digest than larger prey. It was observed that the larger stages (3rd and 4th) of C.(L) tigripes were able to swallow 1st- stage prey larvae whole in few minutes without discarding any part of the body. This is because very little sclerotization of the head and siphon had taken place in the 1st-stage prey larvae. Parallel observations of handling durations of different stages of predatory coccinellid beetle, Adalia decempunctata and C. (lutzia) raptor for one prey size have been made by Dixon (1959) and Prakash and Ponniah (1978) respectively. Dixon (1959), however, suggested further that larger predators often search faster, see further, and make a higher proportion of successful attacks than smaller predators exposed to the same size of prey, so that the rate of searching will tend to increase while the handling time will decrease as the predator grows. C.(L) tigripes does not

search for its prey, it waits in one place until a moving prey comes by and then captures it.

The study of the handling times of 4th-stage C.(L) tigripes larvae feeding successively on 2nd stage larvae of C. quinquefasciatus showed that time increased as the predator continued to feed on more prey larvae (Fig. 29). The mean handling times were 11.37 ± 2.18 minutes for the first prey larva, then 17.23 ± 3.0, 27.93 ± 3.67, 40.87 ± 6.75 and 67.7 ± 14.98 minutes for the second, third, fourth and fifth prey larvae respectively, and the increase is significant ($P<0.01$). The results also suggests that as the predator continues to feed on more prey larvae, hunger is decreased and thus as it becomes satiated, more and more time is spent handling successive preys. Observations on mantids and C. (lutzia) raptor by Holling (1966) and Mathavan (1976) respectively, showed similar results. In both cases of insect predators, handling times increased and in addition the number of attacks on the prey organisms decreased as they became satiated. Ellis and Borden (1970) however observed that less and less time was spent handling successive prey as the backswimmer (Notonecta undulata) became satiated or as its response to the prey decreased. Wolda (1961) has suggested response decrement, a lowered responsiveness to subsequent stimuli from prey as another factor affecting handling duration and rate of attack or search. Ellis and Borden (1970) suggested that the length of time which a predator feeds on

a single prey organism appears to depend also on the hunger level and/or the influence of nearby disturbances for example, other prey. Since C.(L) tigripes larvae were starved for 24 hours before the experiment to minimize differences in individual hunger levels and the larvae do not relinquish their captured prey even when they are disturbed by other preys around, the increase in the handling time of C.(L) tigripes with successive preys could only be due to the fact that it was getting full or satiated.

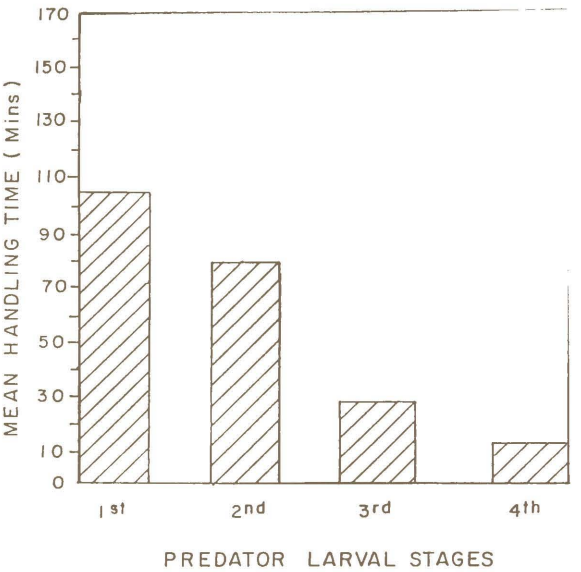

Fig. 27 CHANGES IN HANDLING TIME BETWEEN LARVAL STAGES OF C.(L) TIGRIPES FEEDING ON THE 2nd STAGE PREY LARVAE

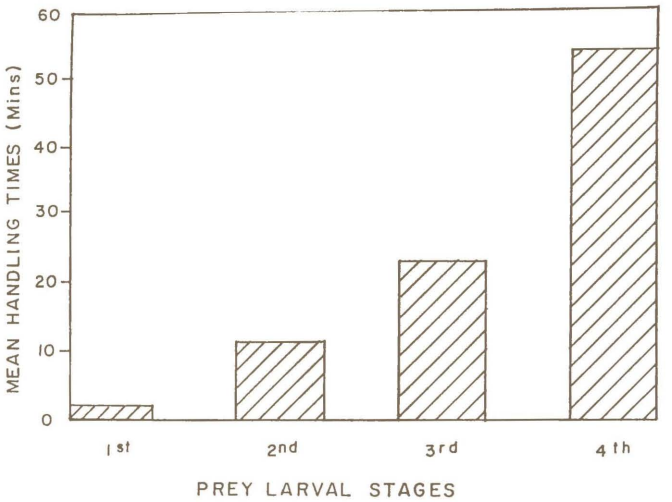

Fig. 28 CHANGES IN HANDLING TIME OF FINAL LARVAL INSTAR OF C. (L) TIGRIPES FEEDING ON DIFFERENT STAGES OF PREY LARVAE

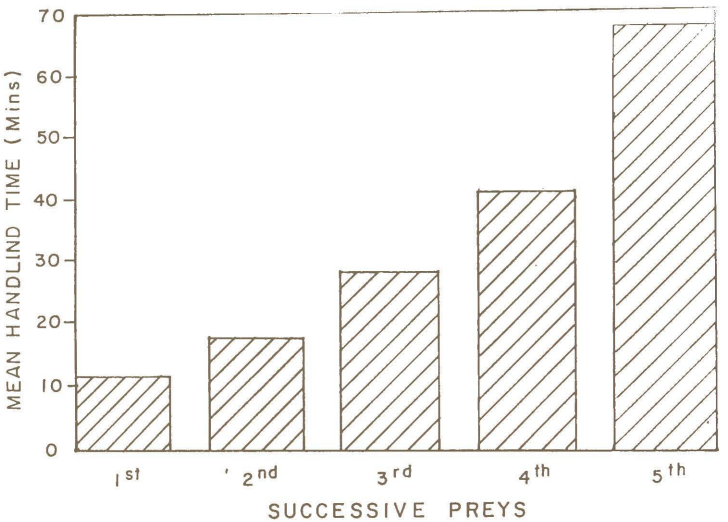

Fig. 29 CHANGES IN HANDLING TIME OF C.(L) TIGRIPES WITH SUCCESSIVE FEEDING ON THE SAME STAGE OF PREY LARVAE

4.3.8 Cannibalism

Table 23 gives the incidence of cannibalism observed in newly emerged 1st-stage larvae of C.(L) tigripes from eggs collected in the field. It indicates that cannibalism occurred within hours after emergence from the eggs; 65.08% (246 out of 378) of the emerged larvae were cannibalised in less than 24 hours. This high rate of cannibalism may be attributed to the fact that in the laboratory there were no prey larvae immediately available. The results of experiments to determine the effect of predator stages on cannibalism are given in Tables 24 and 25. Table 24 indicates that the early (1st and 2nd) stages of the predator readily resorted to cannibalism, compared to the later (3rd and 4th) stages. The mean numbers of C.(L) tigripes larvae cannibalized in the different stages in 24 hours were 18.4 $\pm$ 0.70, 17.4 $\pm$ 1.17, 12.8 $\pm$ 1.62 and 5.9 $\pm$ 1.52 for the 1st, 2nd, 3rd, and 4th- stage larvae respectively, and the difference is highly significant ($P<0.001$). However, the rate of cannibalism among the 1st and 2nd stages were not significantly different. It was observed that the older larval stages, especially the final stage (4th) did not attack each other readily even though they are the most voracious of all the larval stages. It was observed that when a 3rd or 4th stage larva of the predator attacks a member of its own stage, the attacked larva usually manages to free itself of the hold by swimming quickly and violently, except when it is grasped firmly. However, when a small larva is

attacked by a larger member of its own stage it is easily seized and devoured. The long strong hairs on the body of the final instar might probably protect it against cannibalism. When one 4th-stage larva of the predator was exposed to different stages of the predator, it fed more actively on the smaller predators than on the larger ones (Table 25). The smaller predators can therefore serve as food for the larger ones. The 4th-stage larvae does not successfully attack its own pupae as shown by low kill of 0.10 ± 0.31 compared to 19.35 ± 0.79 of first instar larvae. The few pupae killed died out of body injuries inflicted on them by the mandibles of the larvae. The results of the effect of crowding of the larvae on cannibalism are presented in Table 26. It indicates that crowding increases the rate of cannibalism. As stated earlier, if the larvae are at very high densities they are expected to frequently bump into each other and so tend to capture each other more frequently. The mean values of the rate of cannibalism at various levels of crowding are significantly different for both stages tested. Table 27 gives the results obtained on the predatory activity of C.(L) tigripes offered a choice between, its own species and other prey species. The 4th-stage predatory larvae preyed

Table 23 Incidence of cannibalism in the newly emerged 1st-stage larvae of C. (L). tigripes

No. of eggs collected	No. of eggs hatched	No. survived 1st stadium	No. cannibalised	No. of larvae dead
80	77	38	39	0
55	51	21	30	0
100	58	44	14	0
54	44	32	12	0
46	43	19	24	0
78	73	43	27	3
128	128	66	57	5
162	158	115	43	0
Total 703	632	378	246	8
$\bar{X} \pm SD$	79 ± 42.14	47.25 ± 31.11	30.75 ± 15.12	4 ± 1.27
%	89.90	59.81	65.08	2.12

Table 24 Cannibalism among different larval instars of C. (L.) tigripes

No. and stage of lutzia/bowl	No. of trials n	Mean No. killed/24hrs ($\bar{X}$ ± SD)	F
20 1st instar	10	18.4 ± 0.70a	190.68 P<0.001
20 2nd instar	10	17.4 ± 1.17a	
20 3rd instar	10	12.8 ± 1.62	
20 4th instar	10	5.9 ± 1.52	

Numbers followed by the same alphabets are not significantly different (P>0.05 - Duncan's multiple range test)

Table 25 The rate of cannibalism of a 4th-stage C. (L.) tigripes on other stages

No./ bowl	Stage of L. tigripes/ bowl	No of trials	Mean No. killed/24hrs $\bar{X}$ ± SD	F
20	1st	17	19.35 ± 0.79a	234.73
20	2nd	17	18.14 ± 1.86a	P<0.001
20	3rd	17	12.88 ± 2.23	
20	4th	17	5.82 ± 1.42	
20	pupae	15	0.10 ± 0.31	

Table 26 Effect of crowding of larvae of C.(L) tigripes on the rate of cannibalism

Stage of L. tigripes	No. of L. tigripes/ water volume	No. of trials	Mean No. killed/24hrs X ± SD	F
4th	15/15ml	20	8.5 ± 2.59	135.59 P<0.001
	15/30ml	20	5.65 ± 1.09	
	15/60ml	20	2.96 ± 1.36	
	15/120	20	1.20 ± 0 95	
2nd	15/15ml	10	17.2 ± 0.97	139.88 P<0.001
	15/30ml	10	12.9 ± 1.37	
	15/60ml	10	8.7 ± 1.20	
	15/120	10	3.30 ± 2.50	

Table 27 Effect of the presence of mosquito prey larvae on the rate of cannibalism of C. (L) tigripes

No. and stage of L. tigripes	No. and stage of larvae/bowl	No. of trials	Mean No. killed/24hrs X ± SD	T-test
One 4th stage	10 2nd L. tigripes 10 2nd C.quinquefasciatus	22	4.82 ± 1.56 9.27 ± 1.03	11.16 P<0.001
One 4th stage	10 2nd L. tigripes 10 4th C.quinquefasciatus	15	3.67 ± 1.95 8.27 ± 0.80	10.28 P<0.001

more on the Culex prey larvae than on the members of its own species. In the presence of 4th stage prey larvae, more prey were still selected than the smaller species of the predator. These results indicate that C.(L) tigripes larvae will kill more larvae of its own species in the absence of alternative prey larvae, and will kill more of the prey than members of its own species when there is a choice. The presence of alternative prey therefore reduces the rate of cannibalism. Horsfall (1955) reported that C.(L) tigripes larvae are not cannibalistic, and Hopkins (1936) stated that they eat one another with reluctance, in the absence of other food. The present study shows clearly that the larvae of C.(L) tigripes are cannibalistic at all larval stages, even in the presence of other food, although they are less cannibalistic when other preys are present.

CHAPTER 5. GENERAL DISCUSSION AND CONCLUSION

C. Lutzia tigripes show plasticity in the choice of their breeding habitats; they were found to breed in a wide variety of habitats which are also occupied by the larvae of other mosquito species (Table 1). Their preferred habitats are usually sunlit with little vegetation and few known mosquito predators. They seldom breed in small collections of shallow water either on the ground or in tree holes, tins and cans etc. Apart from the fact that such places are more likely to dry up, the water may heat up to high temperatures during the day. The temperatures of all the breeding places were not measured but those measured from a concrete drain, could go as high as 31.1°C during the dry season (Fig.8). Service (1971) observed that small collections of water on the ground which were also the preferred breeding habitats of An. gambiae in Nigeria, could be heated to 40°C. Such high temperatures would definately be lethal to C.(L) tigripes, since the 1st-instars could not develop at 34°C and the 4th-instar larvae and pupae could withstand temperatures of 37°C and 38°C for only 30 minutes respectively (Appendix Table 12). The tendency of small habitats to dry up frequently makes them suitable for species which can complete their development in a relatively short time (Service 1971), so species like C.(L) tigripes which takes about 10 days or more to complete development would be placed at a biological disadvantage, since temporary pools are available for only a short period.

In comparison, developmental duration of Ae. vittatus that inhabits small collections of water (rock holes) in Nigeria was found to be 5-6 days, and it was considered to be longer than expected in a species whose habitats are liable to frequent desiccation (Boorman 1961). In most of the places breeding C.(L) tigripes in the field, mosquito prey larvae were more abundant than the predator (Appendix Table 3), so it appears that the predator larvae could not destroy all of them. However,if one considers that the predator can consume a minimum of about 145 to 229 larvae of various stages before completing its development depending on the temperature, and may sometimes kill more prey larvae in excess of its food requirement, then the possibility of reducing the population of its prey in a habitat is high. The high rate of cannibalism observed in the early stages, particularly, immediately after emergence from the eggs (Tables 23 and 24), may contribute greatly in keeping the population of the predator low.

There was no measurable correlation between the fluctuations in the population of C.(L) tigripes and the variations in the physical and chemical properties measured. This does not mean that the physical and chemical properties measured are not important determinants of C.(L) tigripes breeding site selection, because the development of mosquito larvae under natural conditions does not depend on one but on many factors. The very existence of one factor is often

dependent solely on the presence or absence of another (Senior-White 1946). Smorodinzew and Adowa (1930) showed that there was some correlation between larval incidence of Anopheles maculipennis and pH and calcium content but on studying these factors separately they concluded that Calcium alone had no effect. More data need to be collected to determine the physical and chemical factors which act as the important determinants of a suitable breeding site of C.(L) tigripes.

The shortest developmental duration and the lowest mortality of the immature stages occurred at 30°C. Even though larval development was retarded at 20°C and below and also at 32°C and above, there was sufficient survival to perpetuate the populations. The ability of C.(L) tigripes to survive and develop at varying rates in such a wide range of temperatures is a favourable attribute to a predator whose preferred food are mosquito larvae. The prolongation of larval life at temperatures above and below the optimum again enables the predators to consume more preys (Table 13), thus increasing the impact of predation on the prey population. The effect of temperature on the rate of development and the predaceous behaviour shows that the development of larvae and pupae of C.(L) tigripes can be speeded up during colonization in the laboratory without increasing mortality and the quantitative effect of the preys. Non-living diets used to rear the predator were not suitable, but since one larva

reared on milk casein was able to develop to the adult stage, this suggests that even though mosquito larva is the most preferable food for development, further studies should be carried out to evaluate other diets for economic rearing of this species. This study again suggests that the predator larvae can survive relatively long periods in a habitat without prey, and may be a favourable attribute if the predator is the first to appear in the habitat.

The studies on the predatory activities of C.(L) tigripes show that they do not search for their prey, but lie in ambush until the prey becomes available. The level of predation achieved by the predator in any locality will therefore depend to a large extent on their occurrence in the same breeding places with the prey, and on the densities of the predator and prey. Since mosquito larvae are usually the most common arthropods present in the predator's natural habitats, they are presumed to be their chief prey and this has been confirmed by the preferential feeding tests (Table 19). In general, the predation rate of C.(L) tigripes increases with increase in the size of the predator and prey density and also with a decrease in the prey size. There were large day to day variability in the consumption of prey at all densities, but this variability seems to characterise other invertebrate predators as well (Padgett and Focks 1980, Trimble and Smith 1978). The results on predatory activities also suggest that if C.(L) tigripes occurs in the same habitat with other

mosquito larvae which develop faster than the predator, then a large larval population could conceivably not be greatly suppressed by the C.(L) tigripes population, because the predation rate even though increases with increase in prey density, its magnitude diminishes from low to high prey density (Fig. 22). Many predaceous larval arthropods have important limitations as potential regulators of prey density, because their generation times, compared to those of their prey, are often too long to permit an effective numerical response to short-term changes in prey density (Holling 1959a, 1966).

The type of prey selected has been shown to depend on a number of factors including mobility, size, posture, the density and the extent to which prey and predator occur in the same habitat. The prey killed in nature will depend also on which stages of both prey and predator occur simultaneously in the same habitat. Palatability of a prey may also influence prey selection but in this study it was assumed that all the prey species offered were equally palatable since all were consumed (see section 4.3.4.1). Predation on prey pupae shows that the size of the pupa together with its ability to swim powerfully, its spherical shape and the posture in water enable the pupa to evade predation by C.(L) tigripes. The handling capacity of the predator is also an important factor which can influence prey selection. The prey captured by mantids is partly determined by the handling capacity of the

predator's grasping forelegs (Holling 1966). However, when two prey species of almost equal size (Culex and chironomid larvae) were offered to C.(L) tigripes, the Culex was preferentially preyed upon suggesting that other factors also come into play during prey selection. Chironomid larvae spend most of their time resting on the bottom of the water usually in tubes, surfacing only occasionally to replenish their oxygen supply, so they are not as vulnerable to C.(L) tigripes as mosquito larvae which rest at the surface and move up and down the water frequently. The normal activities of a prey species must bring it near C.(L) tigripes for the latter to prey upon it. This is confirmed by the apparent preference of C.(L) tigripes for Ae. aegypti to An. gambiae and C. quinquefasciatus, and also the preference of C. quinquefasciatus mosquito to chironomid, and larvae to pupae. Ae. aegypti was found to move more frequently in water than either C.quinquefasciatus or An. gambiae and moreover, Ae. aegypti larvae usually spend a long time crawling at the bottom of water browsing for food. These normal activities of the larvae make them more vulnerable to predation by the C.(L) tigripes. Because there are many variables involved in prey selection, the laboratory results may only approximate what occurs in the field.

C.(L) tigripes exhibited wasteful killing behaviour to some extent but they do not kill all the prey which share the same container with them. Thus it seems this behaviour of

killing more prey than required for consumption may be due to other reasons but not necessarily to ensure the survival of their pupae as postulated by Corbet and Griffiths (1963). Compartmentalized processing of food in the gut, and regeneration of the peritrophic membrane are characteristics of arthropods physiology (Campbell and Brunstock 1968) and it has been further shown by photographic documents of gut contents of damselfly naiads that during feeding, the foregut often becomes full before the midgut, leading to the hypothesis that wasteful killing occurs when hunger in the midgut motivates capture but, fullness of the foregut precludes eating (Johnson et al 1975). This hypothesis may also explain the killing behaviour in C.(L) tigripes. When wasteful killing is a normal component of hunger - motivated feeding behaviour, it has sometimes also been explained by hypothesizing the existence of a hunger threshold which is higher for eating than for capture.

Morphologically, C.(L) tigripes is well equipped to capture, manipulate and quickly subdue its prey. The mandibles are well developed with sharp claws and spines and they are the main prehensile organs, supported by specialised mouth brushes which are highly sclerotized with serrated lamellae. Preys are usually captured from two locations, at the surface and at the bottom of the water. The predator usually changes its normal posture after capturing its prey, so that the victim becomes submerged in the water and cannot

REFERENCES

Bates, M. (1941) Field studies of the anopheline mosquitoes of Alabama, Proc. ent. Soc. Wash. **43**: 37-58

Bates, M. (1965) The Natural History of Mosquitoes. Harper and Row, New York 379pp.

Beattie, M.V.F (1932) The physico-chemical factors of water in relation to mosquito breeding in Trinidad. Bull.ent. Res. **23**: 477-496.

Beddington,J.R., Hassell, M.P.and Lawton,J.H.(1976) The components of arthropod predation. II The predator rate of increase. J. Anim. Ecol. **45**: 165-85

Beirne, B.P.C. (1962) Trends in applied biological control of insects. Ann. Rev. Ent. 7:387-400

Beukema, J.J. (1968) Predation by three - spined stickle back (Gasterosteus aculeatus L.): The influence of hunger and experience. Behaviour **31**: 1- 125

Blunck, H. (1924) Die Entwicklung des Dytiscus marginalis L. Vom E. bis zur image II. Die Metamorphose. Z. Wiss Zool. **121**: 171-191

Boorman, J.P.T. (1961) Observations on the habits of mosquitoes of Plateau Province, Northern Nigeria, with particular reference to Aedes (Stegomyia) vittatus (Bigot). Bull.ent.Res. **52**:707-725

Boyd, M.F. (1949), Malariology. A comprehensive survey of all aspects of this groups of diseases from a global standpoint. W.B. Saunders, Co. London. Volume 1

XXI+787pp.

Breland, O.P. (1949) The biology and the immature stages of the mosquito Megarhinus septentrionalis Dyar and Knob. Ann. ent. Soc. Amer. **42**: 38-47

Brett. J.R. (1971) Satiation time, appetite, and maximum food intake of Sockeye Salmon (Oncorhynchus nerka). J. Fish Res. Bd. Canada. **28**: 409-415.

Brett, J.R. and Higgs, D.A. (1970) Effect of temperature on the rate of gastric digestion of fingerling sockeye salmon. Oncorhynchus nerka J. Fish. Res. Bd. Canada. **27**: 1767-1779

Brust, A.R. (1967) Weight and development time of different stadia of mosquitoes reared at various constant temperatures. Can. Entomol. **99**: 986-993

Buxton, P.A (1934) Further studies upon chemical factors affecting the breeding of Anopheles in Trinidad Bull. ent. Res. **25**: 491-494

Campbell, G. and Brunstock, G. (1968) Comparative physiology of gastrointestinal motility. In. C.F. Code (ed) Handbook of Physiology. Sect. **6**:101 IV: 2213-66

Chan,K.L.(1968) Observations on Toxorhynchites splendens (Wiedemann) in Singapore. Mosq. News **28**: 91-95

Chinery, W.A. (1969) A survey of mosquito breeding in Accra, Ghana, during a two year period of larval mosquito control. I- The mosquitoes collected and their breeding places. Ghana Med. J. **8**: 266-274

Chinery, W.A. (1970) A survey of mosquito breeding in Accra, Ghana, during a two-year period of larval mosquito control. II - The breeding of Culex (Culex) pipiens fatigans Wiedmann and Anopheles (Cellia) gambiae Gilles, in Accra . Ghana Med.J. **9**:109-116

Chiszar, D. and Windell, J.T. (1973) Predation by bluegill sunfish, (Lepomis macrochirus rafinesque) upon mealworm larvae (Tenebrio molitor). Anim. Behaviour **21**:536-543

Christensen, and K. Rowley, F.C. (1978) A study of mosquito behavior. An experimental laboratory study of Aedes communis (Deg.) Diptera:Culicidae. Amer. Midland Natur. **40**: 365-270

Christophers, S.R. (1960) Aedes aegypti (L) The Yellow Fever Mosquito. It's life history, bionomics and structure. Cambridge University Press. vii + 736 pp.

Christophers, S.R.(1945) Structure of the Culex egg and egg raft in relation to function (Diptera). Trans. Roy. ent. Soc.Lond. **95**: 25-34

Coker, W.Z.(1989) The medical entomologists contribution towards health for all by the year 2000. An inaugural lecture delivered at the University of Ghana, Legon.

Colless, D.H. and Chellapah, W.T. (1960) Effects of body weight and size of blood-meal upon eggs production in Aedes aegypti (l) (Diptera: Culicidae). Ann.trop. Med. Parasit. **54**:475-482

Coluzzi M. (1964) Maintenance of Laboratory Colonies of

Anopheles Mosquitoes. Bull. W.H.O. 31:441-443

Connel, J.H. (1961) Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides Ecol. Monogr. 31: 61-104

Corbet, P.S. (1963) Observations on Toxorhynchites brevipalpis conradti Grunb in Uganda. Bull ent. Res. 54:9-17

Corbet, P.S., Griffiths, A.(1963) Observations on the aquatic stages of two species of Toxorhynchites in Uganda. Proc. R. ent. Soc. London. Ser. (A) 38:125-35

Crans, W.J. and Slaff, M.E. (1977) Growth and behavior of colonized Toxorhynchites rutilus septentrionalis. Mosq. News. 37: 207-11

De Meillon B. (1947) The Anophelines of the Ethiopian Geographical Region (S. Afr. Inst. for Med. Res.) 272 pp.

Deevey, E.S. (1947) Life tables for natural populations of animals. Quart. Rev. Biol. 22: 283-314.

Dempster, J.P. (1960) A quantitative study of the predators on the eggs of larvae of the broom beetle. Phytodecta olivacea Forster, using the precipitin test. J. Anim. Ecol. 29: 149:167

Dickson, K.B. and Benneh, G. (1970) A New Geography of Ghana. Longman group. London. 173 pp.

Dixon, A.F.G. (1959) An experimental study of the searching

behaviour of the predatory coccinellid beetle Adalia decenpunctata (L) J. Anim. Ecol. **28**: 259-81

Ellis, R.A. and Borden, J.H. (1970) Predation by Notonecta undulata (Heteroptera: Notonectidae) on larvae of the yellow fever mosquito. Ann.ent.Soc. Amer. **63**: 963-973

Elson P.F. (1962) Predator- Prey relationships between fish-eating birds and and Atlantic salmon. Bull. Fish. Res. Bd. Can. **133**: 1-87

Focks,D.A.,Seawright,J.A.and Hall,D.W.(1978) Laboratory rearing of Toxorhynchites rutilus rutilus (Coquillett) on a non-living diet. Mosq. News **38**: 325-328

Foerster, R.E. and Ricker, W.E. (1941) The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus lake. J. Fish. Res. Bd. Can. **5**: 315-336

Fowler, H.W. (1972) Rates of insemination by induced copulation of Aedes vexans (Diptera: Culicidae) treated with three anaesthetics. Ann. ent. Soc. Amer. **65**: 293-6

Furumizo. R.T. and Rudnick, A. (1978) Laboratory studies of Toxorhynchites splendens: Biological observations. Ann. ent. Soc. Amer. **71**: 670-73

Gendre, E. (1909) Bull. Sco. Path. Exot. 2: 147-150

Gibb, J.A. (1958). Predation by tits and squirrels on the eucosmid Ernarmonia conicolana (Heyl). J. Anim. Ecol. **27**: 375:396

Gibbons, E.G. (1932) A note on the relative size of the anal gills of mosquito larvae in salt and freshwater. Ann. trop. Med. and Parasit. **26**: 551-554

Gillett, J.D. (1971) Mosquitos. The World Naturalist, Weidenfeld and Nicolson, London. 244 pp.

Gillett, J.D.(1972) Common African Mosquitoes and Their Medical Importance. William Heinemann Medical Books Ltd.London. 105pp.

Gillies, M. T & De Meillon, B. (1968). The Anophelinae of Africa South of the Sahara (Ethiopian zoogeographical region) - 2nd edn. Publs. S. Afr. Inst. Med. Res. 54, 343 pp.

Haddow, A.J. (1942) A note on the predatory larva of the mosquito Culex (Lutzia) tigripes Granpre & Charmoy (Diptera) Proc. R. Ent. Soc. London (A) **17**: 73-74

Hancock, D.A and Urquhart, A.E. (1965) The determination of natural mortality and its causes in an exploited population of cockles (Cardium edule L) Fish Invest. Lond. **1124**. (2): 1-40.

Harris,W.V.(1942) Notes on Culicine mosquitoes in Tanganyika territory. Bull.ent.Res. **33**: 181-193

Hassell, M.P., Lawton, J.H. and Beddington, J.R. (1976) The components of arthropod predation. I. The prey death rate. J. Anim. Ecol. **45**:135-164

Hassell, M.P. and May R.M. (1973) Stability in insect host-parasite models. J. Anim. Ecol. **42**: 692- 726

Hati, A.K. and Ghost, S.M. (1965) Laboratory studies on the predaceous habits of the dragonfly nymph (Brachytron pratenuse) on diptera prey. Bull. Calcutta Sch. trop. Med. **13**: 61-62

Haufe, W.O. (1957) Physical environment and behaviour of immature stages of Aedes communis (Deg.) (Diptera: Culicidae) in sub-arctic Canada. Can. Ent. **89**:120-139

Hinman, E.H. (1934) Predators of the Culicidae (mosquitoes) I. The predators of the larvae and pupae, exclusive of fish. J. trop. Med. Hyg. **37**: 145-150

Hiyama,Y., Nose,Y., Shimizu,M., Matsubara,J., Onodera,K., Kodama,Y.and Suzuki,N. (1960) Predation on rainbow trout fry traced by radioisotope. Bull. Jap. Soc.-Scient. Fish. **26**:863-867

Holling, C.S. (1959a) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Ent. **91**: 293-320

Holling, C.S. (1959b) Some characteristics of simple types of predation and parasitism. Can. Ent. **91**: 395-398

Holling, C.S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. Mem. entomol. Soc. Can. **45**: 1-60.

Holling C.S. (1966) The functional response of invertebrate predators to prey density. Mem. entomol. Soc. Can. **48**: 1-86

Hopkins G.H.E. (1952) Mosquitoes of the Ethiopian Region I.

Larval bionomics of mosquitoes and taxonomy of culicine larvae, 2nd ed. London Brit. Mus. (Nat. Hist.) 355 pp.

Horsfall, W.R. (1955) Mosquitoes: Their bionomics and relation to disease. 1st Ed. Constable and Co. London. 723pp.

Horsfall, W.R. and Taylor, M.C. (1967) Temperature and age as factors in inducing insemination of mosquitoes (Diptera: Culicidae). Ann. ent. Soc. Amer. **60**: 118-120

Horton, P.A. (1961) The bionomics of brown trout in a Dartmoor stream. J. Anim. Ecol. **30**: 311-338

Howard, L.O. (1910) The mosquitos of South Western America and the West Indies. A preliminary report No 32A (Carnegie Institution, Washington)

Ikeshoji, T. (1966) Bionomics of Culex (Lutzia) fuscanus. Japan J. expt. Med. **36**:321-334

Irving-Bell, R.J., Okoli, E.I., Diyelong, D.Y., Lyimo, E.O. and Onyia, O.C. (1987) Septic tank mosquitoes: Competition between species in central Nigeria. Medical and Veterinary Entomol. **1** (3):243-250.

Iynegar, M.O.T. (1920) Preliminary report of a malaria survey of Calcutta and environs. Rev. Appl. Ent. **9**: 124-8

Johnson, D. M., Akre, B.G. and Crowley, P. H. (1975) Modelling arthropod predation, wasteful killing by damselfly naiads, Ecology, **56**: 1081- 93

Kennan, R.H. (1915) Report of the Senior Sanitary Officer.

(Ann. Rep. Med. Dept. Sierra Leone for the year ending 31st December 1914) pp, 83-112

Kirk, R. (1941) An epidemic of yellow fever in the Nuba mountains, Anglo-Egyptian Sudan. Ann. of trop. Med. Parasit. **35**: 67-112

Knight, F.B. (1958) The effects of woodpeckers on populations of the Engelmann spruce beetle. J. econ. Ent. **51**: 603-607

Knight, K.L. (1964) Quantitative methods for mosquito larval surveys. J. med. Entomol. **1**:109-115

Koch, H.J. (1938) The absorption of chloride ions by the anal papillae of Diptera larvae. J. exp. Biol. **15**: 152-160

Laird, M. (1946) Some natural enemies of mosquitoes in the vicinity of Palmalwal, New Britain. Trans. roy. Soc. New Zealand. **79** (3): 453-476.

Lawton, J.H., Hassell, M.P. and Beddington, J.R (1975) Prey death rates and rate of increase of arthropod predator populations. Nature, Lond. **255**: 60-62

Lea, A.O.and Edman,J.D.(1972) Sexual behavior of mosquitoes.3 Age dependence of insemination of Culex nigripalpus and C. pipiens quinquefasciatus in nature. Ann. ent. Soc. Amer. **65**:290-293

Lea, A.O. and Evans D.G. (1972) Sexual behavior of Mosquitoes. 1. Age dependence of copulation and insemination in the Culex pipiens complex and Aedes

taeniorhynchus in the laboratory. Ann. ent. Soc. Amer. 65: 285-289

Lee. F.C. (1967) Laboratory observations on certain mosquito larval predators. Mosquito News 27: 323-328

Lewis, D.J. (1947) General observations on mosquitoes in relation to yellow fever in the Anglo-Egyptian Sudan. Bull ent. Res. 37: 543-566

Lounibos, L.P. (1979). Temporal and spatial distribution, growth and predatory behaviour of Toxorhynchites brevipalpis (Diptera: Culicidae) on the Kenya Coast. J. Anim. Ecol. 48: 213-236

Lumsden, W.H.R. (1951) The night-resting habits of monkeys in a small area in the edge of the Semliki Forest, Uganda. A study in relation to the epidemiology of sylvan yellow fever. J. Anim. Ecol. 20: 11-32

Lumsden, W.H.R. (1952) The crepuscular biting activity of insects in the forest canopy in Bwanba Uganda. A study in relation to the sylvan epidemiology of yellow fever. Bull. ent. Res. 42: 721-760

Macan, T.T. (1965) Predation as a factor in the ecology of water bugs. J. Anim. Ecol. 34: 671-698

Macfie, J.W.S. and Ingram, A. (1916) The domestic mosquitoes of Accra. Bull. ent. Res. 7: 161-178

Macfie,J.W.S. and Ingram,A. (1923) The early stages of West African mosquitoes VI. Bull. ent.Res. 13:409-442

MacGregor, M.E. (1927) Mosquito Surveys - A handbook for

anti-malarial and anti - mosquito field workers. Wellcome Bureau of Scientific Research London. 293 pp.

Maclellan, C.R. (1959) Woodpeckers as predators of the Codling Moth in Nova Scotia. Can. Ent. **91**: 673-680

Mathavan, S. (1976) Satiation time and predatory behaviour of the dragonfly nymph Mesogomphus lineatus. Hydrobiologia **50**: 55-64

Mattingly, P.F. (1969) The Biology of Mosquito-Borne Disease. George Allen and Unwin, viii + 184pp.

Mead, .A.P (1980) A dreadful way to die - a new mosquito killer. Overseas Universities No. 27: 9-17

Miner, R.W. (1955) Regulation of hunger and appetite. Ann. N.Y. Acad. Sci: **63**: 15-43

Ministry of Health (1980)- Ten year report of the Epidemiology Division. Surveillance of communicable diseases in Ghana, 1969-1979.

Morrow, R.H. Smith, P.C. and Nimo, K.P. (1981). A quantitative method of assessing the health impact of different diseases in less developed countries. Int. J. Epidem. **10** : 73-80

Murdoch, W. and Oaten, A. (1975) Predation and population stability. Adv. ecol. Res. **9**:1-125

Muspratt, J. (1951) The bionomics of an African. Megarhinus and its possible use in biological control. Bull. ent. Res. **42**: 355-70

Nakamura, K. (1977) A model for the functional response of a predator to varying prey densities based on the feeding ecology of wolf spiders.
Bull. Nat. Inst. Agri. Sci. Ser. (C) **31**: 29-89

National Acadamy of Sciences (1973) Mosquito Control: Some perspectives for developing countries. Nat. Acad. Sci. Washington. D.C. 64 pp.

Nielsen, E.T. and Haeger, J.S. (1954) Pupation and emergence in Aedes taeniorhynchus (Wied).
Bull. ent. Res. **45**: 757-768

Nieschulz, O.,Bedford, G.A.H. and Du Toit,R.M. (1934) Results of a mosquito survey at Onderstepoort. Onderstepoort. Journ. vet. Sci. and Anim. Industry. **3**: 43-77

Nijhout,H. F.(1975) A threshold size for metamorphoses in the tobacco hookworm, Manduca sexta.
Biological Bull. **149**: 214-225

Nnakumusana, E.S. (1985) Susceptibility of mosquito larvae to Coelomomyces indicus
Indian J. of med. Res. **82**: 316-320

Padgett, P.D. and Focks, D.A. (1980) Laboratory observations on the predation of Toxorhynchites rutilus rutilus on Aedes aegypti (Diptera-Culicidae)
J. med. Entomol. **17**: 466-472

Pal, R. ard Ramalingam, S. (1981) Invertebrate predators of mosquitoes WHO/VBC/81 799 18 pp.

Pandian, T.J. (1967) Intake, digestion, absorption and conversion of food in the fishes, Megalops cyprinoides and Ophiocephalus striatus. Mar. Biol. 1: 16-32

Pearson, O.P. (1966) The prey of carnivores during one cycle of mouse abundance. J. Anim Ecol. 35: 217-233.

Petreisceva, P.A. and K.P.Cagin (1947) Some observations on Lutzia vorax, Edwards Zoologiceskij Zurnal, 26: 293.

Prakash, R.N and Ponniah, A.G. (1978) Predatory behaviour of Lutzia on Culex fatigans. Hydrobiologia 57:159-162

Rajasekaran, P.T. and Chowdiah, B.W. (1972). Biological markers in feeding experiments of mosquito larvae (Culex (Lutzia) raptor). Experimentia 28: 981-982

Reddy, S.R. and Pandian, T.J. (1974a) Effect of volume of water on predatory efficiency of the fish, Gambusia affinis Curr. Sci. 42: 644-645

Reddy, S.R. and Pandian, T.J. (1974b) Effect of water current on the predatory efficiency of Gambusia affinis. Oecologia 16: 253-256

Reiter, P. (1978) The influence of dissolved oxygen content on the survival of submerged mosquito larvae. Mosq. News. 38: 334-337

Rogers D.J. (1972) Random search and insect population models. J. Anim. Ecol. 41: 369-383

Russell, P.F., West L.S., Manwell, R.D and Macdonald, G. (1963). Practical Malariology. Oxford University Press, London. xiv + 750 pp.104.

Russo, R. (1985) Surplus killing patterns of Toxorhynchites. Proc. 2nd Annual meeting N.J. Mosquito Control Assoc. Inc. Atlantic City N.J. pp. 182-187

Sailer, R.I. and Lienk, S.E. (1954) Insect predators of mosquito larvae and pupae of Alaska. Mosquito News **14**: 14-16

Sasa, M. (1950) Mosquitoes in Japan (Nippon no. ka). Japan DDT Assoc. Tokyo p. 40

Senior-White, R. (1926) Pysical factors in mosquito ecology Bull. ent. Res. **16**: 187-248

Serie, C. (1968) Etudes sur la fievre jaune en Ethiopie. Bull. W.H.O. **38**: 879-884

Service, M.W. (1971) Studies in sampling larval populations of the Anopheles gambiae complex. Bull. W.H.O. **45**: 169-180

Service, M.W. (1973), Mortalities of the larvae of the Anopheles gambiae complex and detection of predators by the precipitin test, Bull. ent. Res. **62**: 359-369

Service, M.W. (1976) Mosquito Ecology Field Sampling Methods. Applied Science Publishers Limited, London. 583pp

Service, M.W. (1990), Handbook to the Afro-tropical toxorhynchitine and culicine mosquitoes excepting Aedes and Culex. British Museum (Natural History) London - 207pp.

Shimizu, M., Matsubara, J. Onodera, K. Kodama, Y. and

Suzuki, N. (1960) Predation on rainbow trout fry traced by radio-isotope
Bull. Jap. Soc-Scient. Fish. **26**: 863-71.

Sinha, V.P. (1976), Further observations on the physico-chemical factors of the breeding places of Culex quinquefasciatus Say = fatigans Wied.
Mosq. News **36**: 358-360

Smith, B.D. (1966) Effects of parasites and predators on a natural population of the aphid Acyrthosiphon spartii (Koch) on broom (Sarothamnus scoparius L.)
J. Anim. Ecol. **35**: 255-267

Smithburn, K.C., Haddow, A.J.and Lumsden, W.H.R. (1949) Outbreak of sylvan yellow fever with Aedes (Stegomyia) africanus. Theobold as principal vector and insect host of virus. Ann. trop. med. parasit. **43**: 74-89

Smorodinzew, I.A. and Adowa, A.N. (1930) The role of calcium in the ecology of Anopheles larvae.
Bull. Soc. Path. Exot. **23**: 34-43

Snow, W.F. (1978) The host feeding of some culicine mosquitoes (Diptera: Culicidae) in The Gambia.
Bull. ent. Res. **68**: 695-706

Snow, W.F. (1983) The attractiveness of some birds and mammals for mosquitoes in The Gambia, West Africa,
Ann. Trop. Med. Parasit. **77**: 641-651

Snow, W.F. and Boreham, P.F.C. (1973) The feeding habits of some West African Culex (Diptera: Culicidae)

mosquitoes. Bull. ent. Res. 62: 517-526

Solomon,M.E.(1949). The natural control of animal populations J. Anim. Ecol. 18: 1-35

Someren, Van G.R.C. (1943) Notes on the mosquitoes of British Somaliland. Bull ent. Res. 34: 323-328

Southwood,T.R.E. (1966).Ecological Methods With Particular Reference To The Study Of Insect Populations. Methuen, London, xiv + 391 pp.

Southwood, T.R.E., Murdie, G., Yasuno, M., Tonn, R.J. and Reader, P.M. (1972). Studies on the life budget of Aedes aegypti in Wat Samphaya, Bangkok, Thailand. Bull. Wld. Hlth. Org. 46: 211-226

Standard Methods For The Analyses Of Water And Sewage (1975) American Public Health Association, New York 12th ed.

Surtees,G. (1959) Functional and morphological observations of the larval mouthparts in the subfamily Culicinae (Diptera) with a review of some related studies by Montschadsky. Proc. Roy. ent. Soc. (A) 34: 7-16

Swift, M.C. and Fedorenko, A (1975) Some aspects of prey capture of Chaoborus larvae. Limnology and Oceanography 20: 418-425

Thompson, W.R. (1948) Observations of the mating behavior of Culex vexans (Diptera: Culicidae) Can. Entomol. 52:261-72

Thompson, D.J. (1975) Towards a predator-prey model incorporating age-structure: The effects of predator

and prey size on the predation of Daphnia magna by Ischnura elegans. J. Anim. Ecol. **44**: 907-916

Tinbergen, L. (1960) The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Arc. Neevl. Zool. **13**: 265-336

Toth, R.S. & Chew, R.M. (1972) Development and energetics of Notonecta undulata during predation of Culex tarsalis. Ann. ent. Soc. Amer. **65**: 1270-1279

Trimble, R.M. and Corbet P.S. (1975) Laboratory colonization of Toxorhynchites rutilus septentrionalis.(Diptera: Culicidae) Ann. ent. Soc. Amer. 217-219

Trimble, R.M. and Smith, S.M (1978) Geographic variation in development time and predation in the tree hole mosquito. Toxorhynchites rutilus septentironalis. Can. J. Zool. **56**: 1256-65

Trpis, M.(1970) Effect of constant temperature on the larval development of Aedes vexans (Diptera: Culicidae) Can. Entomol. **102**: 1048-51

Trpis, M. (1972). Development and predatory bahaviour of Toxorhynchites brevipalpis in relation to temperature. Environ. Entomol. **1**: 537-546.

Trpis, M. and Shemanchuk,J.A. (1969). The effect of temperature on pre-adult development of Aedes flavescens (Diptera: Culicidae) Can. Entomol. **101**: 128-132.

Trpis, M. and Shemanchuk,J.A. (1970). The effect of

constant temperature on the larval development of Aedes vexans. Can. Entomol. **102**: 1048-1051

Turnball, A.L. (1960) The prey of the spider Linyphias triangularis, (Clerk) (Araneae: Linyphidae) Can. J. Zool. **38**: 859-73

Varley, G.C. and Gradwell, G.R. (1970) Recent advances in insect population dynamics. Ann. Rev. Ent. **15**: 1-24

Vyas - Patel, N. (1988) Parasitism of Kenyan mosquito larvae (Diptera: Culicidae) by Romanomermis culicivorax (Nematoda: Hemithidae). J. of Nematology **20**: 96-101.

Ware, D.M. (1972) Predation by rainbow trout (Salmo gairdneri): the influence of hunger, prey density, and prey size, J. Fish. Res. Bd. Canada, **29**: 1193: 1202

W.H.O. (1967) Scientific Group on Mosquito Ecology. Technical, Rep. Ser. No. 368 World Health Organization. Geneva.

W.H.O. (1975) Manual on Practical Entomology in Malaria part II methods and techniques. World Health Organization. Geneva. 191 pp.

W.H.O. (1985) Tropical diseases research. 7th Programme, Report on malaria . Geneva

W.H.O. (1986) - Prevention and control of yellow fever in Africa. World Health Organization, Geneva. 94 pp.

W.H.O. (1990) Tropical diseases in media spotlight. TDR News No. 31 page 3

Wigglesworth, V.B. (1933) The effects of salts on the anal gills of the aquatic larva; the adaptations of mosquito larvae in salt water. J. exp. Biol. **10**: 1-37.

Wijngaarden, A. Van and Morzer Bruyns, M.F. (1961) Mustela erminea L., van Terschelling The ermines, Mustela erminea L., of Terschelling Lutra **3** : 35-42

Windell, J.T. (1967) Rates of digestion in fishes. In Gerking SD. ed., Biological Basis of Freshwater Fish Production. pp. 151-173 Blackwell Scientific Publications, Oxford.

Woke, P.A., Ally, M.S and Rosenberger, C.R. (1956). The numbers of eggs developed related to the quantities of human blood ingested in Aedes aegypti (Diptera: Culicidae) Ann. ent. Soc. Amer. **49**: 35-41

Wolda, H. (1961) Response decrement in the prey - catching activity of Notonecta glauca (L) (Hemiptera). Arch. Neer. Zool. **14**: 61-89

Young, A.M. (1967) Predation in the larvae of Dytiscus marginalis (L) (Coleoptera: Dytiscidae) Pan-Pac. Entomol. **43**: 113-7

Appendix Table 1 Data form for extensive Survey of Predatory Mosquitoes C. (L.) tigripes

Date: Time:
Location:
Breeding Sites:
Description of breeding sites:

1. (a) Permanent
   (b) Temporary

2. (a) Natural
   (b) Artificial water

3. (a) Stagnant water
   (b) Flowing water

4. (a) Clean water
   (b) Unclean water

5. (a) Shaded
   (b) Not shaded

6. (a) Vegetation in water
   (b) No vegetation in water

7. (a) Lutzia larvae present
   (b) No. of Lutzia
   (c) Lutzia larvae absent

8. (a) Other mosquitoes preser
   (b) Other mosquitoes absent

9. (a) Species of mosquitoes present
   (b) No. of species

10. (a) Other predators present
    (b) Other predators absent

11. Type of present predators

12. Physico-chemical factors of water
    (a) Temperature
    (b) pH

13. Remarks

Appendix Table 2 Data Form for intensive survey of a predatory mosq
C. (L.) tigripes

SITE: DATE:
TIME:

Temp °C pH

A. Lutzia
1. Egg count: (a) No./raft (b) Total # of Eggs
2. Larval stage count
(a) 1st stage (b) 2nd stage
(c) 3rd stage (d) 4th stage
3. Pupal count:
(a) # of Pupae (b) Pupa exuviae

B. Other Mosquitoes: Name:
1. Egg count: (a) No./raft (b) Total # of Eggs
2. Larval stage count
(a) 1st stage (b) 2nd stage
(c) 3rd stage (d) 4th stage
3. Pupal count:
(a) # of Pupae (b) Pupa exuviae

C. Other Mosquitoes:
1. Egg count: (a) No/raft (b) Total # of Eggs
2. Larval stage count
(a) 1st stage (b) 2nd stage
(c) 3rd stage (d) 4th stage
3. Pupal count:

(a) # of Pupae (b) Pupa exuviae

Appendix Table 3 Numbers of C. (L). tigripes and other mosquito larvae collected in the extensive survey

Species	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	TOTAL	%
C. (L) tigripes	70	95	110	88	43	25	55	37	12	25	42	10	612	2.50
C.quinquefasciatus	825	1254	1850	1600	1374	1010	1220	946	214	214	340	135	11240	47.06
An. gambiae	80	215	520	325	255	220	370	310	129	216	268	40	2948	12.35
Ae. aegypti	210	490	800	1030	573	632	800	210	94	307	200	54	5400	22.61
Ae. vittatus	67	137	210	331	207	101	97	67	54	175	183	40	1669	6.99
C. univittatus	96	60	107	133	54	68	105	71	42	95	91	0	922	3.86
C. decens	62	95	103	96	37	75	54	28	0	19	30	7	606	2.54
C. thalassius	5	20	24	45	21	50	73	31	0	13	15	0	297	1.24
C. duttoni	0	12	21	30	11	10	45	30	8	0	17	2	186	0.78

Appendix Table 4 Frequency distribution of C. (L.) tigripes from a man hole (Site A) and a concrete drain (Sites B)

Extensive Survey

SITE A		SITE B	
No. of larvae/dip	No. of dips	No. of larvae	No. of dips
0 - 3	519	0 - 3	472
4 - 7	73	4 - 7	69
8 - 11	22	8 - 11	29
12-15	6	12 - 15	10
16-19	6	16 - 19	4
20-23	5	20 - 23	3
24-27	1	24 - 27	1
28-31	0	28 - 31	1
32-35	1	32 - 35	0
Mean (X)	2.75	Mean (X)	2.87
Variance (s^2)	12.01	Variance (s^2)	11.71
$s^2 > X$		$s^2 > X$	
P (X_2) < 0.001		P (X_2) < 0.001	

	Pupa	4	139	13	0
	Eggs	18	3946	0	0
	Total	80	5589	29	1
Oct.	I	50	3811	0	0
	II	12	1616	0	0
	III	0	1017	0	6
	IV	13	1404	1	1
	Pupa	6	650	0	0
	Eggs	232	6097	0	0
	Total	313	14,595	1	7
Nov.	I	84	867	0	0
	II	15	550	0	0
	III	29	508	0	0
	IV	28	985	0	0
	Pupa	22	176	0	0
	Eggs	315	2948	0	0
	Total	493	6034	0	0
Dec.	I	17	784	0	0
	II	22	635	0	0
	III	26	976	0	0
	IV	38	724	0	0
	Pupa	21	125	0	0
	Eggs	183	760	0	0
	Total	317	4004	0	0
Jan. '90					
	I	46	1033	6	0
	II	6	802	0	0
	III	2	459	0	0
	IV	41	557	6	0
	Pupa	11	290	0	0
	Eggs	294	3386	0	0
	Total	400	6527	12	0
Feb.	I	6	299	0	0
	II	8	199	0	0
	III	12	296	0	0
	IV	25	698	0	0
	Pupa	10	624	0	0
	Eggs	0	2104	0	0
	Total	61	4220	0	0
March	I	34	868	0	0
	II	21	761	2	0

III	4	301	0	0
IV	23	692	0	0
Pupa	15	366	12	0
Eggs	82	2783	0	0
Total	179	5771	14	0

Appendix Table 6 The number of various species and stages of mosquito larvae collected from a concrete drain (Site B)

Month	Immature stages	lutzia	Culex spp.	Aedes spp.	Anopheles spp
April '89	I	33	72	68	0
	II	27	231	175	0
	III	4	30	98	0
	IV	20	150	97	0
	Pupa	2	25	101	0
	Eggs	74	618	0	0
	Total	160	1126	939	
May	I	117	247	201	0
	II	98	117	176	17
	III	65	207	515	0
	IV	144	150	937	4
	Pupa	13	31	320	0
	Eggs	96	332	0	0
	Total	533	984	2149	21
June	I	11	137	171	13
	II	25	86	99	69
	III	20	67	51	21
	IV	86	101	230	39
	Pupa	27	40	260	27
	Total	236	746	811	169
July	I	11	276	376	54
	II	29	192	39	44
	III	90	90	128	88
	IV	130	138	419	97
	Pupa	62	92	263	38
	Eggs	70	371	68	13
	Total	392	1159	1293	334
Aug.	I	81	342	219	12
	II	13	119	307	20
	III	10	197	63	2
	IV	24	258	115	8
	Pupa	17	81	42	3
	Eggs	60	310	193	0
	Total	205	1326	939	45

Sept.	I	23	210	477	30
	II	11	183	137	23
	III	14	33	210	8
	IV	20	127	418	32
	Pupa	0	104	77	8
	Eggs	0	101	0	0
	Total	68	758	1319	101
Oct.	I	88	533	238	63
	II	32	217	430	18
	III	20	201	121	9
	IV	50	417	500	80
	Pupa	29	102	91	20
	Eggs	39	690	10	0
	Total	258	2160	1390	190
Nov.	I	50	83	38	1
	II	27	30	127	3
	III	41	215	69	0
	IV	22	437	139	10
	Pupa	10	120	27	1
	Eggs	0	411	0	0
	Total	150	1296	400	15
Dec.	I	41	67	15	27
	II	16	41	4	40
	III	30	19	0	1
	IV	38	288	11	8
	Pupa	13	37	29	16
	Eggs	0	200	0	0
	Total	138	652	59	92
Jan. 1990	I	12	321	0	1
	II	9	111	1	6
	III	4	131	0	0
	IV	7	248	26	0
	Pupa	1	11	51	1
	Eggs	0	0	0	0
	Total	33	821	78	8
Feb.	I	11	173	3	0
	II	19	84	1	0
	III	11	37	2	0
	IV	7	141	0	0
	Pupa	4	38	0	0
	Eggs	0	107	0	0
	Total	50	580	6	0

March				
I	37	191	67	73
II	21	20	29	34
III	7	47	28	0
IV	28	120	2	2
Pupa	5	47	0	0
Eggs	0	217	0	0
Total	98	642	126	109

Appendix Table 7 Numbers of immature stages of C. (L.) tigripes collected each day in 100 samples from a man hole (site A)

Collecting Days	Number Collected				
	Instar I	Instar II	Instar III	Instar IV	Pupa
1	41	33	23	7	1
2	54	46	20	11	0
3	35	22	36	10	3
4	25	42	19	8	0
5	63	25	27	21	2
6	51	32	20	14	4
7	45	40	28	19	0
8	35	29	21	9	1
9	63	21	13	12	2
10	49	28	14	8	1
Total	461	328	221	119	14

Appendix Table 8 Numbers of immature stages of C. (L.) tigripes collected each day in 100 samples from a man hole (site B)

Collecting Days	No. Collected				
	Instar I	Instar II	Instar III	Instar IV	Pupa
1	21	20	17	10	1
2	31	23	13	7	0
3	26	26	27	6	2
4	23	26	18	10	0
5	22	20	16	8	1
6	28	25	17	9	1
7	31	21	14	8	0
8	23	28	20	10	3
9	29	25	15	8	0
10	30	23	19	12	1
Total	264	237	170	88	9

Appendix Table 9 Life Table for C. (L.) tigripes in a manhole (Site A)

x	nx	lx	dx	px	qx	ex
0	379	1000	137	0.8630	0.1370	3.0090
1	327	863	164	0.8100	0.1960	2.4079
2	265	699	206	0.7053	0.2947	1.8560
3	187	493	216	0.5619	0.4381	1.4220
4	105	277	172	0.3791	0.6209	1.1410
5	40	105	39	0.6286	0.3714	1.1900
6	25	66	53	0.1970	0.8030	0.5980
7	5	13				

Appendix Table 10 Life Table for C. (L.) tigripes in a concrete drain (Site B)

x	nx	lx	dx	px	qx	ex
0	300	1000	167	0.833	0.1670	3.0025
1	250	833	187	0.7755	0.2245	2.5042
2	194	646	163	0.7477	0.2523	2.0844
3	145	483	183	0.6211	0.3789	1.6190
4	90	300	150	0.5000	0.5000	1.3017
5	45	150	93	0.3800	0.6200	1.1033
6	17	57	27	0.5263	0.4737	1.6877
7	9	30	23	0.2333	0.7667	0.6167
8.	2	7				

Appendix Table 11 Physico-chemical analysis of water from a man hole and a concrete drain (sites A and B)

Months	pH		Chloride		Total alkalinity		Dissolved oxygen		Temp oC		Total No.			
											Predator		Preys	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B
APR	8.0	7.1	45	41	87.58	80.7	4.67	4.91	26.30	27.7	318	160	3031	2065
MAY	7.6	7.2	45	43	89.13	83.4	4.93	5.06	26.5	28.3	952	533	8676	4131
JUN	7.4	7.2	46	41	90.33	85.91	5.01	5.4	28.1	27.8	944	236	7081	1726
JUL	7.5	7.1	48	48	80.25	84.7	5.53	4.2	27.2	25.9	80	392	1557	2786
AUG	7.5	7.3	48	45	90.03	90.03	5.08	4.71	24.3	25.1	323	205	3213	2310
SEP	7.2	7.2	46	49	98.33	91.2	3.38	4.39	25.6	26.7	80	68	5619	2178
OCT	7.3	7.1	42	37	78.75	91.7	4.58	4.5	27.5	27.3	313	258	14603	3740
NOV	7.3	7.5	44	41	81.43	91.11	3.43	4.0	27.5	28.1	493	150	6034	1711
DEC	7.4	7.4	45	44	91.63	85.13	3.97	4.11	28.2	29.6	317	138	4004	803
JAN	7.3	7.4	41	46	92.17	83.7	4.31	4.83	27.8	29.8	400	33	6539	908
FEB	7.4	7.5	41	46	89.25	83.2	4.83	4.07	28.6	30.7	61	50	4220	586
MAR	7.3	7.8	42	49	90.73	82.6	3.68	4.0	28.9	31.1	179	98	5785	877

Appendix Table 12 Ability of larvae and pupae of C. (L.) tigripes to withstand high temperature

Instar	Period of exposure (mins)	Temp (°C)	No. Surviving/ No. tested	% Surviving	Remarks
4th	Control	Room Temp.	15/15	100	
	15	34	16/16	100	
	30	34	15/15	100	
	60	34	15/15	100	
	15	36	15/15	100	
	30	36	15/15	100	Active
	60	36	13/15	86.67	sluggish
	15	37	10/12	83.33	Larvae moribund
	30	37	5/12	41.67	
	60	37	0/12	0.00	All died
Pupae	Control	Room Temp.	15/15	100	
	15	34	10/10	100	
	30	34	10/10	100	
	60	34	10/10	100	
	15	36	10/10	100	
	30	36	10/10	100	
	60	36	12/13	92.31	Active.
	15	37	12/12	100	
	30	37	7/12	58.33	
	60	37	4/12	33.33	
	15	38	4/15	26.67	Pupae were inactive.
	30	38	1/15	6.67	Pupae died after exposure to water at room temperature
	60	38	0/15	0	All died

Appendex Table 13 Summary of the Colonization of C. (L) tigripes in the laboratory

	NO.	% Surviving	% Mortality
Total Eggs (from field)	1352	-	0
Eggs hatched into larvae	1108	81.95 (hatching)	-
No. of 1st instar larvae entering 2nd instar	853	76.99	23.01 (1st instar)
No. of larvae pupated	582	68.23	31.77 (developing larvae)
No. of adults emerged	579	99.48	0.52 Pupae
No. of adults that survived	568	98.10	1.90 Adult
Adult Females	303		
Adult Males	265		
Total Females	303		
Females blood fed	102 (33.66%)		
Blood fed females which laid eggs	13 (12.75%)		
No. of eggs/female	20-128		

Appendix Table 14 Number of eggs laid by C. (L.) tigripes and the time taken to mature eggs in the laboratory

Adult mosquito	No. of eggs laid	Time to mature eggs (days)
1	43	7
2	56	7
3	20	8
4	81	6
5	65	10
6	37	6
7	58	7
8	67	6
9	101	6
10	39	12
11	99	11
12	128	10
13	28	9
Total	792	105
X ± SD Range	60.92 ± 32.55 20-128	8.08 ± 2.10 6-12

Appendix Table 15 Longevity of adult C. (L.) tigripes under laboratory conditions

Day	Male	%	Female	%
1	54	100	60	100
7	53	98.10	59	98.30
14	50	92.59	57	95.00
21	43	79.62	49	81.67
28	31	57.41	40	66.67
35	22	40.74	29	48.33
42	12	22.22	19	31.67
49	5	9.26	15	25.00
56	2	3.70	9	15.0
63	0	0.00	4	6.67
70	-	-	0	0.00

Appendix Table 16 Average composition of Cerelac Infant cereal per 100 as given by the manufacturers (Food Specialities Ghana Ltd)

Fat	-	9.0	Vitamin E	-	3.0
Protein	-	15.5	Vitamin C	-	35.0
Carbohydrate	-	66.9	Folic Acid (mcg)	-	22.5
Dietary fibre	-	2.8	Thiamine B1 (mg)	-	0.8
Mineral Ash	-	3.3	Riboflavin (B2)	-	0.3
Moisture (water)	-	2.5	Niacin (PP) mg	-	4.0
Energy value KCal	-	411.0	Vit B6 mg	-	0.3
KJ	-	1720.0	Vit B12 mg	-	25.0
Linoleate	-	1.1	Pantothenic acid mg	-	1.5
Vit A (IU)	-	1030.0	Ca (mg)	-	530.0
Vit D	-	200.0	Phosphorus	-	430.0
			Iron (mg)	-	7.5
			Sodium (mg)	-	160.0

Appendix Table 17a Average composition of Dog biscuits by weight as given by the manufacturers (Nippon Pet Food Co. Ltd., Japan)

Crude Protein	-	32.0%
Crude Lipid	-	13.0%
Crude fiber	-	3.0%
Crude Ash	-	10.0%
Water	-	1.2%
Ca	-	1.2%
P	-	1.0

Appendix table 17b Average composition of Milk Casein by weight per 100gm as given by the manufacturers

(Wako Pure Chemicals Ltd., Japan)

Protein	-	86.2	Ca	-	26 (mg)
Energy	-	378KCal	P	-	120.0
Water	-	10.6	Fe	-	0.8
Lipid	-	1.5	Na	-	10.0
Ash	-	1.7	K	-	2.0

Appendix Table 18 Effect of Predator stages, prey stages and prey densities on the number of C. quinquefasciatus consumed by C. (L) tigripes.

Prey stage	Prey density	Predator instar 1 n (X ± SD)	Predator instar 2 n (X ± SD)	Predator instar 3 n (X ± SD)	Predator instar 4 n (X ± SD)
1st	D1	15 8.27 ± 2.15	12 9.5 ± 0.08	10 5.0 ± 2.83	10 6.0 ± 2.0
	D2	9 13.14± 4.14	11 17.67± 2.07	12 16.5 ± 2.74	12 18.0 ±3.52
	D3	12 17.8 ± 4.34	12 31.5 ± 7.66	12 34.67 ± 9.18	34 34.43±2.88
2nd	D1	14 3.43 ± 0.53	14 5.21 ± 1.53	12 8.5 ± 1.17	16 8.31± 2.47
	D2	12 9.67 ± 5.39	12 12.58 ± 3.50	14 16.33± 4.18	14 16.5 ± 8.09
	D3	14 12.57 ± 0.79	17 20.89 ± 7.98	10 28.3 ± 4.50	11 37.86± 1.46
3rd	D1	10 1.1 ± 0.88	11 2.71 ± 0.95	12 7.33 ± 1.83	10 9.2 ± 0.79
	D2	12 4.67 ± 1.21	12 12.83 ± 1.72	12 12.83± 4.83	14 14.0 ± 2.37
	D3	12 6.33 ± 0.52	12 7.75 ± 2.76	14 26.56± 3.47	12 38.17 ±2.86
4th	D1	11 0.14 ± 0.38	10 1.2 ± 0.42	11 2.38 ± 1.30	16 7.19 ± 2.10
	D2	11 1.55 ± 1.37	12 3.67± 1.97	11 6.83 ± 1.72	14 16.0 ± 2.45
	D3	15 2.2 ± 1.15	12 4.0 ± 1.83	12 4.33 ± 0.82	12 32.89± 7.66

D1 = 10 larvae/bowl
D2 = 20 larvae/bowl
D3 = 40 larvae/bowl

n = number of replicates
x = mean of n trials
SD = standard deviation

Appendix Table 19 Duration of spontaneous movements of mosquito larvae

Expt.	An. gambiae	C. quinquefasciatus	Ae. aegypti	C. (lutzia) tigripes
1.	12,16,7,10,6	9,5,3,17,7	11,16,32,41,38	1,2,3,1,2
2.	3,5,8,12,8	12,18,11,9,20	31,7,29,23,20	2,1,3,3,2
3.	2,1,1,1,1	2,6,11,9,10	5,14,25,14,20	1,2,3,4,2
4.	3,1,19,10,6	2,1,6,1,1	23,8,14,30,24	2,3,1,2,2
5.	5,3,3,2,2	5,7,1,4,9	26,6,16,4,5	1,1,1,1,1
6.	1,4,6,3,5	3,15,20,2,3	17,11,6,19,8	2,1,1,2,1
7.	5,1,1,4,2	1,3,2,4,1	10,27,19,20,15	2,2,1,2,1
8.	1,2,1,2,1	20,11,9,7,9	3,15,21,10,7	1,2,1,1,1
9.	3,1,1,2,1	3,1,1,2,2	2,2,8,8,1	2,1,1,2,1
10.	2,4,3,1,1	1,2,1,1,1	7,1,3,2,2	1,2,1,3,1
Total	205	311.0	726.0	83.0
X±SD	4.3 ± 4.44	6.22 ± 5.68	14.52 ± 10.30	1.66 ± 0.77

Each value is the duration of spontaneous movement of each larva within one minute

b) The total number of seconds moved by a larva out of 5 mins.

Appendix Table 20 Duration of Induced movements of mosquito larvae

Expt.	An. gambiae	C. quinquefasciatus	Ae. aegypti	C. (lutzia) tigripes
1.	3,1,1,1,2	2,4,6,2,2	12,6,7,7,21	7,4,6,6,2
2.	2,2,3,1,1	2,4,6,1,4	7,3,7,9,7	2,6,4,2,4
3.	3,2,2,4,4	1,3,3,2,3	11,8,6,10,7	2,4,6,7,3
4.	4,3,4,2,1	1,3,1,2,2	36,9,6,5,3	7,5,3,5,4
5.	5,3,0,5,1	3,3,2,2,1	20,7,6,11,4	3,5,7,4,2
Total	60	65	235	110
X±SD	2.4 ± 1.38	2.6 ± 1.38	9.4 ± 7.03	4.4 ± 1.76

Each value is the duration of movement in seconds per minute of each larva after stimulation by tapping the bowls

Appendix Table 21 Duration of Induced movements of mosquito larvae

Expt.	An. gambiae	C. quinquefasciatus	Ae. aegypti	C. (lutzia) tigr
1.	2,1,2,3,1	4,3,3,1,3	7,10,5,16,8	5,2,3,4,1
2.	2,1,3,2,1	3,3,5,2,6	20,7,24,9,11	4,2,2,3,5
3.	2,3,1,3,2	2,4,1,2,3	1,23,7,14,9	5,2,3,3,3
4.	2,2,1,2,3	3,4,2,1,2	13,9,3,7,6	4,3,5,3,2
5	4,1,3,2,1	2,3,4,2,3	2,18,6,3,9	7,3,4,2,1
Total X±SD	50 2.0 ± 0.87	71 2.84 ± 1.21	247 9.88 ± 6.24	81 3.24 ± 1.42

Each value is the duration of movement in seconds per minute of each larva after stimulation by tapping the larvae

Appendix Table 22 Mean number of C. quinquefasciatus eaten or killed but not eaten by the final(4th instar larvae of C. (L) tigripes

	Day 1		Day 2		Day 3		Day 4	
Prey density No. of larvae/ container	A	B	A	B	A	B	A	B
40	26.2 ± 4.95 (n = 20)	0.00	24.9 ± 7.04 (n = 20)	0.00	19.5 ± 1.81 (n = 20)	0.00	-	-
60	30.1 ± 2.27 (n = 20)	0.00	26.7 ± 1.22 (n = 20)	0.00	18.2 ± 2.61 (n = 16)	2.0 ± 1.21	8.08 ± 1.51 (n = 4)	6.5 ± 1.07
100	38.9 ± 2.07 (n = 20)	0.00	29.8 ± 1.28 (n = 20)	0.00	20.4 ± 2.63 (n = 14)	9.45 ± 2.99	4.65 ± 1.82 (n = 6)	14.36±2.76

A = Number of prey killed and eaten
B = Number of prey killed but not eaten

Appendix Table 23 Functional Response of C. (L). tigripes to prey density

No. of Prey/ 30mls of water	Mean No. of Prey killed or consumed/predator in 24 hrs	No. of trials
10	6.63 ± 2.45	18
20	12.64 ± 3.26	18
40	21.33 ± 3.37	16
60	27.38 ± 3.34	16
80	29.00 ± 1.35	14
100	30.00 ± 1.36	14
120	30.14 ± 1.63	15

Appendix Table 24 Feeding preference of C. (L). tigripes, when offered a choice of 3 mosquito prey species.

Order of Prey Selection

	An. gambiae			C.quinquefasciatus			Ae. aegypti		
	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd
No. consumed	7.0	18.0	17.0	17.0	10.0	15.0	27.0	14.0	1.0
% consumed	16.7	42.9	40.5	42.9	23.8	35.7	64.3	33.3	2.38