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ECOLOGICAL FACTORS IMPORTANT IN INSECTICIDAL AND ALTERNATIVE MEANS OF MOSQUITO CONTROL

by

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1. Introduction

At present large-scale mosquito-control operations rely mostly, if not only, on insecticidal means although many alternative means have been used in the past and many more may be employed in the future.

These alternative means can be listed under several headings: environmental sanitation, use of predators, use of pathogens, genetic control; furthermore integrated control operations can be developed associating one or several of these alternative means and some of the presently used chemical approaches.

A large, but not always sufficient, background of information is available on the facets of the vector ecology related to the conventional means of vector control which deal mostly with female mosquito destruction by residual sprays and with larvicidal control of some major pests. Far less data are available on male ecology and even on female and larval ecology of some important tropical vectors.

The intelligent use of any of the alternative means presupposes a far better knowledge of vector ecology than presently available and will generally involve also a thorough study not only of the vector but also of its hosts, parasites, predators and general environment and of all the relationships between these. Furthermore the study of behaviour genetics and of population genetics will be, in many instances, of the utmost importance.

To some extent insecticides also must be considered against the same criteria as living organisms in that they migrate, they can be destroyed by living organisms or by inimical environments, and they have a behaviour varying greatly according to their formulation and site of application. So their "ecology" cannot be ignored.

2. Insecticidal methods

Insecticidal methods are constantly being improved, with the replacement of the most residual compounds, the organochlorinated ones, by new toxicants which belong generally to the organophosphate and carbamate groups and are much more easily biodegradable (Brown, 1967; Hayes, 1967). The insecticide application is focused more and more on the very area or spot where the vectors are, in order to decrease both the environmental contamination and the operational costs, and this involves serious ecological investigations before planning any mosquito control programme. Special recommendations relative to the optimal use and safety margins of pesticides are periodically issued by WHO and other agencies (Anonymous, 1963 and 1967). Although some general antimosquito measures can be applied, the methods vary usually with the species and are distinct according to their use against adults or against larvae.

2.1 Against adult mosquitos

The first large-scale programme against adults has involved anopheline mosquitos for malaria control operations and represents up to now the biggest collective operation against a vector-borne disease; it has been based from the beginning on the application of residual sprays inside houses, which is the most economic and practical vector control method in rural areas (Rafatjah, 1965). Efficient house-spraying implies a thorough geographical reconnaissance for the location of houses and other human shelters as well as the determination of the main seasons of house-building, wall-replastering, and so on. So human ecology is at least as important as vector ecology. The efficacy of the spraying depends on the feeding habits of the vector, on its resting habits immediately before and after taking a blood meal, as well as on the human ecology. Species with exophilic and exophagic tendencies, but biting from dusk onwards, may be controlled very well by residual sprays if humans stay inside houses from dusk to dawn whereas the vectors may not be affected if humans chatter outside after dusk or sleep outside part of the night, depending on the biting cycle of the epidemiologically dangerous females (Chauvet et al. 1968; Chow, 1968; Elliott, 1968 and 1969; Hamon, 1967; Hamon et al. 1964a, 1964b and 1969; Scanlon et al. 1968). With endophilic species a partial spraying of the houses may be as effective as the complete spraying, depending on the exact resting sites of the vectors. Where mosquito bed-nets are of general use and vectors are night biters, a residual treatment restricted to these nets could be as effective as the complete spraying of the house. It must be stressed that, in malaria control or eradications operations, the official purpose of the treatment is to decrease the man-vector contact and the longevity of the vector to such an extent that malaria transmission becomes impossible, one important point being the destruction of the female vectors before they reach an epidemiologically dangerous age (usually two weeks in tropical countries). Very few other methods of mosquito control can achieve such a result, which is also required for filariasis control, as they usually interfere only with the density of the vector, but not with their behaviour or longevity.

Space-sprays are mainly used for controlling exophilic and exophagic pest mosquitos, specially if they are day-time or dusk-time biters. They began to be used also for stopping arbovirus epidemics by killing all vectors at a time, including infected ones, over large areas (Kilpatrick et al. 1968; Kilpatrick and Adam, 1967; Knapp and Roberts, 1965; Stevens and Stroud, 1966). They are also used sometimes for larviciding (Burgoyne et al. 1967). The efficacy of such sprays can be greatly enhanced if the exact resting places and peak period of emergence of the vectors are known, which allows the application to be restricted to the very periods and locations (Anonymous, 1967c; Clarke, 1967). The nature of the spray and the size of the droplets must be selected for reaching the vectors on the wing or at their resting sites through the vegetation and shelters.

Against exophilic species with a restricted flight range, perifocal spraying in the immediate vicinity of the breeding places or of the hosts to be protected may complement very efficiently house-spraying or larviciding operations (Gabaldon et al. 1963).

Recommendations to humans during epidemics must also be closely related to the vector ecology. In French-speaking West Africa it was traditional, during the past yellow fever epidemics, to restrict movements out-of-doors to day-time hours, in the belief that vectors were night-time biters. It was of little use as the main urban vector has its activity peak during the late afternoon and bites all the day long whereas several of the most important silvatic vectors are also day-time and dusk biters.

2.2 Against mosquito larvae

In many instances it is more convenient and cheaper to kill the pre-imaginal stages than the adult mosquitos, specially in densely inhabited areas and with pest mosquitos. The large number of toxicants and formulations available for larviciding offers the possibility of dealing with almost any particular situation (Hamon et al. 1965; Mulla, 1969). Furthermore some of the pesticides which are the most toxic for humans, such as parathion, can be widely used as larvicides because of the very low dosages employed and their rapid disappearance from the treated area by biological degradation (Anonymous, 1967c).

The organization of larviciding must be based both on a complete geographical survey of all potential breeding places and on the effective flight range of the vector (Dow, 1965; Fussell, 1964; Lindquist et al. 1967; Rafatjah, 1965; Schoof, 1967). Checking the positivity of breeding sites is often more costly than carrying on blind spraying of all potential sites, but this alternative increases the contamination of the environment; a good knowledge of the vector ecology must allow the spraying to be restricted to the small number of really important breeding sites (Rioux et al. 1967, 1968; Rafatjah, 1965). The timing of applications must be closely related to the speed of preimaginal development and to the vector population dynamics in order to destroy the vector when it is the most vulnerable. For example in the irrigated areas of the United States of America, larviciding has to be carried out two or three days after each water introduction (Anonymous, 1967c), whereas against some tropical vectors the residual breeding places of the dry season appear to be the most vulnerable (Surtees, 1960).

When preflood treatment of the potential breeding places is preferred to the larviciding of the actual breeding sites, the same problem of the exact location of the areas to be treated arises.

For minimizing the practical importance of the environmental contamination it is vital, when planning operations and selecting the insecticide, its dosage and formulation, to take fully into account not only the vector ecology but also the population dynamics and ecology of all major animal components of the treated areas (Butler, 1963; Dubos, 1967; George, 1963; Hamon et al. 1965; Mulla, 1969; Mulla and Isaak, 1961; Patterson and von Windeguth, 1964; Rongsriyam et al. 1968), including eventually beneficial micro-organisms (Noguchi et al. 1965) as well as mosquito competitors (Service, 1966; Gilotra et al. 1967).

Wherever some of the breeding places are man-made, human ecology becomes an important factor; for example in the Senoufo country of West Africa the small jars which contain traditional medical macerations of vegetal origin are usually stored in concealed places within houses and never deliberately shown to foreigners, constitute the main permanent Aedes aegypti breeding places during the long dry season (Pichon and Sales, 1967).

3. Environmental sanitation

Environmental sanitation has been the first mosquito control measure widely used in the past, sometimes with great success (Muirhead-Thomson, 1951; Rafatjah, 1965). It has been largely abandoned, in most tropical areas, with the advent of the modern residual insecticides and the consequent reappearance of acute mosquito problems in many urbanized and even rural areas; however it has always been in use on a large scale in many temperate countries, most of the available literature coming from the United States of America (Anonymous, 1967c). The main aspects of environmental sanitation are direct source reduction and prevention, water level management, and ecological modification of the environment.

3.1 Direct source reduction and prevention

Direct source reduction implies either the mechanical elimination of breeding places or the prevention of their creation. It supposes a minimum knowledge of vector and human ecology in order to avoid misdirected and useless work (Laurence, 1965) and regulations, as well as a good geographical reconnaissance. It can involve more or less elaborate devices such as fern planting in tree holes, coco-nut protection from rats and even rodent control, (Bonnet and Chapman, 1956, 1958; Chapman, 1967a, 1967b; Pichon et al. 1969; Tadzhieva, 1965). It is usually a very cheap, but often unpopular, method of mosquito control as it must be accompanied by laws and their enforcement.

The systematic organization of irrigation systems, with land levelling, water control, intermittent application, and drainage of excess water, belongs in this category and involves more problems of human behaviour than of mosquito ecology (Davis, 1959; Stivers, 1957). It constitutes also a transition to water level management.

3.2 Water level management

Mosquito control through water level management involves usually one or several of the following in conjunction or in sequence: drainage, ditching, dyking, levelling, flooding, opening to wave action, periodic alterations of the water level. This requires a very good ecological knowledge not only of the vector to be controlled but also of all potential vectors and pests which could successfully colonize the newly created environment. Furthermore, all actions of this type have immediate consequences on the wildlife as well as on the economic potentialities of the treated areas. So water level management is usually a costly affair and is mainly employed in developed temperate countries often in conjunction with complementary insecticidal applications (Anonymous, 1967c; Clements and Rogers, 1964; Christopher and Bowden, 1957; Edman, 1964; Graham, 1967; Philen and Carmichael, 1956; Travis, 1957).

In many coastal areas the permanent flooding of salt-marsh areas, by water pumping, produces less mosquitos than intermittent flooding by rainfall and high tides. Sometimes the mosquito species favoured by permanent flooding may be eliminated by introducing a proportion of sea-water into the flooded areas or reduced in numbers by fish predation (Clements and Rogers, 1964; Phelin and Carmichael, 1956).

Along dammed rivers prevention of mosquito breeding and purposes of the dam building are often conflicting and very elaborate systems have been built, such as by T.V.A. authorities, with a complex time-table of operations to deal with all aspects of the situation, variations in the water level increasing the possibilities of fish predation on mosquitos and the efficacy of insecticidal applications (Christopher and Bowden, 1957).

The periodic flushing of river courses, used in the past against some malaria vectors (Muirhead-Thomson, 1951), belongs also to this category of mosquito control means, as well as the periodic agitation of the water surface by sprinkling (Schober, 1966).

3.3 Ecological modification of the environment

The ecological modification of the environment was largely used in the past. It consisted in modifications of the breeding sites rendering them unfavourable, or at least less favourable, for the vectors. It has relied mostly on either overshading or else exposing breeding places to the sun, or in introducing sea-water in fresh-water lagoons, etc. (Muirhead-Thomson, 1951; Travis, 1957). It must be noted that the success of such ecological manipulations depends on the absence of alternative vectors able to exploit the new type of environment.

Some renewal of interest for such modifications has been recently manifested, studies having been carried out on tree planting (Smith et al. 1969), on hostile vegetation of small size (Lemna, filamenteous algae, Phragmites reeds (Kuhlhorn, 1965)), and on the possible selective destruction of flowering plants on which the male mosquitos feed in semi-desert areas (Abdel-Malek, 1963). Further investigations should be interesting on the latter.

4. Use of predators

Predators, like parasites, are self-perpetuating organisms, and may be helped or exploited in several ways (Beirne, 1965):

in removing from the environment the factors preventing them from increasing in numbers;

in adding or increasing environmental factors favourable for them;

in increasing the numbers of already present predators by mass rearing and release;

in importing, rearing and releasing predators not existing locally.

It is also important to avoid eliminating the predators during the application of other mosquito control means.

The principally studied mosquito predators are fishes, but many other organisms play a predatory role in the natural regulation of mosquito populations.

4.1 Fish

Fish have been used more or less effectively for mosquito control for at least 50 years (Gerberich and Laird, 1966) but suffered from a lack of interest with the advent of residual insecticides. However their study has never been abandoned and new developments depend on a better understanding of their ecology and potentialities. They are widely used in the United States of America as a biological measure supplementary to insecticides and other control measures, and this is probably their best use (Anonymous, 1967c).

Many indigenous fish destroy mosquito larvae all over the world but, in the past, attention has been focused mainly on two small-sized species which have no economic value except as mosquito-eaters, namely Gambusia affinis and Lebistes reticulatus. Various strains of these species are known, covering most of the ecological conditions found in temperate and tropical permanent waters, including brackish ones, but none of them is drought-resistant. The discovery of species of fish with desiccation-resistant eggs ("annual fishes"), in Africa and in South America, has recently opened a new field for the use of fish as mosquito control agents (Bay, 1966, 1967a, 1967b; Bay and Anderson, 1965; Hildemann and Walford, 1963). However many fish strains have a narrow tolerance and can only be efficiently used within certain physico-chemical limits (Laird, 1967a). The main successes have been reported from the USSR for the regional use of Gambusia on a sound ecological basis, whereas their introduction without any prior reference to the ecological parameters of the species strain and of the vector either failed completely or at best gave inconclusive results (Gerberich and Laird, 1965).

Phytophagous and carnivorous fish can be employed in association, one species destroying the vegetation protecting the mosquito larvae and the other eating the larvae (Nagakawa and Hirst, 1959). Fish can even be used in association with insecticides, many compounds being far more toxic for the mosquito larvae than for the Gambusia and Lebistes, the highest safety margin being observed with Abate, while the use of fenthion and fenitrothion is feasible (Mulla and Isaak, 1961; Rongsriyam et al. 1968; Sasa et al. 1964). Furthermore some strains of Gambusia are resistant to organochlorine insecticides and can be introduced into water highly contaminated by these toxicants, with the risk of transferring these compounds into bigger organisms along the food chain (Vinson, 1968). A Lebistes population, in Bangkok, is highly tolerant to organic pollution and occurs in large numbers in canals, ditches and ponds contaminated by domestic refuses, faeces, and so on, and could by itself reduce by 90% the Culex p. fatigans population of the city (Sasa et al. 1964); such a strain appears to offer unique opportunities for introduction in polluted waters of tropical areas.

Mosquito-eating fish, however, cannot solve all problems; they have general zoophagic habits and eat mosquito larvae amongst other aquatic organisms and very often co-exist with mosquito larvae in most of the areas they inhabit. They are usually efficient only when they reach high densities or when they cannot find any food but mosquitos; they multiply also more slowly than mosquitos and, in temporary breeding sites, cannot control the first mosquito brood following the site flooding. So mosquito-fish must mainly be considered as adding their weight to the pre-existing mosquito population limiting factors, if they do not replace them by destroying other predators as well as mosquito larvae.

In all instances mosquito-fish species must be considered as general feeders, self-perpetuating, which will permanently affect the environmental equilibrium from their very introduction. Their impact on aquatic organisms and wild life cannot be underestimated and may be worse than one of any insecticide application. So introducing a predatory fish in a new area must only follow a thorough assessment of all probable implications, including competition with the already occurring fish and predators.

4.2 Predators other than fish

A very long list of mosquito predators other than fish has been established by Jenkins (1964) and some more recent for complementary data are available, but few of the species involved have yet been considered as of practical use.

Ants and Carabidae beetles prey on Aedes eggs (James, 1966). Chaoboridae larvae, dragonfly adults and larvae, Dytiscidae adults and larvae, Ephemoptera larvae, Empididae adults, Gammarus, Corixidae, Nepidae and Notonectidae bugs, as well as tadpoles, have been all recorded as playing a role as mosquito predators (Boorman, 1961; Christie, 1958; Kulhorn, 1965; Laurence, 1965; O'Connor, 1959; Pritchard, 1964a, 1964b; Sailer and Lienk, 1954; Service, 1965a, 1965b). None of them appears very promising for mass production and release, although some of them could be very efficient in small breeding sites and when they do not have any other prey available but mosquitos.

Some Eretmapodites and Armigeres mosquitos have obligatory or facultative predaceous larvae and may destroy mosquito larvae of other species sharing their breeding places, but their biting habits as adults do not recommend their use as mass-produced mosquito predators (Corbet, 1964; Ikeshoji, 1965).

Toxorhynchites and Culex (Lutzia) mosquitos have obligatory predatory larvae; the former are exclusively nectar-feeders whereas the latter are mostly, if not only, ornithophilic and have never been involved in the transmission of any disease. The different studied species of Toxorhynchites (brevipalpis, b. conradti, splendens) and of Lutzia (tigripes, vorax, fuscanus) occur usually at low natural densities but have sometimes an important impact on mosquito populations of other species, especially in small breeding places (Corbet, 1964; Chan, 1968; Haddow, 1942; Ikeshoji, 1960c; Laurence, 1965; Laurence and Samarawickrema, 1966; Masuda, 1965; Mellanby, 1956; Muspratt, 1951, 1963; Nakagawa and Hirst, 1959; Yasuno, 1965).

Both Toxorhynchites and Lutzia larvae can attack and kill larvae of their own species but whereas the former do so as a rule before pupation the latter attack to a large extent only when the food is scarce, or with smaller larvae. Lutzia larvae can withstand some starvation and Toxorhynchites can starve for several weeks, resuming development when food becomes available again. Lutzia may occur apparently in any tropical environment and are somewhat common in urban areas, whereas Toxorhynchites are restricted to rural areas as the adults feed exclusively on flowers. Toxorhynchites females lay eggs in small containers, including plant-axils; Lutzia females deposit their egg-batches in almost any type of breeding place except plant-axils.

Despite their lower daily consumption of other mosquito larvae, Lutzia have a predatory role probably no less important than Toxorhynchites. All available studies underline that Lutzia can eradicate other mosquito species from small breeding places and kill a large proportion of them in larger breeding places. However it must be noted that, from an overall point of view, both Toxorhynchites and Lutzia, as well as most of the other predators of the same category, are of relatively limited importance by comparison with other population-regulating factors. The general ecology, including dispersal and population dynamics, of Lutzia and Toxorhynchites has yet to be investigated for assessing the precise role they could play in integrated control operations. The mass production for release of Lutzia species has never been attempted whereas this has been done for at least two Toxorhynchites species.

The introduction of Toxorhynchites species in new areas has been performed on a small scale only and has not yet been very successful, (Laird, 1963; Nakagawa and Hirst, 1959).

Without being predators, the mucilaginous seeds of several Crucifera have been observed to entrap and kill the mosquito larvae which attempt to feed on them (Reeves and Garcia, 1969). This phenomenon is very original but does not seem very promising for large-scale use.

5. Pathogens

Many mosquito pathogens are known and the number of pathogenic agents and of affected mosquito species has increased at a steady rate in the last several years. The lists of pathogens includes viruses, bacteria, protozoa, nematodes and fungi. The situation has been recently summarized by several specialists, either from a general point of view or for a limited group of pathogens (Jenkins, 1964; Jenkins and West, 1954; Kellen, 1960, 1962; Madelin, 1966; Roberts, 1969; Weiser, 1963). Furthermore lists summarizing recent identifications of pathogens and hosts have been published by Briggs (1967, 1968).

5.1 Bacteria and protozoa

Bacillus sphaericus has been observed in mosquito larvae only and did not appear to be harmful for other aquatic organisms. It has been successfully introduced in natural breeding places but its incidence on larval mosquito densities was usually low. It has been cultivated in the laboratory where it has infected easily all mosquito species tested, inducing heavy mortality. To be pathogenic it must be ingested in such large quantities (8 000 000 to 85 000 000 spores per ml) that it does not appear of any practical use as it stands (Kellen et al. 1965).

Ciliates and Vorticella sp. have been found occasionally infecting and killing mosquito larvae (Muspratt, 1945; Micks, 1950, 1955; Scholer, 1967). Vorticella can induce heavy mortalities but appeared as being very specific, destroying only one of the three mosquito species at risk (Micks, 1950).

Microsporidia, belonging mainly to the genus Thelohania and Stempellia, have been mostly observed in Europe and the United States of America, where they have been extensively studied (Anderson, 1968; Bailey et al. 1967; Kellen, 1960, 1962; Tsai et al. 1969). Some recent observations deal also with Venezuelan anophelines (Dary and Gamey, 1966). They can induce heavy mortalities in some species and within certain breeding places but seem often to be highly specific. In Venezuela, amongst more than 10 000 larvae examined only An. pseudopunctipennis larvae were infected, but their infection rate was 44%. In the United States of America many unaffected mosquito species were developing side by side with other species densely infested by Thelohania or Stempellia. The laboratory transmission of these pathogens has hitherto been very erratic.

5.2 Helminths

With the exception of one observation carried out in Bulgaria and dealing with trematode larvae in An. maculipennis (Kovchazov, 1963), all helminths recorded from mosquitos belong to the Mermithid nematodes. They have been observed in temperate areas as well as in tropical ones. Several species have been successfully cultivated in the laboratory over a wide host range within the family Culicidae, which agrees with field observations (Artjuhovski and Kolyceva, 1965; Chapman et al. 1967; Coz, 1966; Petersen and Willis, 1969; Muspratt, 1945, 1965; Petersen et al. 1967; Tsai et al. 1969).

In field conditions the infection rate by Mermithidae can be very high and many of the species sharing the same breeding places are infested by apparently the same species, as observed in Zambia and in the United States of America with Romanomermis sp. (Muspratt, 1945, 1965; Petersen et al. 1969), and in the United States of America with Reesimermis nielseni (Tsai et al. 1969). The Romanomermis both of Zambia and the United States of America have been colonized and could apparently be produced in some numbers, infesting most of the species offered to them. However the Agamomermis observed in Louisiana parasiting Ae. sollicitans was relatively specific, inducing at the most low percentage infections in other mosquito species as against 94-100% infections in Ae. solicitans (Petersen and Willis, 1967).

Mermithidae infections are usually fatal to the affected larvae which die before pupation. Females, when they harbour the parasite, do develop ovaries (Coz, 1966).

5.3 Fungi

While many observations have been made recently on a variety of entomophagous fungi (Clarke et al. 1967, Novak, 1965, 1967; Weiser and Novak, 1962), the only systematic investigations have been carried out on Coelomomyces species (Chapman and Woodard, 1966; Gad et al. 1967; Laird, 1962, 1966; Madelin, 1964, 1965, 1967; Muspratt, 1963; Rajapaksa, 1964). Coelomomyces, which is a genus of fungi restricted to mosquitos with a few exceptions, appeared at one time to be amongst the most promising pathogens for mosquito control (Laird, 1962). At least some of the species, such as Coe. indicus and Coe. stegomyiae, are apparently not highly specific and have been naturally observed in several mosquito species and genera, or have been passed on them (Muspratt, 1963; Gad, 1967; Laird, 1966; Rajapaksa, 1964). However laboratory cultivation of the most promising species has not yet given any conclusive results (Madelin, 1967).

In Zambia, Muspratt has shown that Coe. indicus can persist up to 20 years in the same sub-permanent breeding places, with few if any natural dispersion, infected pools occurring side by side with uninfected ones without any conspicuous ecological difference between the two categories. Muspratt succeeded in infesting new pools by transferring infested larvae but never got any infection in plastic containers. He suggested that in nature Dytiscid beetles could play a role in the Coelomomyces spore dissemination.

In one of the Tokelau Islands, Nukunono, the deliberate introduction of the pathogen together with infected mosquito larvae has been successful, and the pathogen Coe. stegomyia is slowly expanding itself through the island, the rate of Ae. (St.) polynesiensis infection increasing with the passing years (Laird, 1966). This is interesting but not very promising since most of the natural breeding places of the island are yet uninfected and the proportion of infected mosquitos within the whole island mosquito population is very low.

It is interesting to note that the global incidence of Coelomomyces infection is very variable from place to place, ranging from 0% in Venezuela (Dary and Camey, 1966) to 0.7% in Ceylon (Rajapaksa, 1964), but with local peaks situated between 20 and almost 100% for individual species and breeding places (Gad et al. 1967; Chapman and Woodard, 1966; Muspratt, 1963).

5.4 General comments

Most of the mosquito pathogens discussed here are sufficiently specific and, as such, may be handled without any risk for human beings and for the environment. Several of the genera, and even some of the species, have a large distribution and can locally affect a high proportion of the mosquito host(s), but on a larger scale they usually affect a very low percentage of the mosquito population. They have also very often, where they occur, a patchy distribution which could persist unaltered for years. This implies a restricted host range, or a low capacity for dispersal, or very narrow ecological limits within which the host infection is possible, or all these characteristics at the same time.

The use of such pathogens will probably require as usual an ecological study of the vector stages under attack, but the most needed investigations will deal with the ecology and population dynamics of the pathogens themselves. The factors determining the distribution and prevalence of the pathogens must be fully understood before the planning of any large-scale use of these biological agents. Such investigations can also give the clue to the laboratory colonization and mass production of pathogens for subsequent release.

As the characteristics of the principal pathogens so far studied do not appear very promising, a constant search must be made for more plastic strains and, during laboratory culture it should be worthwhile to attempt a selection for increased adaptability and larger host range, as advocated by Craig (1963).

The pathogens which are not specific for mosquitos involve a major risk for the environment from the beginning, and a thorough ecological study of the biocenose and of all possible relationships between the pathogen and the micro- and macro-fauna will be a vital necessity before any large-scale use of such agents.

It must be noted that a recently published paper stresses that some pathogens could be susceptible to insecticides, their prevalence being lower in a treated area than in an untreated neighbouring one (Tsai et al. 1969).

6. Genetic control

The field of genetic control is very large, as it involves the use of any condition or treatment that can reduce the reproductive potential of noxious species by altering or replacing the hereditary material. It may also be extended to the replacement of inimical genes (vector ability, anthropophily, etc.) by favourable ones (inability to carry the disease, zoophily or autogeny, etc.) within the same species. It can finally include the improvement of the characteristics of vector parasites, pathogens or predators. A very large bulk of theoretical information is already available, the main possibilities having been recently summarized by several authors (Anonymous, 1964, 1968; Craig, 1963, 1968; Kitzmiller, 1969; Knipling, 1955; Knipling et al. 1968; LaChance and Knipling, 1962; Laven, 1968; Mouchet, 1969; Smith, 1963). All authors stress that nothing can be done without a full knowledge of vector ecology and genetics, vector population dynamics, and determination of natural densities; some authors added that, at the time of writing (1962), no known insect fulfilled all the requirements. This explains why, despite a large number of theoretical papers, very few practical field experiments have been carried out, and they were usually successful.

The main possibilities may be listed as follows:

- male sterilization, using either radiations or chemosterilants, and release;
- release of cytoplasmically incompatible males;
- release of sterile hybrid males;
- deleterious gene introductions;
- gene replacement.

6.1 Male radiosterilization and release

Laboratory and field studies have involved three of the best known mosquito species, namely An. quadrimaculatus, Culex p. fatigans and Ae. aegypti.

Preliminary laboratory studies on the radiosterilization of A. quadrimaculatus were carried out by Davis et al. (1961) and suggested the possibility of releasing sterilized males with only a partial loss of sexual competitivity. Large-scale field experiments, however, were entirely unsuccessful (Weidhaas et al. 1962; Dame and Schmidt, 1962), and it was shown later that the failure was not due to the sterilization, but to the differences in sexual behaviour between the laboratory strain released and the wild A. quadrimaculatus.

Preliminary laboratory studies on the radiosterilization of C. p. fatigans were carried out by Ramakrishnan et al. (1962) and were very promising. A small field experiment was unsuccessful, inducing only a low rate of non-hatching in the egg-rafts laid by the wild females (Krishnamurthy et al. 1963). The scheme failed apparently because the size of the wild population had been underestimated and the number of released sterilized males was far too low.

Mass production (Fay et al. 1963) and sterilization of Ae. aegypti were achieved quite early, but the large-scale field experiments carried out by Morlan et al. (1962) were entirely unsuccessful. It was realized then that the irradiation dosage employed for sterilization was too high, altering seriously the sexual competitivity of treated males (Weidhaas and Schmidt, 1963). It appears also that, the effective flight range of Aedes aegypti being very short, released sterile males could not compete in due time with the wild males emerging from the breeding places side by side with the females (Schoof, 1967; George, 1967).

Very detailed laboratory investigations have been carried out with An. pharoensis but as yet without any field developments (Abdel-Malek et al. 1966, 1967a, 1967b; Tantawy et al. 1966, 1967a, 1967b).

6.2 Chemosterilization

Chemosterilants offer wider possibilities of male and female sterilization than radiations, as they can be applied easily to almost any stage of the insect and in various ways; some of them apparently do not seriously affect the sexual competitivity (Dame et al. 1964; Das, 1967) although they could affect the behaviour (Judson, 1967). The possibility of development of resistance to chemosterilants appears to be low (George and Brown, 1967) but not nil (Dame et al, 1964). The chemosterilants, being general toxicants for all living organisms, cannot be used for large-scale field applications but could probably be applied in conjunction with attractants (as it was done so successfully against Ceratitis capitata, in conjunction with insecticides, (Steiner et al. 1961) if specific and powerful ones could be developed. However, the presently known mosquito attractants do not fulfil the requirements (Fay and Eliason, 1966; Hudson and McLintock, 1967; Ikeshoji, 1966a, 1966b; Lea, 1965).

Applied to wild mosquitos the chemosterilants can interfere with the development of transmitted parasites. The laboratory experiments carried out with Brugia patei, Plasmodium gallinaceum and Pl. cynomolgi bastianelli have shown that the chemosterilants decrease the number of parasites reaching the infective stage but do not interrupt the transmission (Bertram, 1964; Jamnback, 1967; Ward et al. 1965). A mutagenic action of the sterilants on the parasites cannot be excluded.

Field evaluation of a chemosterilant, apholate, has been carried out with Culex tarsalis in an isolated oasis of California, by direct application of the compound to the breeding places, under close supervision. It was partly unsuccessful, because the duration of the experiment was shorter than the life of the wild C. tarsalis females emerging before the first apholate application. So the failure was due to an underestimation of the life expectancy of C. tarsalis females.

6.3 Release of cytoplasmically incompatible males

Intraspecific forms, differing each from another by cytoplasmic incompatibilities, are very well known in the Culex pipiens complex (Laven, 1967); and a similar phenomenon has been described between closely related species of the Aedes scutellaris group (Laven, 1968). Incompatible males, when released within a heterologous population, inseminate wild females but the egg-batches either do not hatch or give rise to a very low number of parthenogenetic females belonging to the cytoplasmic group of the mother.

A field evaluation of this control method has been performed with C. p. fatigans in a very small Burmese village, Okpo, in the Rangoon area. The experiment was almost completely successful, the last observed egg-batches being 100% sterile, but it was interrupted by the monsoon before the total disappearance of the wild C. p. fatigans population (Laven, 1967; Laird, 1967).

6.4 Release of sterile hybrid males

Crosses between closely related species (or between semi-species) can give rise to a hybrid F_1 progeny, the males of which are sterile whereas the females are normal. Due to the heterosis the hybrids males are more vigorous than normal males and fully sexually competitive in cage conditions. Such situations are known in the An. gambiae complex (Davidson, 1967; 1968) and in the Ae. mariae complex (Coluzzi and Sabatini, 1968). The An. gambiae complex is specially interesting as some crosses are producing almost nothing but sterile males. Accurate computations were made for planning a field experiment (Cuellar, 1969a, 1969b; Davidson, 1969). The small-scale experiment carried out in a small voltaic village, Pala, in the Bobo-Dioulasso area, was unsuccessful because most of the sterile males, which were overwhelming the wild males, did not mate with the wild females, due probably to differences in sexual behaviour (Davidson and Coz, personal communication).

6.5 Deleterious gene introduction

Deleterious genes exist within natural populations, from which they can be selected by in-breeding. They can also be produced by irradiation. Amongst the various possibilities are the recessive lethals, the sex distorter, the chromosome translocations.

The gene for sex distortion is known only from one species, Aedes aegypti, where its expression is erratic (Hickey and Craig, 1966) and for this reason it cannot be of any practical use (Laven, 1968).

The chromosome translocations can be induced by irradiation and maintained in pure strains which may be perfectly normal. If "translocated" males mate with normal females, the resulting F_1 progeny will be partially sterile and this partial sterility will be transmitted by the apparently normal adults of each generation to the following ones (Anonymous, 1968; Laven, 1968). However if the translocation is situated on an autosome the accidental release of "translocated" males and females could create problems by establishing a man-made population with unknown and perhaps harmful characteristics.

If the chromosome translocations are male linked they cannot be fixed in nature and can therefore be used without any restriction, the accidental release of some females being unimportant (Laven, 1969).

All these hypotheses await field trials for assessing their practical value but as many difficulties must be expected as with the sterile-male release experiments, for the same general reasons.

6.6 Gene replacement

It has been advocated that populations be replaced with harmful characteristics by populations of the same species lacking these characteristics, examples being Ae. aegypti with and without the gene for Wuchereria and Brugia susceptibility, Ae. communis autogenous and zoophilic for replacement of anthropophilic populations, zoophilic Ae. simpsoni for the replacement of anthropophilic ones (Craig, 1963). For the present, the preceding is no more than an enumeration of wishes.

6.7 Comments

All the genetic methods assume that the mass production of vector strains does not alter those behavioural characteristics without which the released males carrying the unfavourable characters will never meet and mate with the wild females. This is an unlikely assumption, because most of the vectors are very difficult to handle in the laboratory due to their mating behaviour and their colonization will depend on an alteration of this behaviour; this would be expected to be incompatible with their further use for genetic control operations.

The number of mosquitos to release depends on the actual number of the existing wild mosquito populations, and may well reach astronomical numbers (Laurence, 1965). The mosquitos will have to be scattered by some law over the whole controlled area to supplement their inherent dispersal potential which, for some species, is very limited. Despite all precautions, mass-produced mosquitos will be more homogeneous in their characteristics than wild ones (Craig, 1964b); so they will compete easily with those of the wild populations which are of their "average type" but will fail to interfere with the development of the populations having extreme characteristics (Craig, 1961; McClelland, 1967) exactly as do the traditional means of vector control.

Some of the genetical methods proposed presuppose the setting-up of "mosquito factories", and thus will be much more rigid and slower in their application than any chemical means of control; they could be also much more costly and for this very reason seem rather to be applicable as experimental ventures of some developed states than as established practices for developing tropical countries. Some others, based on the self-distribution of deleterious genes, are very appealing as they involve very simple procedures and no elaborate network for field releases. On the other hand chemosterilants may offer very bright prospects if specific attractants are discovered.

All these methods offer additional possibilities, although remote ones, to solve some problems of vector control, and cannot be neglected.

7. Conclusions

All methods of control are used to their best advantage when the vector and host ecology is well known. The "alternative" methods of control will require much more investigation than the insecticidal ones. Few of them are promising alone, and they will have to be employed in association with or reinforcing each other; they will probably not rule out the use of insecticides. Each method having its peculiarities and setbacks, and all relationships between vectors, hosts, parasites, pathogens, predators and vector-borne human pathogens having to be taken into consideration, the rational planning of integrated control operations will soon exceed human possibilities and will involve the necessary reliance on computers for handling them (Conway, 1969).

These new fields offer enormous research opportunities in ecology in its broadest definition.

All these researches will help to build a better world in the future but we cannot forget that epidemic and endemic mosquito-borne diseases prevail in most of the tropical areas and that insecticides constitute our main weapon for the present time and the near future.

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