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BIOLOGY AND CONTROL OF *CULEX PIPIENS QUINQUEFASCIATUS** SAY, 1823 (DIPTERA, CULICIDAE) WITH SPECIAL REFERENCE TO AFRICA

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Abstract—This paper is an attempt to synthesize information available on *C. p. quinquefasciatus* in Africa. The latter is presently found in most urban areas of the African continent and in rural settlements which show some trends towards urbanization. In East Africa, and the islands of the Indian Ocean, *C. p. quinquefasciatus* is one of the major natural vectors of *Wuchereria bancrofti*. In addition it can also transmit, under laboratory conditions, some other pathogenic agents.

Preimaginal forms develop in different kinds of man-made breeding-places, especially those containing polluted water. The situation in each African region is reviewed in detail.

Female behaviour during the different phases of the gonotrophic cycle is analysed, together with population dynamics.

Control methods by synthetic insecticides are discussed in relation to resistance problems and the characteristics of the breeding sites. Other control methods based on the use of growth regulators, genetic manipulation, biological agents (parasites and predators) and environmental management have been investigated as well. Most of them cannot be easily applied or are not yet applicable for control operations.

Key Words: Culex pipiens quinquefasciatus, Africa, distribution, role in public health, preimaginal stages, adult mosquitoes, chemical control, insecticide resistance, alternative control methods

Résumé—Cet article est un essai de synthèse des informations concernant *C. p. quinquefasciatus* en Afrique. Ce moustique se rencontre actuellement dans la plupart des zones urbaines du continent Africain et également dans de nombreuses zones rurales presentant certains caractères d'urbanisation. En Afrique de l'Est et dans les îles de l'Océan Indien, *C. p. quinquefasciatus* est l'un des vecteurs majeurs de la filariose de Bancroft. En laboratoire il peut également transmettre d'autres maladies.

Ses formes préimaginales se développent surtout dans des gîtes à eaux polluées; d'origine anthropique. Les situations propres à chacune des grandes régions Africaines sont passées en revue.

Le comportement des femelles au cours des différentes phases du cycle gonotrophique et la dynamique des populations sont analysés en détail.

Les moyens de lutte par l'emploi d'insecticides de synthèse sont examinés en relation avec les problèmes de résistance et la nature des gites larvaires. Il existe d'autres possibilités de lutte, basées sur l'utilisation de régulateurs de croissance, de méthodes génétiques, d'agents biologiques (parasites et prédateurs) et sur l'aménagement de l'environnement. Cependant la plupart d'entr'elles sont difficilement applicables ou non encore opérationnelles.

Mots Clés: Culex pipiens quinquefasciatus, Afrique, répartition, rôle en santé publique, formes préimaginales, adultes, lutte chimique, résistance aux insecticides, lutte non chimique

INTRODUCTION

DESPITE scientific advances and the efforts of the health services it has not yet become possible to effectively control certain tropical diseases whose causal agents are transmitted by one or more arthropod species. In the case of some of these diseases, the situation has even become worse (GRATZ, 1974a). This applies to bancroftian filariasis, whose incidence is increasing every year. The prospects in regard to this disease are not encouraging, particularly in Asia and Africa (MATTINGLY, 1962; GRATZ, 1974b; WHO, 1974).

The sanitation problems inherent in the rapid urbanization taking place in some of these regions for the last few decades have been only partially overcome by the responsible departments. This applies especially to the disposal of waste-water in open drains, which constitutes an ideal breeding place for *Culex pipiens quinquefasciatus*, one of the main vectors of bancroftian filariasis. For this and other reasons that will be considered later, this mosquito is present in vast numbers in most tropical cities, creating a vector or pest control problem everywhere. In Africa, its prevalence may well extend filariasis transmission to all the cities south of the Sahara (HAMON *et al.*, 1967), thus creating throughout the whole continent a situation similar to that now present in the coastal areas of East Africa and in certain towns south-west of the

*Formerly *Culex pipiens fatigans* Wied. 1828 (SIRIVANAKARN and WHITE, 1978)

Indian Ocean. In addition to rural filariasis (transmitted most often by *Anopheles* spp. or sometimes by both *Anopheles* spp. and *C. p. quinquefasciatus*), urban filariasis transmitted by *C. p. quinquefasciatus* could become established throughout the continent. *C. p. quinquefasciatus* seems capable of invading the whole environment in town or country as a result of changes caused by the habits of the population and various aspects of modern life (CHINERY, 1968; SUBRA, 1975). For that reason, all aspects of the study of this mosquito are of primary importance in order to better understand how to control it most effectively. The present review is an analysis of information available on this subject as a whole.

GENERAL CONSIDERATIONS

Distribution

Geographical distribution. C. p. quinquefasciatus is widely distributed in the tropical and subtropical areas of the world; it has been found in the southern United States (in the Nearctic Region) and in the southern part of Japan (in the Palearctic Region).

In the case of Africa, *Culex pipiens pipiens* and *C. p. quinquefasciatus* are both present. While *C. p. pipiens* has a limited distribution, usually in mountainous areas, more rarely at low altitudes (Mauritania and Cameroon) (HAMON *et al.*, 1967), *C. p. quinquefasciatus* is now a very common mosquito over most of the African continent, although its presence in the north of Africa seems to be debatable. KNIGHT and MALEK (1951) did not encounter it during a study of the *Culex pipiens* complex in the Cairo region, nor did VERMEIL (1955) in Tunisia. However GAABOUB *et al.* (1971) tested the susceptibility to insecticides of larvae of the *C. pipiens* collected 20 miles (32 km) from Alexandria and assigned them to the *C. p. quinquefasciatus* subspecies. On the other hand, *C. p. quinquefasciatus* is widespread in the Ethiopian region, i.e. on the African continent south of the Sahara (HAMON *et al.*, 1967) and in the neighbouring islands: Madagascar, the Mascarenes and the Comoro Archipelago (BRUNHES, 1975), the Seychelles and the Chagos Archipelago in the Indian Ocean (LAMBRECHT, 1971), Sao Tome and Fernando-Po in the Gulf of Guinea, and the Cape Verde islands in the Atlantic (HAMON *et al.*, 1967).

C. p. quinquefasciatus occurs in all climatic zones, ranging from forest to semi-desert. Altitude does not seem to limit its distribution, since it has been found as high as 2770 m in India (BHAT, 1975) and at 2130 m in Sri Lanka (ABDULCADER *et al.*, 1965). However, it is not generally found at such a high altitude and the upper limit of its altitudinal distribution in other regions is said to be at about 1600 m, e.g. 1680 m in the South Pacific (DOBROTWORSKY, 1967) and 1600 m in Réunion (HAMON *et al.*, 1967).

The distribution of *C. p. quinquefasciatus* in continental Africa deserves special attention since it has changed considerably during the last few decades. Only a summary will be given here, since this has been the subject of reviews by HAMON *et al.* (1967) and SUBRA (1975). In West Africa, before the Second World War, *C. p. quinquefasciatus* was known only in a few scattered localities, mainly on the coast where it represented only a small percentage of the culicid fauna, though in Accra (Ghana) MACFIE and INGRAM (1916) found this subspecies in 14.86% of all positive larval collections in domestic water containers. After the Second World War, the number of places where it became the prevalent species increased considerably. This phenomenon seems to have accelerated during the last 20 years, and today *C. p. quinquefasciatus* is the dominant if not the sole species of mosquito in most of the urban areas in West Africa. It is found only very sporadically in rural environments. In Central Africa, *C. p. quinquefasciatus* was known in some localities at the beginning of the century and became common before 1940, particularly along the Congo River. In subsequent years it spread widely, becoming prevalent in a large number of urban areas and also in certain large villages in the Cameroons, though this does not seem to be the general rule as yet; recent surveys in the Central African Republic showed that it was still only present in the big towns, a situation similar to that found in West Africa. The situation in East Africa is quite different, particularly in the coastal areas and in certain islands of the Indian Ocean. The first authors to study the insect fauna of this area at the beginning of the century remarked upon the rapid expansion of this species in the Mascarenes (D'EMMEREZ DE CHARMOY, 1908–1909) and Zanzibar (ADERS, 1917). Since that time, *C. p. quinquefasciatus* has become even more widespread in these regions. Here its distribution is not restricted to urban areas as it is also very abundant in a number of rural localities. Usually this occurs in large villages which are constructed on a town-like pattern, several hundred houses built along streets and lanes, and where a certain percentage of the population is no longer engaged in traditional activities, such as farming and fishing. As in most tropical towns, space is limited in the centre of these localities; thus people have to dig pit latrines and cesspools to eliminate waste and used water. In small villages of around 10 or so scattered houses, there is little problem of waste elimination, and *C. p. quinquefasciatus* remains rare or completely absent, finding no breeding places to support it.

The case of the Seychelles deserves special attention. In these islands, *C. p. quinquefasciatus* was relatively uncommon even as recently as 25 years ago, and was concentrated round Port Victoria, the capital (MATTINGLY and BROWN, 1955). Some 15 years later, LAMBRECHT (1971) found it was abundant throughout the Archipelago, where it had colonized not only its classical larval habitats but other less suitable types as well. Thus *C. p. quinquefasciatus* was successful in adapting to an environment where only a short time before it occupied only a relatively restricted habitat.

In East Africa, as in West Africa, *C. p. quinquefasciatus* densities do not seem to have stabilized. In an analysis of data from 1954 to 1971 in Dar es Salaam, for example, they have been shown to be increasing more or less steadily each year as observed by BANG *et al.* (1973b).

Relationship to human environment. The distribution and density of *C. p. quinquefasciatus* in tropical Africa are therefore two constantly evolving phenomena for which different explanations have been suggested. Here again reference is made to the reviews on the subject by SERVICE (1966), HAMON *et al.* (1967) and

SUBRA (1975). Apart from the development of rapid modes of transportation which promote the dispersal of *C. p. quinquefasciatus* (HIGHTON and VAN SOMEREN, 1970) though not its establishment, there are two essential reasons which lead to the rapid multiplication of this mosquito: the utilization of insecticides and rapid urbanization. The excellent results obtained with organochlorine insecticides for the control of medically important insects led to their use in many tropical areas. Unfortunately, however, *C. p. quinquefasciatus*, which is less susceptible to these compounds than many other species, soon became highly resistant to them. In as much as species like *Culex nebulosus* and *Culex cinereus* with which it was formerly in competition for larval breeding places had been eliminated by the insecticides, *C. p. quinquefasciatus* was able to make use of the newly available sites (SERVICE, 1966). Furthermore, the number of such breeding places has considerably increased with the growth of towns and poor sanitation. In Africa, the natural population increases and subsequent growth in size of towns has often been compounded by large migratory movements of people to the cities, which has led to the overcrowding of numerous quarters. The sanitation services in most cases have been unable to deal adequately with this influx of people. The disposal of the various types of waste has been left partly to the initiative of the inhabitants themselves, who have often dug poorly constructed, insanitary latrines or soakage pits. *C. p. quinquefasciatus* has therefore been able to colonize easily all those breeding places which insecticides had previously cleared of possible competitors.

Urbanization is often accompanied by an abandonment of the traditional way of life in favour of different habits and the amenities provided by the modern world. Thus detergents are now used on a large scale by numerous African housewives. Such products in waste-water could also well play a part in eliminating species in competition with *C. p. quinquefasciatus*, which itself tolerates high levels of pollution and seems to adapt easily to these new type of habitat. This would partly explain the recent expansion of breeding of this mosquito in those urban areas where there has never been any insecticide spraying and where it has remained susceptible to organochlorine insecticides (SUBRA, 1973).

Public health importance of C. p. quinquefasciatus *as a disease vector*

A distinction will be drawn under this heading between diseases which *C. p. quinquefasciatus* is known or presumed to carry, and diseases whose causal agent may be maintained or may develop in this mosquito, but only in the laboratory.

In nature. C. p. quinquefasciatus plays a major role in the transmission of bancroftian filariasis. It has a more restricted role as a vector of viral diseases of man and animals.

In most tropical areas where *C. p. quinquefasciatus* became established several decades ago, it transmits filaria in the towns and in areas where urban life has led to the creation of its favourite larval breeding places. This is also the case in the neotropical and oriental regions (HAWKING, 1973) and in part of the Australian region, where the periodic form of *Wuchereria bancrofti* is encountered (CHOW, 1973).

So far as Africa south of the Sahara is concerned, the vector role of *C. p. quinquefasciatus* has been demonstrated in East Africa by NELSON *et al.* (1962) and WHITE (1971a). Similar observations have been made in the islands of the south-west Indian Ocean by BRUNHES (1975) and in the Seychelles by LAMBRECHT (1971). The situation in Central Africa is not clear, since there has not been any adequate recent work. However, in 1964 COSTA MOURAO discovered in *C. p. quinquefasciatus* females on Sao Tome the sausage-shaped forms of filariae, suggesting that the risks of transmission in nature in this area are quite serious. In West Africa, where the spread of this mosquito is comparatively recent (after the end of the Second World War), a considerable amount of research has failed to demonstrate that this species plays any role at all in the transmission of filariasis (SUBRA, 1973; BRENGUES, 1975). Various laboratory observations on the other hand demonstrated that microfilariae could develop up to the infective stage in Upper Volta (SUBRA, 1965) and in Nigeria (OGUNBA, 1971), but with low infection rates. In Liberia the susceptibility of *C. p. quinquefasciatus* to *Wuchereria bancrofti* has been found to be only 28% as high as that of the anophelines (MAASCH, 1973). This could explain why *C. p. quinquefasciatus* is not yet a natural vector in this area (BRENGUES, 1975; KUHLOW, 1976). The susceptibility of this mosquito to *W. bancrofti* seems to be under the control of at least two genetic factors (ZIELKE and KUHLOW, 1977). In addition, BRENGUES (1975) found a different intensity of infection between strains which can be differentiated by cytoplasmic incompatibility.

In addition to bancroftian filariasis, *C. p. quinquefasciatus* was found to be infected with Chikungunya virus during an epidemic that occurred in 1953 in southern Tanzania (quoted in WHITE, 1971b). More recently in Senegal, WILLS *et al.* (1976) demonstrated the presence of hepatitis B virus on the mouthparts of these mosquitoes. Reovirus type 3 can be picked up by *C. p. quinquefasciatus* larvae and it is maintained through the pupal stage to the first days of adult life. It could also be an important vector of Rift Valley fever virus: in Egypt this virus has been isolated from mosquito specimens collected in the home of a RVF patient (WHO, 1978).

In India, *C. p. quinquefasciatus* can be one of the vectors of West Nile virus (RAO, 1975), and in the Americas it can transmit St. Louis encephalitis virus (GILLET, 1972). It also is of importance in veterinary medicine, since in Australia it is the main vector of fowl pox virus (LEE *et al.*, 1958).

In the laboratory. In Madagascar, BRYGOO and SUREAU (1962) found that poliomyelitis virus persists for 24 hr without losing its virulence in *C. p. quinquefasciatus* hatched from larvae raised in aquaria containing the virus. In 1946 the species was suspected by GALVEZ GOMEZ (1947) of being responsible for the transmission of poliomyelitis virus in Havana. Its role as a vector of this virus had not been directly demonstrated, the author basing his hypothesis merely on the fact that the number of cases were localized near *C. p. quinquefasciatus* breeding places and the number decreased after those breeding places had been eliminated. This mosquito can also transmit the yellow fever virus in the laboratory as was demonstrated by MUSPRATT (1956) in South Africa. Nevertheless, *C. p. quinquefasciatus* does not seem to play a role either in the natural transmission of yellow fever as stated by this author or in the epidemiology of Burkitt's tumour (MCCRAE *et al.*, 1968).

Laboratory work in other regions of the world has shown that *C. p. quinquefasciatus* was also mechanically able to transmit smallpox virus, which it could harbour for about 72 hr (SARKAR *et al.*, 1973). In the same way, it can transmit Wesselbron virus (SIMASATHIEN and OLSON, 1973) and Venezuelan equine encephalitis virus (KRAMER and SCHERER, 1976). On the other hand, multiplication of rubella virus (TESH and ROSEN, 1975) or the trans-ovarial transmission of La Crosse virus (TESH and GUBLER, 1975) does not occur.

Nuisance role. In addition to its role as a vector of pathogenic agents, *C. p. quinquefasciatus* frequently causes considerable annoyance to people exposed to its constant biting, particularly when they cannot afford to buy mosquito nets. Thus in Bamako (Mali) SUBRA *et al.* (1965) observed several hundred bites per man per night indoors by this species. This situation is common in most large African towns. Its effects are difficult to measure, but there is no doubt that the loss of sleep involved reduces the productivity of numerous workers. In this way, therefore, it has economic repercussions.

BIOLOGY

Eggs

C. p. quinquefasciatus eggs are laid in the form of rafts which can float on the surface of the water. At the time of laying, they are whitish but they darken within a few hours. An average of 155 eggs per raft was observed by SUBRA (personal observation) in East Africa, but there may be very important variations from one female to another. Generally, females that have fed on birds lay a greater number of eggs than those that have fed on man (KRISHNAMURTI and PAL, 1958).

In tropical countries, hatching usually occurs one day after egg-laying. Nevertheless, in some cases, the crossing of two different strains gives no offspring because of cytoplasmic incompatibility which results in the death of the embryo in the egg. It is usually uni-directional: crosses between two strains are fertile in one direction but sterile in the other. In some cases (less common) it may be both ways, crosses being sterile in both directions.

Larvae

Larval development. The two main factors that regulate mosquito larval growth are nutrition and the temperature of the water in the breeding places (CLEMENTS, 1963). In the southern United States during the coldest months, pre-adult life lasts 48 days on the average (HAYES, 1975). In the tropics, it is much shorter. In Rangoon, where the mean temperature varies little throughout the year, DE MEILLON *et al.* (1967b) studied the duration of the different stages. At a temperature around 28°C, the egg incubation period is approximately 27 hr, and the male and female larvae hatch out simultaneously. However, the duration of the larval stages in the males (about 118 hr) is shorter than that in the females (about 135 hr) while the reverse is true for the pupal stage. In Africa, field studies by SUBRA (1973) at Bobo Dioulasso showed that the average time elapsing between oviposition and hatching ranged from 24 to 36 hr. The larval stage lasted between 6 and 8 days and pupal stage about 40 hr. The wide range of the incubation and larval periods observed by SUBRA (1973) may be due to temperature differences of the larval breeding places in various types of soakage pits: a difference of several degrees was observed between surface water at ground level and that deep down in the pits.

C. p. quinquefasciatus develops mainly in habitats containing highly polluted water rich in organic matter that the larvae can use for nourishment. Thus food supply is a factor which can be disregarded in most cases, since food is usually available in excess in their numerous breeding places. A shortage of food obviously leads to a low production of pupae in the breeding places concerned. SUBRA (1973) reported on one such breeding place where daily pupal production was only 20 or so pupae, even though the daily average of stage I larvae which hatched was something like 35,000. The effects of the amount of nourishment available in the breeding places are reflected not only in the number and size of the pre-imaginal forms but also in the size of the adults, which are larger when a greater amount of nourishment is available (KURIHARA, 1963; SUBRA, 1971a, b).

Types of larval breeding places. While the pre-imaginal stages of *C. p. quinquefasciatus* develop mainly in polluted water, a study of the literature on this mosquito throughout the world shows that though waste-water represents the main breeding sources, the larvae can develop in virtually any type of breeding place found in the human environment. Most breeding sites are of medium size (a few cubic metres) or small (a few litres), and the species can develop in either sunny or shady places. The classification adopted here for these larval breeding sites is based on their location in relation to human dwellings. There are two main categories: man-made and naturally occurring breeding places which cover all the tropical areas of the world where *C. p. quinquefasciatus* has been found. The situation in Africa will be discussed in more detail below.

(a) *Man-made or man-modified larval breeding places.* These are by far the most important and depend on man for their establishment.

Breeding places in highly polluted water. In this group latrines are the most widespread type of breeding place in most countries. In flat areas, they may often be excavated down to the underground water-table, particularly in high-rainfall regions where the table is very close to the surface. The water mixed with excreta therefore constitutes a highly polluted environment perfectly suited to *C. p. quinquefasciatus* larvae. Furthermore, since latrines are usually protected against heavy rainfall, which may flood other breeding places, their production of larvae during the rainy season continues practically uninterrupted. Relatively slight fluctuation in the water table usually gives them a great stability; in regions with a marked dry season the level of the underground water-table may fall below that of the latrines, which then cease to be favourable breeding places for *C. p. quinquefasciatus.*

Soakage pits are designed to collect waste washing and cooking water. These consist of holes dug in the ground to varying depths, sometimes filled with pebbles. Most are accessible from the outside, as the covered top is rarely completely sealed or mosquito-proofed. Heavy rain may cause the pits to overflow, providing less stable breeding places than latrines. Unlike latrines, however, they contain water throughout most of the year and represent actual or potential breeding places over a longer period. In quarters where housing is modern and of good quality, *septic tanks* form the main breeding places. They maintain high culicid densities almost uninterruptedly throughout the year.

Breeding places in unpolluted or slightly polluted water. These sites allow mosquito breeding during most or all of the year. A distinction will be drawn between fixed receptacles (usually very large) and smaller (usually domestic) containers.

In the absence of polluted water for breeding, *C. p. quinquefasciatus* can utilize sites containing limpid water used for domestic needs of the population. In the Maldives, the 20,000 existing wells represent the most important *C. p. quinquefasciatus* larval habitats (IYENGAR, 1952; VELIMIROVIC and CLARKE, 1975). In the Indian subcontinent, *C. p. quinquefasciatus* is present in rural areas where it develops in wells used for irrigation (YASUNO *et al.*, 1975). The case of tanks and cisterns in Grand Comoro, in which *C. p. quinquefasciatus* larvae are also encountered, will be dealt with later.

Small receptacles or containers represent a very widespread type of breeding place in all tropical areas of the world. In regions where the inhabitants still pursue a traditional way of life, water for domestic use is stored mainly in earthenware jars which may hold up to several dozen litres. In more modern environments, these easily breakable jars are often replaced by metal containers with a capacity of as much as 200 l. When the water is changed irregularly, or at too great intervals (several weeks), mosquito larvae can develop therein. *C. p. quinquefasciatus* and *Aedes aegypti* can be found in such containers.

(b) *Peridomestic breeding places.* Ditches and gutters designed to take away rain-water in towns frequently become breeding places for *C. p. quinquefasciatus* if not properly cleaned. The organic detritus that accumulates pollutes the water often to a very high degree, and furthermore prevents the normal flow, thus providing excellent conditions for larval development. In some regions, brooks and ponds are used as municipal tips where human and animal excreta are also discharged. When pollution reaches its peak, these ponds favour intense breeding of *C. p. quinquefasciatus* (COLLESS, 1957).

Also in this category are breeding places in which water is not highly polluted. They consist of various used containers thrown away through negligence or lack of sanitary education of the inhabitants. They may be the remains of jars, empty tins, bottles, broken metal cans, broken coconut husks, bamboo stalks, and shells. These containers fill up with water in the rainy season and act as mosquito breeding places during that time of the year. In towns, old tyres, which often accumulate in large numbers, constitute important breeding places for *Ae. aegypti* and *C. p. quinquefasciatus.* In seaside communities, abandoned canoes fill with rainwater, and sometimes provide breeding places for both these species.

(c) *Industrial and agricultural breeding places.* Waste-discharge channels at sugar or sisal-processing factories may enable the development of large numbers of the aquatic forms of *C. p. quinquefasciatus.* The organic pollution usually found in the breeding places of this species is supplemented here by a chemical pollution to which the larvae seem well adapted.

C. p. quinquefasciatus larvae may sometimes develop in irrigation channels but these are of secondary importance.

(d) *Natural larval habitats.* Natural sites are usually small and *C. p. quinquefasciatus* is often found breeding with other species. By themselves, they doubtless contribute quite small adult numbers; but they cannot be disregarded in campaigns designed to interrupt disease transmission. Three categories of breeding place have been observed which differ greatly from each other in origin and structure: tree-holes, crab burrows, and coral rock-holes.

Some authors have collected *C. p. quinquefasciatus* larvae from brooks, but if these watercourses have been polluted from man-made sources, they should be placed in the previous category.

The situation in Africa. Madagascar. At Tananarive in the uplands, *C. p. quinquefasciatus* is very abundant in polluted water (CHAUVET and RASOLONIANINA, 1966, 1968), particularly in the lower part of the town where the water-table rises to ground level during the rainy season. Larvae have been gathered from latrines and from pools with water contaminated by various types of rubbish, particularly excreta from pigs (SUBRA, personal observation). They are also found in numerous containers used for storing domestic water and in various peridomestic breeding places, often in company with *Aedes albopictus* Skuse, 1894. The same situation applies in coastal towns. However, on the west coast of Madagascar, *C. p. quinquefasciatus* is associated with *Ae. aegypti* instead of with *Ae. albopictus. C. p. quinquefasciatus* has also been collected from tree-holes by BRUNHES (personal communication) in Tananarive and by SUBRA (personal observation) in the southern part of the island. During surveys throughout the country, only a few soakage pits were seen in Majunga. Such pits do not, therefore, seem to be important breeding places for *C. p. quinquefasciatus* in Madagascar as a whole.

The species is absent from those rural areas with low human densities where people are still living according to old traditions and do not have any problem of water or waste disposal. In the south of Madagascar, which suffers from serious water supply problems, *C. p. quinquefasciatus* is found in various water-storage containers and other peridomestic breeding places. Investigations carried out by the author in rice fields near the big towns did not reveal any *C. p. quinquefasciatus.*

The Mascarenes and the Seychelles. In the case of the Mascarenes, it is difficult to make a distinction between urban and rural environment. In Réunion, *C. p. quinquefasciatus* has long been found in all the inhabited zones, and it can be collected from most types of breeding places including crab burrows (HAMON *et al.*, 1967). In 1950, it was particularly abundant in the waste-water from sugar factories (HAMON, 1953a).

In the Seychelles, *C. p. quinquefasciatus* is found in all types of domestic and peridomestic breeding places already described; and also in tree-holes, rock-holes, cut bamboo, pools next to rice fields, and leaf axils (LAMBRECHT, 1971).

Comoro Archipelago. In Grand Comoro, a volcanic island of recent origin, polluted water and surface water are almost non-existent because of the high permeability of the soil. *C. p. quinquefasciatus* develops in all the containers used for storing water (cisterns, metal cylinders and wash bowls) as well as in peridomestic breeding places. It has also been found in the hollows of trees (BRUNHES, 1975).

In Mayotte, on the other hand, waste-water is generally common in the human environment and soakage pits are constructed for its disposal. Furthermore, during the rainy season the water-table rises sufficiently to reach the latrines. There are therefore two types of highly productive *C. p. quinquefasciatus* breeding places. Their distribution is not uniform, but depends on the ethnic origin of the people concerned (SUBRA and HEBRARD, 1975). The nature of the village site also affects the productivity of the breeding places (BRUNHES and DANDOY, 1973). To these purely man-made breeding sites, must be added the mouth of coastal streams, which are often used as public tips. At certain times of the year, the mouths are obstructed by sand bars and represent excellent *C. p. quinquefasciatus* breeding sites. Other breeding places for this species have been described by SUBRA and HEBRARD (1975) and BRUNHES (1975). Water jars inside dwellings do not contain mosquito larvae, since the water is changed daily.

In the other islands, Moheli and Anjouan, the situation is similar to that of Mayotte except that in Anjouan, coastal streams are less common than in Mayotte.

East Africa. In the coastal regions of East Africa, and in Zanzibar, the same types of breeding place are found both in the towns and big villages. In Mombasa (TEESDALE, 1959) and also in smaller towns in Kenya (WIJERS and KIILU, 1978), latrines are the most common breeding places. A rather similar observation has been made in Zanzibar (MANSFIELD-ADERS, 1927) and in continental Tanzania (WHITE, 1967, 1971b; MENU and KILAMA, 1972; BANG *et al.*, 1975). Soakage pits also provide breeding places for *C. p. quinquefasciatus* (ADERS, 1917; TEESDALE, 1959; WIJERS and KIILU, 1978), although in some localities in north-east Tanzania, larvae were not found (KOLSTROP, personal communication). A noteworthy case was observed by WIJERS and KIILU (1978), in which latrines received waste-water in the absence of soakage pits and therefore mosquito larvae developed for a longer time than breeding places supplied only from the water-table. Waste-water from sisal factories is particularly suitable for the development of *C. p. quinquefasciatus* larvae.

Various containers and peridomestic breeding places can also be colonized by *C. p. quinquefasciatus* (HARRIS, 1942; VAN SOMEREN *et al.*, 1955). The species even develops in rice fields in the interior: SURTEES (1970) gathered specimens in rice-growing areas in greater numbers than in unmodified ecosystems. CHANDLER and HIGHTON (1975), when sampling newly hatched adult mosquitoes in the rice fields, found among them males and females of this species.

Finally, in East Africa, *C. p. quinquefasciatus* larvae can develop in certain natural habitats such as banana leaf axils (TEESDALE, 1941) or tree-holes (VAN SOMEREN *et al.*, 1955). Although *Ae. aegypti* and *Ae. simpsoni* larvae were found breeding in coral rock-holes, *C. p. quinquefasciatus* was not found in that type of site either in Tanzania (TRPIS *et al.*, 1971) or in Kenya (TRPIS, unpublished report).

Central Africa. In the urban environment, numerous *C. p. quinquefasciatus* have been collected in the classical polluted-water breeding places in Zaire (HENRARD *et al.*, 1946), in southern Cameroon (MOUCHET *et al.*, 1960), in Angola (RIBEIRO and MEXIA, 1966) and in the People's Republic of the Congo (HAMON *et al.*, 1967).

In Central Africa, breeding sites with only slightly polluted water or natural sites are usually not colonized. In Angola, RIBEIRO and MEXIA (1966) only very rarely found *C. p. quinquefasciatus* in artificial or natural breeding places. On the other hand, in Sao Tome it is frequent in various containers and is also found in the hollows of trees or the axils of certain leaves (COSTA MOURAO, 1964). In Zaire, it was present 40 years ago breeding in crab-burrows (WANSON, 1935).

West Africa. In urban areas of the savanna zones, the main larval breeding places of *C. p. quinquefasciatus* at the end of the rainy season are soakage pits, ditches filled with polluted water and gutters (SERVICE, 1966; CHINERY, 1969, 1970; SUBRA, 1971a, 1973). In Bobo Dioulasso, the present author found that latrines seemed to play an insignificant role, even at the end of the rainy season. In more humid climatic zones (lower Guinea), *C. p. quinquefasciatus* was found in septic tanks (TOUMANOFF *et al.*, 1956). In Accra, septic tanks and concrete water tanks constituted important perennial breeding places (CHINERY, 1970). In eastern Nigeria, pots and drums used for cassava fermentation can support considerable breeding of this species (IWUALA, 1979).

In rural areas polluted-water breeding places are very rare. Twenty years ago in the southern part of Nigeria, *C. p. quinquefasciatus* was not yet found in domestic water containers. It was also absent from certain natural breeding places such as tree-holes (SURTEES, 1959), although DUNN (1927) had made similar observations but found the species in a few crab-holes in the region of Lagos and Ebute Metta. More recently, it was also found colonizing crab-holes in Accra (CHINERY, 1969).

Discussion. An examination of the various types of *C. p. quinquefasciatus* breeding places in the Ethiopian faunal region as a whole shows two differences: the types of larval habitats in urban and rural areas are not always identical, and the particular types of important breeding place vary in degree of infestation in different regions of the continent. There is a relationship between the establishment and breeding of *C. p.*

quinquefasciatus and its vectorial capacity. Where the species has been established for a long time, it is present in all environments and is an effective vector of *W. bancrofti*. Where it has only recently become established, it is restricted to urban areas and is still only a potential vector. This suggests that, in the future, West and Central Africa may witness a spread of *C. p. quinquefasciatus* to the rural areas followed by the beginning of transmission of *W. bancrofti*.

Adults

After first describing the various phases of adult mosquito life, the work particularly concerned with each of those phases will be reviewed. Most of the observations involve essentially the females, which are of more public health interest than the males because of their role as vectors.

Phases of adult life. After leaving the breeding place where their pre-imaginal development has taken place adults usually fly for a short distance (rarely more than 100 m). By 24 to 36 hr later, most of the females will have been fertilized and will then take a blood-meal at quite a stable rhythm. After the blood has been entirely digested, and the eggs have formed, they will be laid on the surface of various bodies of water generally of man-made origin. A period of from a few hours up to a half a day will elapse between oviposition and the next blood-meal, which will be the beginning of the next gonotrophic cycle.

Adult activities before the first blood-meal. Equal numbers of males and females continuously emerge from the breeding sites but there are nevertheless two peaks, one before sunset and the other, which is very marked, between 20.00 hr and 21.00 hr (DE MEILLON *et al.*, 1967c). Before adults leave the larval breeding place, a rest phase of varying length occurs when they will rest on the banks of ditches or sides of the container. It is followed by a mass departure of the males and females at nightfall (YASUNO and HARINASUTA, 1967). DE MEILLON *et al.* (1967c) have demonstrated that in these flights there are two categories of individual: some aged a few hours, which have emerged during the day and during the emergence peak preceding sunset, the others older, originating from the day before the hatching peak of 20.00 hr to 21.00 hr, which leave the breeding place the following day. In regions where the seasons are more distinct than in the tropics, the females emerge in larger numbers than the males during the colder months (HAYES, 1975).

Mating does not take place immediately after leaving the larval breeding place, but occurs 36 to 48 hr after emergence according to YASUNO and HARINASUTA (1967) or even later (72 hr) according to the laboratory observations of SEBASTIAN and DE MEILLON (1967). These two groups of authors observed that it took place mainly before and after sunset. Usually, the females are fertilized before their first blood-meal, but sometimes fertilization occurs when the females have already taken blood (YASUNO and HARINASUTA, 1967). Climatic conditions may influence the time of fertilization. In India, it takes place at all seasons when the females are 2 to 3 days old, except during the winter when it is sometimes delayed up to the sixth day after hatching (YASUNO *et al.*, 1972). Absence of fertilization does not necessarily mean sterility, for KITZMILLER (1959) has described cases of parthenogenesis in *C. p. quinquefasciatus* in the laboratory.

In the laboratory in Upper Volta, this period between emergence and the first blood-meal was found to be 60 hr by examination of the ovarioles of nulliparous females. However, in nature, it is believed to be only about 48 hr (SUBRA, 1972a).

The blood-meal. Endo-exophagy. Anthropophilic mosquitoes feeding at night, bite man either inside dwellings (endophagy) or outside (exophagy). It may happen that certain individuals of the same species facultatively feed indoors and others outdoors. Furthermore, this behaviour may differ from one region to another. In South-East Asia, at Bangkok, SASA *et al.* (1965b), observed that most females of *C. p. quinquefasciatus* fed indoors. DE MEILLON and SEBASTIAN (1967a) had observed the exact opposite in Rangoon, where the exophagous tendency predominated. The results recorded in Africa seem to show more uniform behaviour of *C. p. quinquefasciatus*, which is markedly endophagous in the Comoro Islands (BRUNHES, 1975), in East Africa (VAN SOMEREN *et al.*, 1958; SMITH, 1961; VAN SOMEREN and FURLONG, 1964) and in West Africa (SUBRA, 1972b). In Mayotte in the Comoro Islands, BRUNHES (1975) observed that the percentage of endophagous females could vary according to locality. In Bobo Dioulasso, endophagy was more marked during the cold season, when the difference between lower and upper extreme temperatures was greater (SUBRA, 1972b).

Biting cycle. The large majority of female *C. p. quinquefasciatus* feed at night. When they bite man it is mainly below the knee if the person is sitting, or on any part of the body if he is lying down (SELF *et al.*, 1969). Similar observations have been made by other authors studying the biting cycle of endophagous females. Most biting specimens were collected after midnight in the Comoro Islands (BRUNHES, 1975), in East Africa (VAN SOMEREN *et al.*, 1958; TEESDALE, 1959; SMITH, 1961; VAN SOMEREN and FURLONG, 1964) and in West Africa (SUBRA, 1972b). In Réunion, however, HAMON (1965) observed most bites in the first part of the night. This discrepancy with the results of other authors might be due to the marked fall in temperature during the night, which led to a decrease in the number of females seeking a blood-meal. SUBRA (1972b) and BRUNHES (1975), who each collected several thousand specimens, place the peak more precisely between 01.00 hr and 02.00 hr. The maximum number of bites outside dwellings occurs in some instances at the same time as indoors (SMITH, 1961) and sometimes earlier (BRUNHES, 1975). In Bobo Dioulasso exophagous females sometimes bite earlier and sometimes at the same time as endophagous females, depending on the season of the year (SUBRA, 1972b). Their age only occasionally seems to affect the biting cycle of *C. p. quinquefasciatus* females. Among specimens that feed away from dwelling places, there is no difference between parous and nulliparous females at any season. In endophagous females and only in the rainy season, a majority of parous individuals has been observed at the beginning and end of the night. This special behaviour of the parous females during the rainy season might be connected with their oviposition rhythm (SUBRA, 1972b).

Host preferences. While most authors (HAMON and MOUCHET, 1967) agree that *C. p. quinquefasciatus* is anthropophilic, the host preferences of that mosquito have been the subject of numerous investigations, often with contradictory results, in the different parts of its area of distribution. This applies also to Africa, where MATHIS (1935) described *C. p. quinquefasciatus* as highly ornithophilic, whereas the majority of authors, both in West Africa (Sierra Leone, THOMAS, 1956; and Upper Volta, SUBRA, 1970) and in East Africa (HEISCH *et al.*, 1959, and CHANDLER *et al.*, 1975, in Kenya; WHITE, 1971a, in Tanzania) have agreed that it is anthropophilic.

The degree of this anthropophily, moreover, varies according to the place where fed females are trapped, and *C. p. quinquefasciatus* may be attracted by various types of bait (LEE *et al.*, 1954). Catches carried out inside occupied dwellings provided a larger percentage of anthropophilic females than those out of doors. Thus, in Upper Volta, 98% of the females captured inside dwellings had fed on man, as against 1.3% on birds and 0.7% on various mammals. On the other hand, with females captured outdoors, the percentage of anthropophilic specimens was only 73%, while the ornithophilic proportion was 20.9%, and those feeding on various mammals (particularly dogs) accounted for 6.1% (SUBRA, 1970). However, here also as in Rangoon (DE MEILLON and SEBASTIAN, 1967b), anthropophily still predominated, whereas in northern Nigeria the percentage of females that had fed on different host species was greater than the percentage of anthropophilic females (SERVICE, 1965). These data, however, were based on a few dozen specimens only.

The practical consequences of host selection are seen in differences in fertility (see section on 'Biology', subsection 'Egg').

Non-blood-meals. The taking of meals other than blood has been discussed by only a few authors, although in this species it may affect the length of the gonotrophic cycle and hence its vectoral capacity and population dynamics. DE MEILLON *et al.* (1967d) demonstrated that feeding on sugar–water delayed oviposition but also reduced daily mortality. These authors discovered this phenomenon under natural conditions, and established that *C. p. quinquefasciatus* has a feeding cycle on sugarcane. The specimens collected under these circumstances included not only newly emerged mosquitoes but also older ones.

Similarly, in Upper Volta, SUBRA (1970) caught parous females that had taken a non-blood-meal. The proportion of this type of female was much higher outdoors than inside dwellings. There seemed to be no such difference in nulliparous females.

The gonotrophic cycle. In the past, the concept of the gonotrophic cycle has been interpreted in two ways. The present author accepts the definition of BEKLEMISHEV (in DETINOVA, 1963) who believed that the gonotrophic cycle was the period between two successive ovipositions (or the period between emergence and oviposition in the case of nulliparous females). This interpretation makes it possible to determine the chronological age of females in which the number of ovipositions is known and to calculate the average duration of the gonotrophic cycle. Determinations of this kind are obviously possible in anautogenous females and if gonotrophic concordance (agreement between the number of blood-meals and the number of ovipositions) is the general rule. Just two cases of autogeny in *C. p. quinquefasciatus* have been reported from Africa, one by MICHEL at Thies in Senegal (in HAMON *et al.*, 1967), the other by BUSHROD (1978) in Tanzania. Autogenesis has not been demonstrated in the laboratory in Dakar (MATHIS, 1935), in Sierra Leone (THOMAS, 1956) or in Bobo-Dioulasso (SUBRA, 1972a). As for the pre-gravid phase said to indicate gonotrophic discordance, it has been observed in West Africa but involved only a limited number of cases—less than 10% of the specimens studied (SUBRA, 1972a). Thus knowledge of the duration of the gonotrophic cycle can be used for determination of chronological age.

The duration of digestion of the blood-meal has been studied during the rainy season in the laboratory and in the field at Bobo Dioulasso, Upper Volta (SUBRA, 1972a). In the laboratory, the author used nulliparous females and found that digestion proceeded at approximately the same rate whatever the time of the blood-meal. In all specimens it was completed by 60 hr, in some it required only 48 hr. The results of field trials using specimens marked with fluorescent powder confirm these observations. Oviposition, if it is not delayed by the taking of a non-blood-meal, occurs a few hours after completion of maturation of the ovaries, at least in the rainy season. The blood-meal following oviposition occurs within just a few hours.

The first gonotrophic cycle would therefore appear to last a minimum of 5 days, the second 3 days, and the subsequent ones 4 days or more, since old parous females require a longer time than primiparae.

Oviposition. Oviposition cycle. If there are no atmospheric disturbances, sunrise and sunset are the preferred times for oviposition in *C. p. quinquefasciatus* females as observed at Rangoon in South-East Asia (DE MEILLON *et al.*, 1967e) and in Bobo Dioulasso in West Africa (SUBRA, 1971b). In the latter case, the most important peak was at sunset. Several authors who have studied other mosquito species estimate that variations in luminosity trigger off the oviposition reflex. However, luminosity does not seem to be the only factor determining the oviposition cycle since DE MEILLON *et al.* (1967e) demonstrated a relationship between the date of the blood-meal and the date of oviposition. Under the humidity and temperature conditions in which these authors were working, the sunset peak corresponded to females which had taken a blood-meal after midnight 3 nights before, while the sunrise peak corresponded to the females which had taken a blood-meal before midnight 2 nights earlier. In Bobo Dioulasso, fluctuations in the number of ovipositions made daily could not be precisely linked with any other phenomenon (SUBRA, 1971b).

Chemical factors determining selection of oviposition sites. On the whole, *C. p. quinquefasciatus* females do not oviposit at random in all potential breeding places, but only in those which contain certain attractive substances. IKESHOJI (1966) showed that breeding-site water contained a factor attractive to gravid female *C. p. quinquefasciatus* and stimulated oviposition. In 1968, the same author separated by gas chromatography four compounds that are attractive to *C. p. quinquefasciatus* females. Later, IKESHOJI and MULLA (1970a) demonstrated that this mosquito sometimes responded positively to attractants peculiar to other species.

In the field in Upper Volta, SUBRA (1971b) tested the attraction of various potential breeding places in the human environment in Bobo Dioulasso, and observed that the water in soakage pits attracted the largest number of gravid females. Furthermore, he found in the laboratory that the attraction of certain of these pits varied from season to season. In particular, some negative breeding places in the dry season were much less attractive than the positive ones. The absence of pre-imaginal specimens could be ascribed, at least in part, to the lack of attractiveness for the females of the water in these breeding places.

Structure of the breeding place determining selection of oviposition sites. The chemical composition of the water in larval breeding places is not the only factor that determines the selection of oviposition sites by gravid *C. p. quinquefasciatus* females. The structure of the breeding places also plays an essential part. In Rangoon, DE MEILLON *et al.* (1966) placed pans containing water from larval breeding places at different levels (from ground level to 2 m), and the number of ovipositions was greater near ground level. In Upper Volta, SUBRA (1971b) using as a model the natural breeding places (soakage pits) studied the influence of three factors: volume of water, distance between the surface of the water in the breeding places and ground level, and the degree to which the opening into the breeding places was obstructed. For an equal surface area, breeding places with the most water attracted the largest number of ovipositions. The number of ovipositions was greater, the further below ground level and surface of the water. Finally, females oviposited more readily in breeding places with an unobstructed entrance than in those in which it was obstructed.

Flight range. Research on this topic has not been very extensive and most of it has been done in South-East Asia. Most of the papers referred to here are concerned with studies using marked mosquitoes released at various points. Large differences (ranging from a few hundred metres to several kilometres) in the flight range of *C. p. quinquefasciatus* have been recorded by the various authors who have dealt with this question. In reality, these facts are more intelligible and easier to interpret if they are considered in relation to the environment in which the test mosquitoes were released—urban, rural or uninhabited.

In Rangoon (Burma), LINDQUIST *et al.* (1967) estimated the flight range of *C. p. quinquefasciatus* at 1 km. In the same city, SELF *et al.* (1971) later made a more or less identical estimate, mosquitoes flying a greater distance being the exception. In fact, most specimens fly less than 500 to 600 m from the point of release. In uninhabited areas, on the other hand, mosquitoes are able to fly for several kilometres (AFRIDI and MAJID, 1938). YASUNO *et al.* (1975) captured nearly 8% of the marked mosquitoes at 1 km from the release point. These authors worked in a situation half-way between the two examples quoted above: they released the mosquitoes in an uninhabited area but near a village in the New Delhi region. However, in the same region in a rural area BROOKS *et al.* (1976) recorded a distance of 11 km—much greater than any known hitherto. Thus, it seems that in its classical environment, an inhabited region, *C. p. quinquefasciatus* rarely flies more than a few hundred metres. However, this distance does not represent potentialities inherent in the species which, in an uninhabited area, can travel much further.

The distances covered may be influenced by the wind (FUSSELL, 1964) and by climatic conditions. YASUNO *et al.* (1973) found that *C. p. quinquefasciatus* moved faster and covered a greater distance in the hot rather than in the cold season. Study of sexual differences has led to contradictory results. According to FUSSELL (1964) and YASUNO *et al.* (1973) sex does not affect the distance covered, but LINDQUIST *et al.* (1967) found that females had a greater flight range than males.

In Africa, in Rèunion, HAMON (1953a) estimated that *C. p. quinquefasciatus* could fly a distance of 8 km by relating the densities observed at a given point to the nearest breeding place capable of producing such numbers of mosquitoes. Movements in urban and rural environments were studied in Bobo Dioulasso, Upper Volta, with the help of insects marked with fluorescent powders (SUBRA, 1972a). In the urban environment, it was found that there was a preferred direction of travel for males and females. No satisfactory explanation could be found for this phenomenon, which in any case does not seem to be the general rule, since YASUNO *et al.* (1973) observed uniform dispersion from the release point. In Bobo Dioulasso, males covered between 400 and 500 m, whereas the females could fly up to 1 km. The distance travelled by females seems to be related to their state of nutrition, since the greatest distances were covered by unfed females, some of which flew for several hundred metres following emergence. In rural areas, the females covered greater distances at a greater speed than in urban areas—up to 3.5 km from the release point (SUBRA, 1972a).

Resting places. As already stated, some *C. p. quinquefasciatus* females have an endophagic behaviour and others an exophagic. In the same way, some specimens choose resting places inside dwellings, while others find shelter outdoors. The tendency of mosquitoes to stay inside dwellings will be called *endophily*, and the opposite tendency *exophily*, although it should be made clear that during the gonotrophic cycle the same female may exhibit both tendencies.

Numerous studies have been carried out on endophilic mosquitoes, undoubtedly because they are easier to catch. In this category, adults of both sexes rest inside dwelling places by day. In Upper Volta, SUBRA (1970) observed that males were significantly more numerous in huts with corrugated iron roofs than in those with roofs of dried mud, the difference perhaps being due to the climatic conditions prevailing in the two types of houses. No such difference was found in females. While the proportions of the different stages varied with the type of house studied or the series of observations concerned, in every case it was recently fed females that made up the largest proportion of the specimens caught. The physiological age of these females varies from one season to another. Unfed females, on the other hand, always include a high proportion of nulliparous specimens, which indicates that newly emerged insects use dwellings as shelters.

Outside dwellings, there are numerous shelters where *C. p. quinquefasciatus* adults take refuge (DE MEILLON *et al.*, 1967a; SUBRA, 1970). In Upper Volta, metal shelters such as cans and cabins of lorries, seem particularly attractive to males. Furthermore, specimens of both sexes were caught in unoccupied houses, sheds and hen-coops, in jars, and in dry wells. The large catches made by SUBRA (1970) in dry wells showed that recently fed females represented the smallest part of the population present in that type of shelter, unfed females and gravid specimens were the more numerous. These unfed females, as in the case of the endophilic mosquitoes, consist mainly of nulliparous specimens which seem to shelter in wells after leaving the breeding places where they emerged.

On the basis of the above data, it is possible to sketch an outline of the behaviour of *C. p. quinquefasciatus* adults during the different phases of the gonotrophic cycle. The mosquito generally spends only a few hours in the vicinity of the breeding place from which it emerged. It then makes one or more flights, which take it to another shelter either inside a house or outdoors. When they reach the appropriate age, the females take their first blood-meal, mostly inside dwellings where they then pass the first few hours after the blood-meal. Most of them then leave the dwellings and digestion is completed outdoors in some shelter. Exophagic females, once they have taken a blood-meal, undergo their gonotrophic cycles in the outdoor shelters already mentioned. Some may even enter inhabited houses after biting man or animals outside. In any case the females, whether endophilic or exophilic, carry out a series of movements by day and night, throughout their gonotrophic cycle (DE MEILLON and KHAN, 1967).

Population dynamics. Most of the data on seasonal fluctuations of *C. p. quinquefasciatus* adults have been based on human-bait catches, since the results obtained by other methods may lead to conclusions of doubtful validity.

In Upper Volta, peak female densities in urban areas have been recorded in the rainy season and at the beginning of the dry season (SUBRA, 1973). The same applies to rural areas, where the species is, however, very much less common (HAMON, 1963). In northern Nigeria, near Kaduna, peak densities occur at the beginning of the rainy season (SERVICE, 1963).

The coastal areas of East Africa have two rainy seasons, one in April and May and the other, less important and less constant, from October to December. In the town of Mombasa in Kenya, TEESDALE (1959) observed two periods of peak densities, during and after these two rainy seasons. In rural areas, VAN SOMEREN *et al.* (1958) made similar observations, as did WIJERS and KIILU (1978). In north-east Tanzania, in a suburban locality, *C. p. quinquefasciatus* densities had two peaks corresponding to the two rainy seasons (WHITE, 1971a), the peak densities occurring during the lesser rainy season. In the Comoro Archipelago, which has only one rainy season, peak densities occur during that season both in Grand Comoro and in Mayotte (BRUNHES, 1975).

From this review, covering several areas of Africa, it clearly emerges that there is a marked relationship between rainfall and the peak breeding periods. A single peak corresponds to a single rainy season (West Africa and the Comoro Islands), while two peaks correspond to the two rainy seasons (East Africa).

The differences between maximum and minimum densities are generally very great. Thus, in West Africa, mean densities in the rainy season are often 10 times as high as in the dry season (SUBRA, 1973). Similarly, in the Comoro Islands, BRUNHES (1975) found an almost complete absence of the species during the dry season in Grand Comoro and in some villages in Mayotte. This was not, however, a general phenomenon, since in other villages, according to the same author, the reduction observed is only by a half between the two seasons; this difference is doubtless due to the nature of the breeding places and sites of the villages studied.

CONTROL

General background

C. p. quinquefasciatus is a species that has proved difficult to control in many areas although the use of insecticides has given satisfactory results in many instances. This species has shown a relatively high tolerance to DDT and other organochlorine compounds (BROWN and PAL, 1973), thus requiring application of high doses of the pesticides.

The increasing resistance to organochlorine insecticides and then to certain organophosphorus insecticides has restricted the use of these compounds and in some cases has led to a return to petroleum larvicides which had been abandoned when organochlorine compounds were originally introduced. New substances (chemosterilants, growth regulators and overcrowding factors) have also been tested, particularly in the laboratory, as have new methods of control (genetic and biological, the use of parasites and predators); but very few trials have been carried out on the African continent. Environmental improvement and integrated control through a combination of several methods have produced positive results and appear to be the most promising solution to the problem of controlling *C. p. quinquefasciatus.*

Methods of control

Chemical control. Synthetic insecticides. In the years following the Second World War, the use of organochlorine insecticides spread throughout Africa and the islands of the Indian Ocean. However, few data are available on the successive or alternative use of the compounds involved. In general, the periods of maximum utilization and effectiveness of these insecticides fall within the years 1950 to 1960, while the appearance of some cases of resistance antedate 1960. Thus, in Brazzaville DDT and HCH were used every year from 1951 to 1957, inclusive. Dieldrin was used in 1957 and alternated with DDT and HCH in the years that followed (ADAM and SOUWEINE, 1962).

In some cases, the use of combination of insecticides and oils has enabled a wider use of organochlorine preparations: for example, malariol (DDT + oil) was applied for many years in Tanzania (MENU and KILAMA, 1972).

From 1960 onwards, however, organophosphorus larvicidal compounds gradually began to replace organochlorines. Experiments carried out in Rangoon (Burma) showed that the routine use of such insecticides and especially fenthion as a larvicide gives extremely satisfactory results against *C. p. quinquefasciatus* (GRAHAM *et al.*, 1972) at a cost lower than that of the oil-based applications used previously (GRATZ, 1973a).

In Africa, starting from 1955, diazinon gave promising results on a small scale against *C. p. quinquefasciatus* larvae in heavily polluted waters (HARVEY, 1956). The most widely used OP compound has been malathion but it has the disadvantage of deteriorating rapidly in polluted waters (WHITE, 1971b). Very good results seem to have been obtained with other compounds of the same group. Thus in Bagamoyo, in Tanzania, *C. p. quinquefasciatus* densities have been considerably reduced when granular chlorfenvinphos (Birlane) was applied to latrines (MENU and KILAMA, 1972). In Zanzibar (Tanzania) the use of chlorpyrifos (Dursban) has produced encouraging results (KILAMA, personal communication) as it has in Dar es Salaam (BANG *et al.*, 1975).

Experiments on a more restricted time-scale and space, but carried out in a more rational way, have also shown the effectiveness of other organophosphorus compounds for controlling *C. p. quinquefasciatus* larvae. In towns in West Africa temephos (Abate) and chlorpyrifos have proved very effective against this mosquito (SUBRA *et al.*, 1969). On the East African coast in a rural area of Tanzania, the utilization of these two compounds has reduced by 95% the number of man-biting females (BUSHROD, 1979). In the same area, excellent results have been obtained with chlorpyrifos in the town of Morogoro, in Tanzania (MROPE *et al.*, 1973), and with temephos on the Kenyan coast (WIJERS, personal communication). In Mayotte, in the Comoro Archipelago, the use of temephos has led to reductions in adult densities in rural areas (SUBRA *et al.*, 1973). However, it is interesting to note that in some African countries, the national or local vector control services prefer to use these products (excepting temephos) as adulticides for intradomiciliary spraying and that larviciding, when carried out at all, is merely supplementary to adulticidal measures. It has been so in Mali with fenthion (SUBRA *et al.*, 1970a) and in Madagascar with malathion (SUBRA, personal observation).

It should be noted, however, that such intradomiciliary spraying is not directed against *C. p. quinquefasciatus* alone but also against anophelines, for which this control measure is often the most appropriate. In addition, they often control populations of other insects (bedbugs) that sometimes cause as much nuisance as mosquitoes, so the human population would favour spraying rather than larvicidal application, and this explains why adulticiding is sometimes given preference.

Choice of pesticides. While *C. p. quinquefasciatus* can develop a high degree of tolerance followed by resistance to these insecticides, it nevertheless is true that, if financially feasible, there is a range of new products particularly larvicides, which if rationally used produce good control results. Judicious alternation of the various compounds available seems, moreover, to be the best way of controlling *C. p. quinquefasciatus* (see HAMON and MOUCHET, 1967).

Four organophosphorus compounds can be especially used as larvicides: chlorpyrifos (Dursban), fenthion, fenitrothion (=sumithion, =folithion) and temephos. As most *C. p. quinquefasciatus* breed in rather small areas (a few square metres or less) it is difficult to estimate a dosage per hectare as is done for other mosquito species. The idea is to introduce into the breeding place a certain amount of insecticide adapted to each case and expressed in p.p.m. The places to be treated include mainly cesspools, latrines, drains, ditches and some artificial containers (drums, cisterns) which contain contaminated water. Pirimiphos methyl (OMS 1424) has also been tried as a larvicide against this mosquito by the WHO Vector Biology Control Research Unit No. 2 in Indonesia: one part per million was effective for 2 weeks.

Although indoor residual application of insecticides is not the method of choice against *C. p. quinquefasciatus*, two OP compounds (malathion and fenitrothion) and one carbamate (propoxur) can be considered under special situations. At 2 g/m^2 the effectiveness may last for about 3 months. The areas to be treated include inside walls, ceilings, sometimes furniture, and verandah, if any.

Malathion has been used in the United States of America in ultra-low volume (ULV) exterior treatments to control encephalitis outbreaks (WHO, 1970). A dosage of 225 ml per hectare proved to be sufficient to control *C. p. quinquefasciatus* outside. Nevertheless, this rate had to be increased to 450 ml to control mosquitoes inside urban housing. See Tables 1–4 for a summary of residual toxicities of larvicides and susceptibility to larvicides.

Methods of chemical application. In most cases, ground equipment is used to apply pesticides for the

Table 1. Susceptibility of fourth-instar colony larvae of *C. p. quinquefasciatus* after 24 hr exposure to various larvicides

Compound	OMS number	LC_{50} (p.p.m.)	LC_{95} (p.p.m.)
Chlorpyrifos	971	0.00071	0.0013
Chlorpyrifos methyl	1155		0.004
Parathion	19	0.0017	0.0026
Temephos	786	0.0016	0.0029
OMS 1211*		0.0023	0.0048
Fenthion	2	0.0028	0.0051
Bromophos	658	0.0058	0.0083
OMS 1210		0.0042	0.0084
OMS 437		0.0057	0.011
OMS 1290		0.0078	0.025
Fenitrothion	43	0.014	0.028
Bromophos ethyl	659	0.018	0.045
Dichlorvos	14	0.044	0.063
OMS 1287		0.053	0.072
OMS 711		0.042	0.085
Malathion	1	0.064	0.098
Tetramethrin†		0.043	0.120
OMS 236		>0.10	
Bendiocarb	1394		0.500
Pirimiphos methyl	1424		0.020
Methoprene	1804		0.010

*O-(2,5-dichloro-4-iodophenyl)O,O-dimethyl phosphorothioate.

†A pyrethrum derivative.

Source: SELF and TUN (1970).

Table 2. Residual toxicities of larvicides against *C. p. quinquefasciatus* in polluted concrete drains

Treatment	Dosage (p.p.m.)	No. of days effective
	Emulsifiable concentrates	
Chlorpyrifos	1.0	25
Chlorpyrifos	0.1	10
Temephos	2.0	15
Temephos	1.0	13
Temephos	0.1	6
Fenthion	2.5	15
Fenthion	1.0	11
Fenthion	0.5	7
Fenthion	0.1	5
OMS-1290	2.5	16
OMS-1290	1.0	11
OMS-437	4.0	14
OMS-437	0.8	11
Bromophos-ethyl	0.5	6
Bromophos-ethyl	0.25	4
OMS-1210	5.0	10
OMS-1210	1.0	7
OMS-1211	5.0	8
OMS-1211	1.0	7
Bromophos	5.0	7
Bromophos	0.1	2
Tetramethrin	5.0	6
Tetramethrin	1.0	3
OMS-1287	5.0	5
OMS-1287	1.0	3
Parathion	7.5	10
Parathion	0.04	1
OMS-236	12.5	9
Fenitrothion	15.0	10
Fenitrothion	0.4	2
OMS-711	18.0	18
Pirimiphos-methyl (OMS-1424)	1.0	14
Altosid (OMS-1697)	1.0	21
Methoprene (OMS-1804)	1.0	7

Treatment	Dosage (USgal/acre;1./ha)	No. of days effective
	Emulsifiable concentrates* + oil†	
Dursban + gas oil		10
Abate + gas oil	80; 760	10
Fenthion + gas oil		10
	Oil alone	
Flit MLO*	80; 760	8
Malariol	80; 760	6
Gas oil	80; 760	6

*Applied at a rate of 1.0 p.p.m.

†Applied at a rate of 0.19 US gallons per 100 ft^2 of water surface.

‡Obtained from the Esso Research and Engineering Co.

Source: SELF and TUN (1970).

control of *C. p. quinquefasciatus*. It can be either hand- or power-operated. In many African countries, hand-operated equipment has been preferred as it is less expensive (in terms of cost and maintenance) and easier to carry (in terms of weight and volume) in sometimes very confined spaces. Aerial equipment was used in the United States of America for the ULV treatments with malathion.

Treatment frequency of pesticides. The frequency of insecticide applications depends on the breeding periods of the species and the persistence of the compound used. In the case of adulticides, it depends amongst other things, on the nature of the substrate on which the product is sprayed. Thus, it is only possible to speak of the mean duration of effectiveness (WHO, 1970): in the case of the most commonly used compounds (malathion and fenitrothion), it is about 3 months. The duration of effect of larvicides also varies and depends on the degree of pollution of the breeding places, a high degree of pollution reducing the duration of effectiveness as well as the flow of water. Thus, in Bobo Dioulasso in West Africa, temephos remained effective in soakage pits for about 2 weeks (SUBRA *et al.*, 1970b), but in Mayotte in the Comoros it was effective for over a month in the same type of breeding place which was apparently less polluted (SUBRA *et al.*, 1973).

Precautions necessary for pesticides. Indoor spraying against adults can be applied only when food and clothing have been removed.

The larvicides available cannot be used indiscriminately in all types of breeding places. Those containing water which may be used for watering animals, or those situated near drinking water wells, must be treated with compounds of low mammalian toxicity. In such cases, temephos is preferred to chlorphyrifos, although the latter has a much longer-lasting effect.

As far as insecticide storage and use are concerned, several measures have to be kept in mind in all circumstances. Pesticides have to be stored in safe places, inaccessible to children. Staff responsible for treatment operations have to be supplied with well-maintained spraying equipment and protective clothing. In addition to this, they must be under regular medical surveillance.

Insecticide resistance. The first case of resistance to organochlorine compounds in *C. p. quinquefasciatus* was demonstrated by HAMON (1953b) in Réunion. In subsequent years, other strains became resistant: in West Africa in 1958, Central Africa (Zaire) and East Africa in 1959, Madagascar in 1961 (BROWN and PAL,

Table 3. Residual toxicities of larvicides against *C. p. quinquefasciatus* in polluted earthen drains

Treatment	Dosage (p.p.m.)	No. of days effective
	Emulsifiable concentrates	
Temephos	0.5	12
Temephos	0.1	9
Bromophos	3.75	21
Bromophos	0.75	10
Bromophos	0.50	9
Fenthion	5.0	21
Fenthion	1.0	11
OMS-1290	1.0	11
OMS-437	1.0	11
Fenitrothion	0.25	7
Parathion	3.0	9
Parathion	2.0	8
OMS-236	5.0	14
OMS-711	2.5	10
OMS-1287	1.0	3
Tetramethrin	1.0	3

Source: SELF and TUN (1970).

Table 4. Residual toxicities of larvicides against *C. p. quinquefasciatus* in polluted pit latrines

Treatment	Dosage (p.p.m.)	No. of days effective
	Emulsifiable concentrates	
Chlorpyrifos	1.0	77
Chlorpyrifos	0.1	31
Temephos	5.0	63
Temephos	1.0	35
Fenthion	2.0	24
Fenthion	1.0	21
Fenthion	0.5	10
OMS-1210	2.5	25
OMS-1210	1.0	20
OMS-1211	2.5	25
OMS-1211	1.0	18
OMS-1290	2.5	27
OMS-1290	1.0	15
OMS-1290	0.5	6
OMS-437	5.0	49
OMS-437	1.0	10
Bromophos	5.0	35
Bromophos	2.5	21
Bromophos	1.0	11
Fenitrothion	5.0	12
Fenitrothion	1.0	10
Parathion	5.0	20
Parathion	1.0	7
OMS-1287	2.5	8
OMS-1287	1.0	6
Malathion	5.0	10
Dichlorvos	5.0	10
Dichlorvos	1.0	7
Tetramethrin	5.0	4
Tetramethrin	1.0	2
	Emulsifiable concentrates + gas oil*	
Chlorpyrifos	1.0	56
Chlorpyrifos	0.5	53
Chlorpyrifos	0.1	30
Temephos	1.0	42
Temephos	0.1	12
Fenthion	1.0	21
Bromophos-ethyl	0.5	13
Gas oil alone	—*	7

*Applied at a rate of 120 US gal/acre, i.e. 0.03 US gallons per 11 ft^2 of water surface (approximately 1140 l./ha).
Source: SELF and TUN (1970).

1973). This resistance became so general that susceptibility tests carried out in 1966 by MOUCHET *et al.* (1968) on West African strains showed that only a very small number were still sensitive to DDT.

Resistance to the HCH-dieldrin group followed resistance to DDT, and showed a similar spread. It was reported in West Africa in 1957, then in Mali (1961) and the Ivory Coast (1966). In 1959 it was found in Central Africa (Zaire), East Africa and Zanzibar; in 1964 in continental Tanzania, and in 1961 in Madagascar (BROWN and PAL, 1973).

At the present moment, resistance in *C. p. quinquefasciatus* to all organochlorine insecticides seems to be general and covers vast regions in Central Africa (MOUCHET *et al.*, 1972).

Oils. Oils were employed before the use of synthetic insecticides became general. Their utilization is still considered for certain types of breeding places or in special circumstances such as when other products are not available. After the treatment of latrines with sump oil in Amani (Tanzania) WHITE (1967) observed a reduction in *C. p. quinquefasciatus* densities and the disappearance of the species from breeding places of this type where it was later replaced by *Culex cinereus* and *Culex nebulosus.* Special oils ('Flit MLO') developed during the last few years for mosquito control have proved to be excellent larvicides. They were recently shown to kill *C. p. quinquefasciatus* eggs (McDONALD, 1976), although trials carried out by WHITE (1971b) in Tanga (Tanzania) were disappointing. According to him, the lack of success could be ascribed to the rapid emulsification of the oil by soaps, detergents and urine contained in the breeding places. The rising price of oils, however, will certainly reduce if not eliminate their use against mosquito larvae.

Insect growth regulators. Insect growth regulators are a new group of products which could be used as substitutes for the larvicides mentioned above. These new pest control agents, in general, pose less hazard to the non-target fauna, man and animals.

Several trials have been carried out with OMS-1804, diflubenzuron (=dimilin) (1-(4-chlorophenyl)-3-(2,6-difluorobenzoyl)-urea), used as larvicide. This growth regulator interferes with the formation of the cuticle and thus causes disturbances during ecdysis. In India, SHARMA *et al.* (1975) found the duration of its efficacy to be about one week. The same product has given much better results in Africa at Bobo Dioulasso (Upper Volta) where SALES and HERVY (1977) found that its effect persisted for about a month. This compound has also been tested in Indonesia by WHO/VBCRU-2 and found effective for 2 weeks (SELF *et al.*, 1978).

Another compound, OMS-1697 (methoprene or Altosid) has been tested at Jakarta by NELSON *et al.* (1976) and SELF *et al.* (1978). It simulates juvenile hormone, and disturbs pupation causing the death of pupae or of adults when they emerge. Its effectiveness was assessed on the basis of the reduction in female population densities in the treated zone. This reduction, which was observed over a long period (between the second and seventh week following treatment), was about 84% in specimens caught on human-bait and 69% in those caught inside dwellings.

Overcrowding. Pre-imaginal forms of mosquitoes breeding in very large numbers in a small space may release substances that slow up growth and cause high mortality among young specimens of the same species. This phenomenon, which was observed as long ago as 1930 by ROUBAUD and TOUMANOFF in *C. pipiens*, has recently been studied in *C. p. quinquefasciatus* by IKESHOJI and MULLA (1970b). These same authors (1974a, b) have isolated and chemically identified the factors responsible for these developmental anomalies. If they prove effective in the field, they could play a considerable role in controlling mosquitoes, especially *C. p. quinquefasciatus*, on which most of the research has been done (HWANG and MULLA, 1976; MULLA, 1976). At the moment, they are still in early stages of testing.

Genetic control. Genetic control would doubtless constitute one of the most satisfactory ways of dealing with the problem of mosquito control since it does not require the use of any chemical product in the field and the risks of pollution are therefore nil. Furthermore, only the target species is affected by such control operations, and thus there is very little disturbance of the natural balance.

Studies on cytoplasmic incompatibility have been carried out on *C. pipiens* (MARSHALL and STALEY, 1937) and later on *C. p. quinquefasciatus* (ROUBAUD, 1956). Crossing experiments in Africa on the latter species have used strains from different areas, and some have resulted in incompatibilities. In West Africa SUBRA (1972c) achieved 57 crosses (out of 72 possible) with nine different strains. With a strain from Thies in Senegal it was possible to classify the various strains tested into six different types according to success or failure in crossing, and in which direction or directions. Thirty crosses carried out by LAVEN (1969) with six strains from West (two), Central (two) and East (two) Africa also demonstrated several cases of incompatibility. On the other hand, six strains of *C. p. quinquefasciatus* caught in Tanzania and Kenya and crossed by MAGAYUKA and WHITE (1972) showed no incompatibilities in 26 crosses achieved (30 possible).

In an experiment carried out in Asia (LAVEN, 1967), non-indigenous males incompatible with the females of the local strain were released in a Burmese village. After a few weeks none of the eggs laid by these females was viable. In a trial based on the release of males sterilized in the pupal stage with thiotepa in the United States of America (PATTERSON *et al.*, 1970), the indigenous population of *C. p. quinquefasciatus* was suppressed 10 weeks after the beginning of the trial. Although these two trials were carried out on a small scale in well-isolated zones, they nevertheless proved that the released males competed with the males of the wild population.

Two trials carried out in the Delhi region (YASUNO *et al.*, 1978; BROOKS *et al.*, 1976), the first using chemosterilized males and the second using males incompatible with the local strains and in which a sex-linked translocation had been introduced, resulted in a high percentage of sterility. However, in both cases the trials did not have the success anticipated because of reinvasion of mosquitoes from the outside.

While genetic control in theory remains one of the most attractive methods of control, at present none of the methods is operational. Prospects of their use on a large scale are not very promising due to reinvasion problems, human factors, and high cost. As GRATZ (1973a) observed, vast difficulties must be overcome and further knowledge acquired before such methods can be used routinely.

Biological control. Predators. Use of larvivorous fish is one of the oldest and best-known methods of controlling mosquitoes. In East Africa, they were introduced several centuries ago by the Arabs who had founded towns and villages along the coast. The fish were placed in tanks ('birikas') where the water was kept for ritual ablutions and where *Aedes aegypti* and *C. p. quinquefasciatus* developed (WIJERS and SUBRA, personal observation). After the Second World War, fish (*Lebistes*) were used in Tanzania in breeding places of the same type (BANG *et al.*, 1973a).

The recent resumption of their use was envisaged especially because it became obvious that synthetic insecticides could not by themselves solve all the problems of *C. p. quinquefasciatus* control. The first obstacle to the use of these predators lay in their inability to adapt themselves to highly polluted waters which are the most productive breeding places for this mosquito. However, work by SASA *et al.* (1965a) showed that in some places, such as Bangkok, *Poecilia reticulata* (ROZEN and BAILY, 1963) developed satisfactorily in polluted breeding places. BAY and SELF (1972), studying the problem in other towns in South-East Asia, considered that larvivorous fish could be used effectively to control mosquito larvae but in restricted situations, since various factors work against their establishment in all types of breeding places. The Maldive Islands would seem to offer a situation exceptionally favourable to the use of fish as the main means of controlling several mosquito species, including *C. p. quinquefasciatus* (VELIMIROVIC and CLARKE, 1975). The larval breeding places are mainly wells in which three different fish species can be introduced (*Poecilia reticulata, Mollienesia sphenops* and *Kuhlia taeniurus*, a marine species adapted to life in wells).

In addition to fish, attention has also been given to other predators, including the mosquito larvae belonging to the *Lutzia* genus, which are able to develop in some of the *C. p. quinquefasciatus* breeding places (GRATZ, 1973b).

Parasites. Field trials have been carried out in South-East Asia and also in the South Pacific. REYNOLDS (1972) succeeded in introducing a microsporidan, *Plistophora culicis* Weiser, into a natural population of *C. p. quinquefasciatus* in Nauru Island in Micronesia but did not succeed in appreciably reducing the density of populations of that mosquito.

Nematodes belonging to the *Romanomermis culicivorax* species have also been tested experimentally to control *C. p. quinquefasciatus.* In the laboratory, a strain of this mosquito from Taiwan proved to be very susceptible to infection by *R. culicivorax*, with infection rates ranging from 90 to 100% (MITCHELL *et al.*, 1974). Nevertheless, a trial carried out in Bangkok by CHAPMAN *et al.* (1972) proved quite disappointing, since the percentage of mosquitoes infected by the parasite was low. Moreover, these authors were not certain that the parasite could survive under natural conditions. Later on, CHEN (1976) in Taiwan observed that this same parasite could complete its life cycle in nature but emphasized the importance of pH as a limiting factor. More recently, in the United States of America, LEVY and MILLER (1977) were able to get 53.7% parasitism in *C. p. quinquefasciatus* larvae breeding in an abandoned sewage settling tank, and it was concluded that this mermithid had potential as a control agent against this species. Nevertheless, it is worth noting that *C. p. quinquefasciatus* can develop resistance to *R. culicivorax* which might reduce the possibilities of its use on a large scale. This has already been reported by PETERSEN (1978).

One of the most promizing pathogen agents seems to be a spore-forming bacterium discovered a few years ago by GOLDBERG and MARGALIT (1977) and identifed as *Bacillus thuringiensis* serotype H-14 (DE BARJAC, 1978). It produces a crystal of toxin protein (delta-endotoxin) which acts as a stomach poison when eaten by the insect. It is active, against several mosquito species, including species of the *Culex pipiens* complex (Garcia and Desrochers, 1979), and it has a high degree of safety for non-target organisms (Dejoux, 1979; Sinegre *et al.*, 1979). To determine whether it might be one of the main tools for future control of *C. p. quinquefasciatus* in developing countries will require large-scale field experiments.

Environmental management. These measures aim at eliminating the breeding places that enable mosquito larvae to develop. A distinction will be drawn between operations aimed at eliminating these sites on a relatively permanent basis (environmental modification), and those which tend only to get rid of unstable and generally small breeding places temporarily (environmental manipulation).

Waste water can be discharged either through well-designed soakage pits in which mosquito larvae can no longer develop, or by building sewers which at the same time avoid accumulation of stagnant rainwater and replace latrines. Disappearance of breeding places of this type would considerably reduce the densities of *C. p. quinquefasciatus* and would lead to large savings in both insecticides and manpower. However, the development of such systems requires large investments often beyond the available resources of a particular state. It is nevertheless the aim to which all concerned should be directing their efforts, even if it is not immediately attainable.

Besides the breeding places mentioned above which are characterized by their stability and large size, are small collections of water resulting from human activity or negligence (tin cans, broken bottles, etc.). Their elimination by the health services or the inhabitants themselves can also help to reduce adult densities. The most important problem here is to convince populations of the need to continue their efforts and thus to avoid a return to the *status quo ante* once the first enthusiasm has died down. Here health education must play a primary role, since there can be no permanent environmental improvement without the cooperation of the local population (WHO, 1975).

Integrated control. Integrated control aims primarily at combining methods, which if applied separately, would not achieve the desired result but together are mutually complementary.

Several pilot field trials have been carried out in South-East Asia. In Rangoon, Mathis (1972) successfully combined the use of larvivorous fish (*P. reticulata*) and the larvicide fenthion with a view to controlling the pre-imaginal females of *C. p. quinquefasciatus* developing in a ditch. In Bangkok Prakong Phan-Urai *et al.* (1975) had achieved a reduction of something like 75% in size of pre-imaginal population by twice a week removing the debris floating on the top of two pools colonized by *C. p. quinquefasciatus.* The introduction of *P. reticulata* also reduced the number of pre-imaginal forms down to only 2% of the level observed before the beginning of the trials. Interruption of the removal of this debris was followed by an increase in the culicid population.

At Dar es Salaam in East Africa, in a large-scale trial affecting several species (*Anopheles*, *Ae. aegypti*, *C. p. quinquefasciatus*), Bang *et al.* (1975) combined environmental improvement and insecticides. A reduction in the number of larval breeding places and the spraying of latrines and polluted water with chlorpyrifos led to a reduction of 92% in adult densities of *C. p. quinquefasciatus* evaluated on the basis of room-pyrethrum spray catches. This is ample proof of the success of the operation.

Evaluation

Evaluation is an essential component of any vector control operation. Its aim is to assess the effects of these operations on vector densities and disease impact. In areas of Africa where *C. p. quinquefasciatus* is only important as a nuisance, the evaluation will deal only with mosquito population densities. When it is considered mainly as a filariasis vector, evaluation will also involve reduction in disease transmission and prevalence.

Mosquito densities. It is essential to collect data on mosquito densities prior to any control operation, then to compare them with the data obtained during and after these operations. When possible, there should be an uncontrolled experimental area in order to evaluate density variations which may not be related to control operations.

Mosquito densities can be measured at each of the development stages: eggs, pre-imaginal forms, and adults. Finding and collecting egg rafts of *C. p. quinquefasciatus* is not always very easy, especially in breeding places which may be several meters deep. Accurate identification requires larvae bred to the fourth stage, which requires time and laboratory space. In addition, important fluctuations in the number of egg rafts laid in the same breeding place from day to day (Subra, 1971) may give a false idea of the size of the mosquito population. In this respect egg sampling cannot contribute to proper evaluation.

Larvae and pupae are sampled at the same time. Several devices have been developed which have been reviewed by Service (1976). Most *C. p. quinquefasciatus* breeding places have a rather limited surface, and it is usually relatively easy to check whether or not they are colonized by this species. However, in cases where water surface is not easy to reach (very deep latrines, cesspools covered with a cement cap), proper pre-imaginal sampling may then be difficult and inappropriate for evaluation.

Adult mosquitoes may be sampled using numerous methods and devices (Service, 1976). The most commonly used in Africa to assess the effects of control operations have been night catches on human baits (Subra *et al.*, 1973; Bushrod, 1979; Wijers, unpublished report) and day catches (either by hand or pyrethrum spray catches) of females resting inside the houses (Subra *et al.*, 1970). The favourable or unfavourable reactions of people living in the area where control operations are taking place is another way of assessing the success of mosquito control. Although it cannot be measured on a scientific basis, it is an indication which has to be taken into account by those responsible for these operations.

Reduction in disease transmission and prevalence. Reduction in disease transmission as well as reduction in disease prevalence are the two major factors which have to be assessed, in addition to density reduction, when the target mosquito is a disease vector. Thus in Tanzania, the success obtained in reducing densities of *C. p. quinquefasciatus* and *Anopheles gambiae* complex species was confirmed by an important reduction of filariasis transmission (BUSHROD, 1979). On the other hand, in Réunion, a large decrease of the number of cases of bancroftian filariasis was observed after intensive antimosquito measures mainly aimed towards malaria vectors (BRUNHES, 1975).

Conclusions

Complete success in operations to control *C. p. quinquefasciatus* is rare. In most instances, the species has been able to overcome the obstacles placed by man in the way of its breeding. It is true that often these efforts to control the mosquito were unsuccessful because new breeding sites were created by man. This situation has led many authorities responsible for vector control to believe that the control of *C. p. quinquefasciatus* is ineffective or at least requires means that are out of reach of their financial resources.

An interesting paper by GRAHAM and GRATZ (1975) has shown that in numerous developing tropical countries the sums devoted to vector control were often considerable. The bulk of the failures seem to be due to faulty planning, execution and surveillance of operations. Thus it becomes essential to strengthen the already existing cadre of mosquito control workers (MACDONALD, 1978) and to carry out cost/benefit studies for the control operations on the basis laid down by CVJETANOVIC and GRAB (1976) to ensure better utilization of the available funds. Perhaps, it would then be possible to maintain *C. p. quinquefasciatus* densities at a sufficiently low level to ensure that the mosquito ceases to be one of the major health problems in the human environment in the tropics.

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