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BIOLOGICAL VARIATIONS IN ANOPHELES DARLINGI AND ANOPHELES GAMBIAE

Their Effect on Practical Malaria Control in the Neotropical Region

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SYNOPSIS

A remarkable range of variation has been demonstrated in the biting habits of *A. darlingi* in South America. At the centre of its area of distribution, the species comprises both anthropo-endophilic and zoo-exophilic individuals, but the anthropophilic tendencies increase progressively towards the periphery of its distributional area. Conditions of travel and migration, imposed by the South American rain forest, have probably favoured the development of a specialized anthropophilic strain on a geographical pattern. There is ample evidence of a similar strain evolution in *A. gambiae*, but on a more confused pattern. *Aëdes aegypti* also presents an outstanding example of variation in biting habits.

A proper understanding of the extent and significance on anthropophilic and zoophilic tendencies is essential for the proper conduct of malaria control campaigns; for the formulation of long-term policies; and for the proper evaluation of the probabilities of resistance to insecticides.

The control of malaria by modern insecticidal techniques rests fundamentally on the biting and resting habits of the anopheline species responsible for its transmission.

In the western hemisphere we have the two following outstanding examples:

(*a*) *A. darlingi* of British Guiana and centro-northern Venezuela, a specifically anthropo-endophilic mosquito; DDT house-spraying *exclusively* has brought about its eradication.

(b) *A. bellator* of Trinidad, a typically exophilic carrier; residual house-spraying techniques have had no effect either on the incidence of this mosquito or on the incidence of the malaria it carries.

All malaria control problems fall within these two extremes and the results of residual house-spraying methods will everywhere be proportionate to the man-biting and house-frequenting propensities of the vector mosquito.

There is abundant evidence that under appropriate conditions vector eradication is not necessary for the attainment of malaria eradication; [16, 18] if, however, malaria is reduced, even if only to minimal proportions, in the presence of a " residual " population of the vector, then a resurgence of malaria may be reasonably expected if control operations are suspended or excessively curtailed.

At the present day under continental tropical conditions, and over wide areas of Africa in particular, the eradication of either malaria or its vectors appears unlikely; on the contrary a very considerable reduction in the prevalence of house-frequenting anopheles and malaria can be reasonably expected wherever modern spraying techniques are properly applied. We have no answer, however, to the long-term problem concerning the maintenance of control in the presence of reduced but still existing reservoirs of human malaria parasite carriers and anopheline vectors.

The object of this paper is to focus attention on variation in behaviour as regards feeding and biting habits within some of the best studied and most dangerous mosquito species, mainly for the purpose of stimulating wider and deeper studies on the modalities, extent and significance of such differences. There appears in fact to be evidence of the existence of vector and non-vector strains within what morphologically present themselves as perfectly well-defined mosquito species. It is obvious that the economics of malaria control upkeep will be placed on a much more practical basis when the " fixity " or " lability " of exophilic and zoophilic variation within dangerous vector species will have been adequately defined and explained.

Anopheles darlingi is the most widely distributed and most dangerous malaria vector of the neo-tropical region. Its area of distribution is huge, ranging from southern Mexico to northern Argentina and from the eastern slopes of the Andes to the shores of the Atlantic and Caribbean. Its position in tropical America can be described as analogous to that of *A. gambiae* in tropical Africa. The most successful and best documented campaigns against tropical malaria have been waged against this vector with results ranging from high degree malaria control (central Brazil) to malaria and vector eradication in northern British Guiana,[22] in centro-northern Venezuela [19] and in French Guiana.[13-15] These successful campaigns have been in progress for very adequate periods of time: since 1945 in British Guiana and Venezuela, since 1946 in Brazil and since 1950 in French Guiana.

A. darlingi was first described by Root in 1926; it was not, however, until the mid-nineteen-thirties that its preponderant role in malaria transmission became apparent. Its presence everywhere has been associated with severe endemic or epidemic malaria. Throughout its area of distribution it is always the prevailing anopheline species captured within houses; early observers emphasized its domesticity.[8, 26] On the British Guiana coastlands, Giglioli [20] found not only that *A. darlingi* was very numerous and the overwhelmingly prevailing anopheline within houses (99.1 % of all captures),

but also that its occurrence in animal shelters and on animal and human bait, in the open at night, was negligible (2.2% of all captures); it thus appeared to be a truly anthropophilic and endophilic mosquito. Extensive observations throughout the colony between 1939 and 1945 only confirmed these findings. Entirely comparable conditions have been reported from Venezuela.

In Brazil, the high frequency of *A. darlingi* in houses was confirmed by Airosa Galvão, Damasceno & Marques [1] and Deane.[9] Deane, Causey & Deane,[10] however, in a wide series of observations conducted throughout Amazonia in the States of Pará, Maranhão, Piauí and Guaporé, found that, in spite of its prevalence in houses (61% of all captures, at an average rate of 5.3 per hour), *A. darlingi* was also very frequently collected on animals in the open (38.3% of all captures, at an average rate of 2.7 per hour). At Belem simultaneous captures in the open on human and on horse bait netted 333 and 482 *A. darlingi* respectively.

With the inauguration in 1947 of the great nation-wide malaria control campaign by the National Malaria Service of Brazil, entomological surveys and systematic resurveys were widely extended; attention was soon focused on the unexpectedly eclectic feeding habits of *A. darlingi*. De Bustamante et al.[5] on the mid San Francisco river, in the central Brazilian states of Bahia and Minas Gerais, reported that though *A. darlingi* accounted for only 6.55% of anopheline larval captures, 90.66% of adults collected in houses belonged to this species. Out of the total *A. darlingi* catches, however, no less than 34.86% were collected in the open on animal or human bait, *A. darlingi* accounting for 12% of total outside captures. The region in which these observations were made is sparsely inhabited and has an abundance of livestock. At Engenheiro Dolabela in Minas Gerais, de Bustamante & Guedes,[4] in the course of observations extending over three months, collected 2397 anopheles in an animal-baited Shannon dawn trap; 89.99% of these were *A. darlingi*. It should be noted that the houses of this area had been subject to regular DDT spraying since 1946. In this same locality de Bustamante and his associates in 1949-50, in the course of 602 night inspections, collected 691 *A. darlingi* resting on the outside walls of DDT-sprayed houses; at Logoa Grande, in the same region and eight months after the last DDT spraying, 2045 *A. darlingi* resting on the outside walls of houses were collected in the course of 140 night inspections. Quite recently (1955) Dr. N. Lacerda, head of the National Malaria Service in the State of Amazonas, informed the writer that in the Maderia-Guaporé area identical conditions had been met: a very high degree of malaria control had been achieved; *A. darlingi* had disappeared from the houses, but it was still found in abundance outside. Further observations by de Bustamante [3, 6] indicate that in the coastal districts of south-eastern Brazil, in the States of Alagoas, Bahia, Espirito Santo and Rio de Janeiro, *A. darlingi* is preponderantly anthropophilic and endophilic, the average capture rate being 6.9

per hour in houses against 1.8 per hour on animal bait in the open; on the other hand, on the central plateau of the interior, in the States of Piauí, Pernambuco, Bahia, Matto Grosso and Goiás, *A. darlingi* is prevalently zoophilic and exophilic, the average capture rate being 21.6 per hour in houses and 45.2 on animal bait in the open. Brazilian workers do not regard exophilia, zoophilia and the resting of *A. darlingi* on the outside walls of houses as a post-DDT effect. In fact at Marques do Reis in the state of Paraná, a virgin locality, de Bustamante [3] found that *A. darlingi* could be caught at the average rate of 37.47 per hour in houses and 35.27 per hour on animal bait in the open (February-April). In this same locality Rachu (quoted by de Bustamante [3]) observed *A. darlingi* resting on the outside walls of houses.

In British Guiana, northern Venezuela and French Guiana, the effect of DDT on *A. darlingi* has been dramatic and has brought about extensive eradication of this vector. This is not the case on the central plateau of Brazil; DDT has brought about everywhere a drastic diminution in the incidence of malaria and the disappearance of *A. darlingi* from the interior of houses; this mosquito, however, still persists outside in variable numbers, particularly in areas with a low density of human population. In the more populated areas extradomiciliary captures appear to be diminishing progressively as a result of the sustained DDT campaign, and in the long run eradication may eventually result. Eradication by house-spraying methods appears, however, unlikely in pastoral, sparsely inhabited districts where the mosquito continues to occur in large numbers.

Gabaldon [17] believes that anopheles are primarily zoophilic; anthropophilism is an incidental quality of some strains; in their centres of dispersion, species which attack man should be comprised of mainly zoophilic individuals; at their peripheral areas of dispersion anthropophilic individuals may prevail. He quotes *A. darlingi* as a typical example:

> " In its probable centre of dispersion (Goiás and the interior of Piauí and Bahia in central Brazil) the ratio of density indexes of zoophilic and anthropophilic adult specimens (mosquitoes collected per man hour on animals/mosquitoes collected per man hour in houses) was 4.7 [showing] that zoophilism was prevailing. On the other hand, these ratios were below zero [in] the surrounding areas of dispersion: 0.51 [in] the North (Amazonia); 0.48 [in] the South (Paraná); 0.26 [in] the East (Litoral); and 0.34 [in] the West (Matto Grosso). In these zones, therefore, anthropophilism was predominant (data from Deane, Causey and Deane, 1948, [10] for Amazonia and from Bustamante, 1951, [3] for other regions). Farther north and west, in Venezuela, British and French Guianas, and in Bolivia, anthropophilism is still greater (Gabaldon 1952, [16] Giglioli 1951, [22] Floch 1952, [13] Moscoso-Carrasco 1953 [personal communication])."

It is obvious, on factual evidence, that the population of *A. darlingi* at the centre of its area of distribution consists of a mixture of individuals, some zoophilic, others anthropophilic. The fundamental question to be answered concerns the relations of these two groups: How far are they

distinct? Do they evolve separately but in parallel to form strains with distinct characteristics? How far are these characteristics fixed?

Once a differentiation in biting habits has developed it is easy to understand the process by which anthropophilic and endophilic specialization increases progressively and centrifugally towards the periphery of the distributional area of a species. Anthropophilic individuals will tend to follow man, this most restless and mobile of all animals, and will do so within the ecological range which the species can tolerate. Such a process must obviously be a slow and progressive one, varying, however, according to human progress in respect to travel facilities. *A. darlingi* must have done most of its early travelling on its own wings, and hitch-hiking on Indians along forest trails and in canoes; more recently we have seen it in launches, trains and planes. *Anthropophilia crescit eundo !*

In British Guiana we have repeatedly observed evidence of penetration of *A. darlingi* into clean areas following the opening up of communications and increased human traffic: in the Rupununi Savannahs about 1930; on the Pakaraima Plateau in 1947 [21] and on the upper Corentyne Coast in 1951.[23] We cannot say whether *A. darlingi* exists as a purely sylvatic mosquito in the immense, totally uninhabited forest of the interior of Guiana. Positive observations in uninhabited areas are few and limited to habitual camp sites along well-beaten lines of communication, trails or rivers, and to forest farms and provision fields, in areas habitually frequented by Indians for centuries. It is evident that in these remote but intermittently inhabited areas *A. darlingi* must survive for considerable periods without the possibility of obtaining human blood. On the Rupununi Savannahs in fact we collected it in considerable numbers at night feeding on horses in the open; its attraction to man, however, remained sufficiently preponderant to bring about its rapid and selective elimination by DDT house-spraying. The adults disappeared from the houses, and the larvae from breeding places in the surrounding areas. Briefly, in recapitulation of what has been said:

(1) *A. darlingi* is a highly efficient malaria carrier with an extremely wide geographical distribution; wherever it occurs it is the predominant anopheline found within houses.

(2) *A. darlingi* at the centre of its area of diffusion appears to be an eclectic feeder; it attacks both indoors and in the open and appears to be equally attracted to man and to animals. In these areas, DDT applied to the interior of houses has brought about: (*a*) a very high reduction in the incidence of malaria; (*b*) the disappearance of *A. darlingi* from the interior of houses, and (*c*) the survival of a more-or-less large population of *A. darlingi* which continues to thrive in the open like any other zoophilic species.

(3) Towards the periphery of its distributional area, *A. darlingi* appears to be preponderantly endophilic and anthropophilic; DDT applied to the interior of houses has brought about: (*a*) a very high reduction in the incidence of malaria, with good promise of early eradication; (*b*) the disappearance of *A. darlingi* from the interior of houses, and (*c*) the quasi-complete disappearance of *A. darlingi* outside.

(4) In the extreme north of its distributional area, in centro-northern Venezuela and the coastlands of British Guiana, *A. darlingi* is strictly endophilic and anthropophilic, and the application of DDT to the interior of houses has both: (*a*) wiped out malaria, and (*b*) eradicated the vector species.

A. gambiae was for long accepted as the prototype of anthropophilic and endophilic mosquitos and the most dangerous and efficient of malaria vectors. It is still unrivalled as regards efficiency; this in itself is an indication of highly specific anthropophilia. Of recent years, however, a very considerable range of variation as regards its biting habits has been brought to light. This range, in fact, appears even wider than anything yet recorded for *A. darlingi*. It is very difficult to reconcile the high vector efficiency of *A. gambiae* with the eclectic feeding habits and zoophilic tendencies which have been discovered; the development of specialized strains within the species suggests itself. Symes [27] reported the finding of *A. gambiae* on the Lume river in Kenya in uninhabited forest. He suggested that under such conditions it lives mainly on animal blood until human settlement brings about a permanent increase in numbers.[28] Symes also reported that in Kenya this species is prevalently anthropophilic.[29] With such an interpretation anthropophilia and zoophilia would only be the result of feeding convenience.

Haddow and his associates carried out extensive ecological and biological investigations on the mosquitos of Bwamba County in Uganda. One of their most remarkable observations was the discovery of both *Aëdes aegypti* and *A. gambiae* in the entirely uninhabited Semliki forest.

A. gambiae was found in very large numbers attacking actively by day and by night; prevalently at ground level but also quite commonly in the forest canopy, 80 feet (25 m) above the ground. It was particularly abundant along the Semliki river, which at no point was separated from the nearest settlement by less than six miles (10 km) of dense rain forest. We quote:

> " The writers (all of whom have had experience of *A. gambiae* in infested urban areas) have never seen this usually domestic species in concentrations approaching these encountered at Mongiro and Mamirimiri, where over 30,000 (representing 93% of the total of all species) were taken in the 40 catches. " [25]

Still referring to the same area:

> " The implications of these records of *A. aegypti* and *A. gambiae* are interesting and difficult to interpret. As the two most dangerous mosquitoes in the world, they have

been the subject of numerous and extensive field studies and the great mass of evidence points to the fact that they are not sylvan or rural but domestic species which haunt human habitations and prefer human blood. In Bwamba, however, both are found under sylvan conditions. *A. aegypti* can rarely be taken biting man and *A. gambiae*, though it bites man freely when opportunity offers, is commonest in an area rarely visted by human beings. It is thus important, when taking up the studies of mosquitoes in forest areas, to do so without preconceived ideas concerning their probable behaviour, particularly in the case of well-known and dangerous species." [24]

These findings should be compared with Vinke's [30] on *A. gambiae* and its reactions to DDT in Katanga, in the Belgian Congo, an area which, like Bwamba, belongs to the Central African zoogeographical region.

In this area endophilia and anthropophilia of *A. gambiae* were indicated by very high and habitual house-infestation indices. This obviously is not in itself a sufficient proof of endophilia and anthropophilia for the species *as a whole*. Aipplcation of DDT, however, brought about: (*a*) practically complete disappearance of *A. gambiae* in treated houses; (*b*) very marked reduction of *A. gambiae* adults in non-sprayed control houses within the treated area; and (*c*) great reduction in the number of *A. gambiae* attacking man in the open or attracted to man-baited Magoon traps.

These results would indicate a quasi-specific endophilia and anthropophilia. From the published report, however, no specific investigations appear to have been made to determine any possible zoophilic tendency in *A. gambiae*, nor are larval indices given, before and after DDT, to indicate the trend of the actual *A. gambiae* population as a whole. Obviously, if *A. gambiae* in this region is entirely anthropophilic, as *A. darlingi* is in British Guiana, for instance, then the disappearance of adults should be followed by a rapid disappearance of larvae from breeding waters.

At Ilaro, within the High Forest Zone in the Western Region of Southern Nigeria, an area of holoendemic malaria, Bruce-Chwatt and his associates in the period 1949-53 found that the systematic application of BHC to all houses caused a 90% reduction of *A. gambiae* within houses, and a similar reduction in larvae of this species within the area.[2] During the campaign *A. gambiae* was rarely collected biting human beings in the open between 9 p.m. and 7 a.m. The experimental area covered only 12 square miles (31 km^2) with a width ranging from 2000 to 5500 feet (600 m to 1600 m). As the surrounding area was not treated and was heavily infested, outside influences were inevitable; however, the entirely parallel reductions in both the house and larval populations of *A. gambiae* suggest a very high degree of endophilia and anthropophilia. It should be noted that captures on animals or in animal-baited traps do not appear to have been made in the course of this important experiment.

Davidson & Draper,[7] in a holoendemic area in a valley in the Eastern Usambara Mountains (some 40 miles (60 km) inland from Tanga), on the coast of Tanganyika, found *A. gambiae* to be 100% anthropophilic. This

conclusion was based on precipitin tests made on mosquitos found resting in houses. From the " scarcity of animals " in the area it was considered that the biting of animals could only have a very slight effect on the anthropophilic index as a whole; what is meant by " animals ", however, is not stated. In tsetse-infested areas, livestock is generally very scarce or absent. This is not a sufficient reason, however, for ruling out actual or potential zoophilia. In the canopy of the uninhabited Semliki forest *A. gambiae* undoubtedly was not feeding on livestock! The bird population of Africa is exceptionally varied and abundant and must be considered.

In central Brazil, as we have seen, *A. darlingi* is by a long way the most endophilic and anthropophilic anopheline species, yet careful and systematic studies have demonstrated that in some areas quite a considerable proportion of its population is naturally exophilic and zoophilic and is thus not affected by DTT.

In Mauritius [11, 12] a condition has developed which is entirely comparable to the one described for *A. darlingi* in central Brazil; unfortunately no preliminary pre-spraying investigations on the local biting of *A. gambiae* were made. *A. gambiae* captures in houses were reduced by 98% in two years, and malaria transmission practically ceased, yet *A. gambiae* continued to breed actively and could be found in animal shelters and also sometimes in new untreated houses. In Réunion and Madagascar, identical results have been obtained in the course of large-scale campaigns with residual insecticides.

In Somalia, the reproduction of *A. gambiae*, in the areas watered by the Webi-Scebeli river, is distinctly intermittent. Suitable breeding conditions occur for only short periods: (*a*) after the peak of the bi-annual floods, in pools and ponds left along the banks by the receding waters; (*b*) at the height of the bi-annual dry seasons, when the river dries up leaving ponds and puddles in its sandy bed. In between these periods, *A. gambiae* activity ceases. Malaria is of endemic and hyperendemic intensity.

During 1955, the writer carried out a survey of the area with Dr C. Guttuso and Dr M. Maffi. No *A. gambiae* adults or larvae could be found during June and the first half of July, when the river was low but still flowing. From the beginning of the second week of July the flow ceased and pools and puddles began to form: the first larva was captured on 18 July, and in the following week larvae were collected in considerable numbers all along the river, quite independently of the distribution of villages. The association of *A. gambiae* with man in this area would therefore appear to be relative and a considerable degree of zoophilia can be expected.

We have dealt with what is only a very small sample of recent but authoritative African literature. All observations refer to regions well within the distributional area of *A. gambiae*. Outside this area, in Brazil and in southern Egypt, *A. gambiae* became so well established as to cause disastrous malaria epidemics; in both countries it was distinctly endophilic

and anthropophilic and it was most successfully eradicated. We believe that it is the natural selection, " for export ", of the more strictly endophilic and anthropophilic strains—which selectively follow man in his ships and planes across the ocean and in his transcontinental peregrinations—that causes the greater eradicability of expatriate mosquito species, rather than an entirely hypothetical adverse effect of the alien environment.

The geographical distribution of anthropo-endophilic strains of *A. darlingi* in South America is characteristic and appears to have developed on a well-defined pattern. This may be explained, to some extent, by the limitations imposed on human movement by the immense equatorial rain forest. Settlement and traffic are nearly exclusively confined to the rivers; mammalian fauna and livestock are relatively rare and limited; cross-country migration is impossible. This peculiar form of ribbon development obviously favours continuous and progressive selection.

If anthropophilia and endophilia can evolve in a centrifugal direction in a mosquito species, as they obviously have in *A. darlingi*, it is reasonable to expect that evolution on similar lines should also take place, to some extent at least, at the centre of the distributional area of the species; under such conditions the development of specialized strains would evolve on more or less parallel lines. On the central plateau of Brazil it may well be that DDT has eliminated the domestic anthropophilic strain of *A. darlingi*, as it has done elsewhere, without affecting the exophilic and zoophilic non-vector strain, which therefore continues to thrive as it did before DDT was introduced. If this were the case the suspension or relaxation of spraying would have no appreciable effect on the degree of malaria control achieved. If, on the other hand, specialization has evolved to a lesser degree, one can envisage the possibility of DDT's eliminating only the most evolved section of the *A. darlingi* population, demoting the species from a first to a second or third class position as regards malaria transmission, independently of the long-term maintenance of DDT control. The " fixity " or " lability " of this demotion remains to be defined and should be clarified.

With *A. gambiae* there is evidence of evolutionary specialization, entirely comparable to what we have described for *A. darlingi*, but the pattern is confused. This is probably the result of different environmental conditions. With the exception of the rain forest area of the great Congo basin, in fact, there are few natural barriers throughout Africa to the migration of both man and animals. An exceptionally varied and abundant mammalian and bird fauna and the extensive and ancient tradition of pastoral nomadism tend to keep man and animals in closer and more constant contact; under such conditions the differentiation of feeding affinities must evolve on slowly divergent lines, favoured or hindered by local environmental factors. Yet the highly anthropophilic *A. gambiae* of Brazil and southern Egypt were obviously already evolved African

" export products "; the same can be said of the highly domestic *Aëdes aegypti* which was exported from Africa to the western hemisphere and to Mauritius.

Obviously the study of variations in feeding habits and their significance within an apparently fully characterized and uniform mosquito species presents difficulties which will tax the ingenuity and patience of researchers to the utmost; colonization of large numbers of strains will be necessary. Nonetheless, such studies appear to have fundamental importance for the proper understanding of the potentialities and limitations of malaria control by residual insecticides and for the intelligent planning of long-term policies.

The development of mosquito resistence to residual insecticides at present preoccupies our minds. In this respect, also, further clarification of anthropophilic and zoophilic tendencies within vector species is essential. It is difficult to see, for instance, in what way the residual post-DDT exophilic and zoophilic population of *A. darlingi* on the mid San Francisco river could make the necessary contact with sprayed surfaces to develop resistance. What then is the position with regard to the exophilic *A. gambiae* of Mauritius and Madagascar?

RÉSUMÉ

Il a été démontré que *A. darlingi*, le vecteur du paludisme le plus dangereux et le plus largement répandu dans les régions néotropicales, manifeste des divergences parfois fort importantes dans sa façon de piquer ses hôtes. Au centre de sa zone de répartition, sur le plateau central du Brésil, l'espèce *A. darlingi* comprend à la fois des individus anthropo-endophiles et des individus zoo-exophiles. Le DDT a permis de maîtriser le paludisme et d'éliminer *A. darlingi* de l'intérieur des habitations, mais cette espèce continue à exister en grand nombre à l'extérieur.

Les tendances anthropophiles de *A. darlingi* s'accroissent progressivement, suivant un tracé géographique bien déterminé, du centre à la phériphérie de sa zone de répartition: en Guyane britannique et au Venezuela (région du centre-nord) l'espèce est si étroitement associée à l'homme qu'elle a été extirpée par le seul traitement des maisons au moyen de pulvérisations de DDT.

Les conditions de déplacement et de migration imposées à l'homme par l'immense forêt sud-américaine ont probablement favorisé le développement, suivant un certain tracé géographique, d'une souche anthropophile spécialisée.

On dispose de nombreuses observations indiquant une évolution analogue des souches chez *A. gambiae* mais suivant un schéma plus confus. Les diverses manières dont *Aëdes aegypti* pique ses hôtes sont un bon exemple de variations qui influent sur les modalités pratiques de la lutte contre les moustiques. Les souches « d'exportation » qui ont suivi l'homme à travers l'océan, jusqu'à l'hémisphère occidental, et jusq'à l'Ile Maurice, sont strictement domestiques.

Pour pouvoir mener des campagnes antipaludiques de façon rationnelle et économique, selon une politique à long terme, et tenir compte de l'éventualité d'une résistance aux insecticides de plus en plus grande dans la population exophile d'une espèce vectrice qui survit aux pulvérisations, il est nécessaire de bien comprendre l'ampleur et la signification

des tendances anthropophiles et zoophiles, ainsi que la fixité ou la labilité de ces deux caractères.

L'indice élévé de domesticité d'une espèce vectrice n'exclut pas l'existence, dans la même localité, d'une souche zoophile. Lors de toute enquête paludologique préliminaire, il convient de rechercher et d'évaluer les tendances zoophiles de l'espèce vectrice.

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