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Ecological studies of Vectors in Malaria Control

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Under the strong selection pressure exerted by residual insecticides over many years, the behaviour of anopheline vectors of malaria has in many cases undergone a change. It is therefore necessary to reinvestigate their ecology in different areas in order that causes of failure to interrupt transmission may be identified and new control strategies developed. Aspects of vector ecology which are relevant to control are discussed, and the type of information which should be obtained briefly indicated.

Key Words: Malaria, Anopheles, Ecology, Control

Introduction

When Sir Ronald Ross, in 1897, saw oocysts on the stomach wall of an anopheline for the first time and realised their significance, very little was known about the biology of mosquitoes. Manson, who had encouraged Ross to take up these studies, believed that mosquitoes died after ovipositing, and that the infection passed into water from their disintegrating bodies and back to man by an oral route. It remained for Ross to elucidate the cycle of development in the mosquito and to show that another blood meal was then necessary to transmit the infection. It was soon realised that it was both impossible and unnecessary to eradicate all anophelines, and the alternative concept of "species sanitation" (in which specific control measures were undertaken against important vectors of each zone) ushered in the serious study of vector ecology.

The tremendous achievements of the early malariologists have provided a solid foundation of ecological information, much of which is still relevant today. However, with the advent of DDT and its wide-spread use in Public Health work after the second World War, it seemed that this type of research was no longer necessary. Drastic reductions in malaria incidence followed residual spraying against every major vector in all parts of India, and it was confidently believed that residual foci could be mopped up with antimalarial drugs. Today, after nearly disappearing, malaria has made a come-back in many parts of the country. With the benefit of hind sight it is clear that research should have been a built-in component of the control programme. It was inevitable that physiological resistance should develop, and that vector behaviour itself should change under the strong selection pressure exerted by residual insecticides over a long period. No easy solutions seem to be possible now, and it is necessary to study each local situation afresh to see whether the old assumptions regarding the identity of vectors and their biology are correct. It may be useful at this stage to review some aspects of the information available, and the type of studies which remain to be carried out in order that effective strategies of control can be devised.

Systematic studies of Anopheles

Ecological studies can only be made on the basis of correct identification of all stages of the life cycle. The pioneering work of Puri on anopheline larvae and of Christophers and others on the adult and egg stages culminated in 1933 in the publication of a volume on Anophelini in the *Fauna of British India* series. In general this is still the standard work of reference today. However, a number of important additions have been made to the Indian list. Colless's revision of the *leucosphyrus* group (1956) led to the recognition of two of the member species in India (Kalra & Wattal 1962), *A. balabacensis* which plays a role in the transmission of human malaria in Assam, and *A. elegans* which has been incriminated as the vector of simian malaria in the Nilgiri hills (Choudhury et al. 1963). Both the *A. barbirostris* and *A. hyrcanus* groups contain member species which have been recognised as vectors of human malaria in southeast Asia, though not in India. A number of species of these groups have been identified in India in recent years (Wattal et al. 1962, Reid 1968 and Harrison & Scanlon 1975), but much more work remains to be done to determine their distribution.

Certain species, such as *A. varuna* and *A. annularis*, are known to be vectors of malaria in one part of India, but not another. Others show markedly different behaviour in different parts of their range. Thus *A. fluviatilis* in many hilly tracts was highly anthropophilic, showing high vectorial capacity and low densities. In the plains the species was characterised by zoophilic behaviour, low vectorial capacity and high densities (Brookworth & Sitaraman 1952). Species like these would repay reexamination, particularly now that cytotaxonomic techniques are beginning to be available, to see whether in fact they are species groups. Identification of the members of such groups would make it possible to draw valid conclusions regarding their biology and vectorial capacity, and perhaps provide the answers to some of the anomalies puzzling malariologists.

Role of incidental vectors

On the basis of a large number of dissections in different parts of India (summarised in 'Vectors of Malaria in India' (1961) ten anopheline species were incriminated as vectors, of which seven were of major importance, and three were considered to be of incidental or local importance only. However, in cases where transmission has continued in spite of the very low prevalence of the recognised vector, the role of other species will have to be reassessed. Thus Rajagopal (1976) has shown that in Burnihat, Assam, *A. minimus*, believed to be the only local vector, has almost disappeared, but low level transmission is being maintained by *A. philippinensis*, previously believed to be unimportant in this area. Investigation of other local situations may reveal hitherto unsuspected vector species whose role should be defined before the ecology is investigated.

Selection of breeding site and immature biology

It has generally been accepted that antilarval measures alone are sufficient to interrupt malaria transmission, but that these may be operationally too difficult or too expensive unless breeding places of the vectors are well-defined and relatively limited in extent. A precise knowledge of the breeding habitats, their extent and epidemiological importance is necessary for the planning of appropriate control measures. A good example of how this may be done is the control of malaria in Bombay following Covell's recommendations in 1928. The vector here was *A. stephensi*, breeding chiefly in wells, overhead cisterns, blocked roof gutters etc. The wells were closed and handpumps installed, overhead-cisterns were provided with mosquito-proof covers and a regular surveillance of other peridomestic breeding sites instituted. These measures proved very successful with proper maintainence of the covers of wells and cisterns.

As early as 1910, Watson had suggested that control might be achieved by slightly altering the character of breeding waters. Such naturalistic methods were widely used in the pre-DDT era, with a considerable degree of success against species with specialised breeding habits such as *A. minimus*. It was observed that this species bred in sunlit streams with grassy edges, and was controlled most successfully on tea-estates in Assam by growing bushes to provide heavy shade along water courses and over marshes. Unfortunately the bushes used began to invade the tea and extra labour had to be employed to cut them back, and eventually it was found most practical to revert to open drains and oiling (Covell 1955). Meanwhile in a series of brilliant studies, Muirhead-Thomson showed that the effect of shading was indirect. The ovipositing females of *A. minimus* actually laid more eggs in shaded situations. However, dense shading killed the grass on the margins of the streams, which were then left bare and unprotected from water movement and this was in fact what prevented egg-laying.

A. culicifacies provides another example of the practical utility of knowledge of specialised egg-laying behaviour. Russell and Rao (1942) found that this species oviposits while performing a hovering dance a few inches above the water surface, and that mechanical obstruction by plants above a certain height prevented egg-laying. This made it possible to control the breeding of this species by planting *Vitex negundo* along the margins of canals in Tamil Nadu (Vectors of Malaria in India 1961).

Larval control measures whether naturalistic or by chemical larvicides, are an important adjunct to adult control measures, even where breeding may be too extensive for them to be used alone. It is essential in any kind of control programme that the important breeding places of the vector species should be accurately known, and that elementary precautions should be taken to avoid creating new and extensive sites. This has happened in Rajasthan where surplus water of the Bhakra and Rajasthan canal system and the Ghaggar Flood Control canal innundated large areas and provided breeding sites for *A. culicifacies*, aggravating the local malaria problem (Kalra 1978).

Adult density

In each locality there is a transmission season, which corresponds with the period of high density of the vector. Careful studies by Russell and Rao (1942), showed that the minimum indoor resting density of *A. culicifacies* for transmission lay between 8–10 and 17–20 per man hour in Tamil Nadu, although in some places anophelism without malaria did occur. Similar "critical densities" have been determined for other species also (Vectors of Malaria in India 1961). In general the concept of acritical density is a valid one, as long as it is remembered that other factors, notably longevity (Macdonald & Davidson 1953) may alter its absolute value under particular circumstances. During and after residual spraying campaigns mosquito resting behaviour has altered, as discussed below, making the number of mosquitoes captured indoors an unreliable index. It is now necessary to make direct measurements of man-vector contact. Macdonald, on theoretical grounds, suggested that the per-man-hour critical density for *A. culicifacies* might correspond to an average of about 2.5 bites per man per night (Macdonald 1952). It would be interesting to know whether biting levels above this can be detected in problem areas today.

Adult resting behaviour

The resting behaviour of a vector species will determine its degree of contact with indoor residual sprays. While at the outset it seemed that spraying was equally successful against all vector species in India, it is now clear that each has reacted differently. For example *A. minimus*, which rested mainly indoors during the daytime, though outdoor resting was also known (Vectors of Malaria in India 1961), has almost disappeared in Assam (Rajagopal 1976 & Kalra 1978), although irritability to DDT was reported for this species (Bertram 1950). *A. culicifacies*, also mainly indoor resting, remains an important vector today and has developed resistance in many parts of its range. Shalaby (1966) showed that even after 10 years of DDT spraying in Gujarat large numbers of this species could be captured in inadequately sprayed huts, although outdoor resting was also detected (Shalaby 1971). This author found that the entry of mosquitoes into unsprayed huts was significantly higher than into sprayed huts, and made the interesting suggestion that this, together with irritablity on contact with DDT, reduced man-vector contact, so that no immediate increase in malaria incidence followed the development of resistance to DDT (Shalaby 1966).

With species which rest outdoors during the daytime contact with sprayed surfaces occurs only at night. When the human population spends much of the night outdoors, transmission may take place without the vector mosquito being exposed to insecticides at all. In other cases, resting behaviour may play an important role. For example in Thailand *A. balabacensis* enters houses and rests on walls before feeding (Scanlon & Sandhinand 1965). This species readily becomes irritated by contact with DDT. By contrast *A. maculatus* feeds directly on arrival and rests on walls after feeding, when it is more sluggish and liable to acquire a lethal dose (Reid 1968).

Critical studies such as these need to be carried out in many situations where there has been failure to interrupt transmission.

Feeding behaviour

Anopheline mosquitoes may feed on animals or man, depending on their innate preferences and on host availability. A highly anthropophilic mosquito could be a dangerous vector even when present in small numbers, like *A. fluviatilis* in the Western Ghats. A zoophilic mosquito must be present in large numbers in order to transmit malaria, but when diverted to man by the absence of cattle, as is the case of *A. stephensi* in cities (Macdonald 1957), a normally weak vector may become highly efficient. Recognising the importance of the anthropophilic index, a large number of precipitin tests were carried out on the stomach bloods of wild-caught malaria vectors in different parts of India (Vectors of Malaria in India 1961) in the years before the Eradication Programme was initiated.

Bruce-Chwatt and his associates (1966) have suggested that residual spraying may have had the effect of selecting for zoophilism. Thus, in Greece a high degree of zoophilism was reported for *A. sacharovi* during and after insecticide spraying, with subsequent reversion to anthropophilism (Boreham & Garrett-Jones 1973). The very low percentages of man feedings reported in recent years for *A. culicifacies* in Gujarat (Shalaby 1969) and near Lahore (Reisen & Boreham 1979), as compared to earlier records for this species, suggests that this is a similar instance. Such changes in feeding behaviour could have important implications for the vectorial potential of important malaria vectors and should be investigated.

Longevity

One of the most important factors determining vectorial capacity is adult longevity. Macdonald (1956) showed how even a moderate reduction in the survival rate could drastically reduce transmission. This was the reason for the initial spectacular success of the indoor residual spraying campaign. Molineaux and colleagues (1979) have recently pointed out that if exposure of the vector population to insecticides is non-uniform, then relatively moderate reductions in average longevity will not be sufficient to interrupt transmission. From field studies of the age composition of *A. gambiae* populations biting man before and after spraying with propoxur, they were able to demonstrate that a section of the vector population, estimated at 37 and 52 % respectively in successive years, was not coming into contact with the insecticide. The observed reduction in the incidence of malaria agreed well with the theory of non-uniform exposure to the insecticide. Studies of the age composition of vector populations, to determine what proportion of the females survive to an epidemiologically dangerous age, are of great importance to control. Such studies are frequently technically difficult to carry out and need to be interpreted with caution, as pointed out by Gillies (1977).

It is not possible, in a brief review to do more than indicate how ecological studies may be of direct relevance in the present situation. It is a challenge to the present generation of medical entomologists to study and interrupt happenings in the field in the light of recent advances in our understanding of the basis of mosquito behaviour, and to develop innovative technologies to overcome the problems which have so far prevented the effective control of malaria in this country.

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