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MOSQUITO EXOPHILY AND ITS IMPORTANCE IN MALARIA ERADICATION

by

The late Professor V. N. Beklemišev¹
Member of the Academy of Medical Sciences of the USSR
Head of the Division of Entomology, Mortsinovsky Institute
of Medical Parasitology and Tropical Medicine, Moscow
Ministry of Health, USSR

From the very beginning of the use of residual insecticides for spraying premises with a view to malaria control, it was clear that this method is only applicable in the case of sufficiently endophilic vectors, since mosquitos that do not fly indoors are not exposed to the risk of contact with sprayed surfaces. In fact, the existence of exophilic vectors has proved one of the most serious obstacles to malaria eradication in a number of countries. However, the term "exophily" embraces a very wide range of essentially different phenomena and when not properly analysed is used by various authors in a somewhat different and not always strictly defined sense. Therefore what is first needed is an analysis of the problem of exophily and of all the phenomena connected with it.

In a general sense the degree of endophily or exophily can be defined as the degree of preference for human dwellings or outdoor resting-places respectively that may be shown at different stages in the life and activity of the mosquito (attack on the host, single-day and many-day resting-places, winter shelters, etc.).

¹ Professor Vladimir Nikolaievič Beklemišev died in Moscow in September 1962. This is one of his last papers. It was presented at the Conference on the Diseases of Countries with Hot Climates, held at Tashkent in September 1961.

There are no mosquitos that are domestic "by nature". All species of mosquitos arose long before man began to build dwellings and they all have their places in nature. It was in accordance with the place occupied in nature by individual species that their individual systems of adaptations also took shape. Because of this, different species of mosquito react differently to the appearance on the scene of man and his dwellings and show various types and degrees of anthropophily and endophily. These differences also affect the epidemiological importance of particular species of Anopheles and their vulnerability when dwellings are sprayed with insecticides.

The actual differences in the degree of adaptation of mosquitos to human dwellings and other buildings or to outside resting-places may depend to a lesser degree on the following factors.

1. Differences in the distance between human settlements and the breeding-places of the species or populations under comparison

Some species inhabit breeding-places situated in landscape features rarely settled by man, as, for instance A. marteri in Central Asia (Kešiš'jan, 1938) and Northern Iran (Beklemišev & Šipicina, 1947), whereas other species may inhabit places not yet inhabited by man. These last species seem to us to be exophilic (obligatorily exophilic species according to the nomenclature proposed by Gillies, 1956)¹ and under the circumstances they are necessarily so, although their reaction to human dwellings, if there were any in the vicinity, might prove to be positive. It is a fact, indeed, that some species with wide areas of distribution and a wide ecological range live over a considerable proportion of their habitat in the neighbourhood of man and are considered to be more or less endophilic. At the same time, some populations of these species have remained in unsettled areas. Examples are A. gambiae in the virgin forests of Uganda, or A. maculipennis messeae in the seaward portion of the Volga delta, where it lives at the expense of colonies of aquatic birds (Bagirov, 1953). Such populations are in practice completely exophilic, although obviously only because they have no opportunity of contact with human dwellings.

¹ An ambiguous term, since "obligate" is usually used to designate some ecological characters specific for the species concerned and possessed by it in any setting. (Author's remark)

2. Difference in methods of finding a host

In this connexion blood-sucking mosquitos can be divided into three groups (Beklemišev, 1944):

- (1) the "liers-in-wait" (e.g. A. bifurcatus);
- (2) active hunters after a scattered and often small host-animal (e.g. Aedes caspius);
- (3) active hunters after gregarious, usually large, animals (e.g. the whole Anopheles maculipennis and A. superpictus group).

There are transitional forms between the typical cases.

The "liers-in-wait" fly for short distances. If there is a human dwelling in the immediate vicinity of their breeding-place they enter it. If it is further away, they do not enter and in such a case they are exophages (see below) and exophils. Thus A. bifurcatus in the village of Moldovka in the Sochi district emerges in springs in the immediate vicinity of houses and flies into houses and stables for feeding purposes (Šipicina, 1941), whereas in Šithale in the Northern Caucasus its breeding-places were discovered at a point several hundred metres away from the village, into which only occasional mosquitos flew. Near the breeding-places, however, this mosquito species made mass attacks on human beings (Markovič).

The mosquitos that hunt after scattered hosts fly about actively and may reach points several kilometres from their breeding-place. In the process they fly into settlements but do not concentrate in them. The bulk of the population both feeds and chooses its resting-places in nature and in this sense is exophagous and exophilic. Such mosquitos have little opportunity of taking a blood meal twice from man during their lives and are, therefore, epidemiologically less important vectors of human diseases. They may, however, transmit the diseases of small mammals, e.g. tularaemia.

Mosquitos that hunt after gregarious (usually large) animals in populated places are attracted by settlements and other large gatherings of human beings and cattle, from which they obtain their blood meals. These hunter mosquitos frequently fly indoors in search of a host or resting-place. As a result, mosquitos showing this

form of hunting behaviour are the most likely to become endophages (see below) and endophils. However, the actual degree of endophily of particular populations of these species depends on a number of further conditions.

3. Differences in the places of attack on the host

Mosquitos that penetrate indoors in search of a blood meal are called endophages by Senior White, while those which attack their host out of doors are known as exophages. He reserves the terms "endophils" and "exophils" in the strict sense for mosquitos that select their daytime resting-places indoors or out of doors respectively. For the majority of Anopheles species the place of attack on the host depends entirely on ecological circumstances. If both people and animals are out of doors during the period of activity of the mosquitos, they are subject to attack. If the host is indoors and the mosquitos are able to penetrate indoors, the attack takes place there. The relationship between meteorological conditions indoors and out of doors is of great importance. If the host species is to be found indoors and outside, the majority of Anopheles species will attack mainly indoors under some combinations of meteorological conditions and mainly out of doors under other combinations. In most cases on one and the same night in one and the same settlement one and the same species of mosquito will attack both out of doors and inside the houses. At the same time the conditions furthering attacks indoors differ for different species. Thus exophagy or endophagy are usually not a species character. However, some species (for example the West Indian A. bellator) are apparently exclusively exophagous. If this is true, such species are the exception.

Differences in the place of attack are in themselves very important for the epidemiology of malaria and have some effect on the diurnal distribution of mosquitos (see below).

4. Differences in the behaviour of fed females

There are two main forms of behaviour of fed females, each of which is characteristic for determination of the species.

(a) A female engorged with blood retains the positive phototaxis to weak light that is characteristic of unfed mosquitos. In view of this, if the female has taken a blood meal indoors she will quickly leave the premises, flying through openings that let in the outside light. If the photosensitivity of her retina is great and the threshold of phototactic reaction low, the fed female will fly towards the light of the night sky (a number of tropical species: Muirhead-Thomson, 1951). If the sensitivity of the retina to light is lower, the mosquito will fly out only towards crepuscular light. Such species are A. hyrcanus, A. bifurcatus and many others. If they have taken a blood meal indoors, they remain there until morning, but at first light fly out and settle for the day in the outside resting-places, (on vegetation, fissures in the rocks, etc.). Only occasional individuals will remain indoors. Species with this type of reaction to light are typical exophils. Their males also are not encountered indoors and the females never over-winter indoors (e.g. A. hyrcanus).

(b) The female when engorged with blood loses her positive phototaxis to weak light. As a result, once she has taken a blood meal indoors, she remains there until digestion is completed, unless driven out earlier by unfavourable conditions. This group includes all subspecies of A. maculipennis, A. superpictus, A. gambiae and many other highly endophilic species. A difference between the reactions to light of fed and empty females of A. maculipennis and A. hyrcanus was discovered experimentally by Ioležev and Sakovič and has often been observed by us and by others under natural conditions in respect of a number of species.

The females of this ecological group, even when they have taken a blood meal in the open air, may in a very large percentage of cases, in response to the irritant effect of light (photokinesis), fly indoors at dawn and stay there if conditions are favourable until digestion is completed. This quite often occurs in A. m. sacharovi, A. pulcherrimus and others, but is particularly frequent in A. superpictus. The males of A. superpictus and the A. maculipennis group are often found indoors in the daytime with the females. Diapausing females may over-winter indoors.

Thus the potentially most endophilic of all Anopheles are those mosquitos that hunt after gregarious animals and lose their positive phototaxis to weak light when fed. The actual distribution of populations between indoor and outdoor resting-places depends on the design of the buildings and their microclimate, the microclimate of the surrounding outdoor resting-places, the distribution of the host, etc.

Thus, whether the host is attacked indoors or out of doors (endophagy or exophagy) depends mainly on conditions but also on the type of "hunting" practised by the different species. The mosquitos that hunt after gregarious animals and concentrate round settlements have wider opportunities for flying indoors in search of food. Distribution in resting-places and outside buildings (i.e. endophily and exophily) depends mainly not only on the females' reaction to light, but also on the type of hunting practised by the species. Because of these factors, some species are only accidentally encountered in indoor daytime resting-places. This applies to species that are exophilic by nature (A. hyrcanus and others). Other species, because of their hunting behaviour and light reactions, stay indoors in most cases during the daytime. These species are potentially endophilic (A. maculipennis, etc.). The actual degree of endophily depends in every case on the ecological situation.

The considerations set forth above allow of a better understanding of the life of anopheline populations and of the conditions under which they are vulnerable to the control measures taken. In particular, they make it possible to study the so called "behaviouristic resistance" of mosquitos to insecticides.

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