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The Chief of the Malaria Section
has the honour to communicate hereunder the
following note:

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BIOLOGICAL VARIATIONS IN ANOPHELES DARLINGI AND THEIR
EFFECT ON PRACTICAL MALARIA CONTROL IN THE NEOTROPICAL REGION.
DOES A. GAMBIAE PRESENT ANALOGOUS VARIATIONS?
HOW FAR IS ANTHROPHILIA A FIXED TRAIT?

by

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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:

- (1) A. darlingi of British Guiana and Centro-Northern Venezuela, a specifically anthro-endophilic mosquito; DDT house spraying exclusively has brought about its eradication.
- (2) A. bellator of Trinidad, a typically exophilic carrier; residual house spraying techniques have had zero effect both on the incidence of this mosquito and 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; 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 will be 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 South Mexico to the Northern Argentine 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 analagous 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, in Centro-Northern Venezuela

and in French Guiana. 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, till 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 (Davis 1931, Shannon 1933). On the British Guiana Coastlands, Giglioli (1938) found that A. darlingi not only was very numerous and the overwhelming prevailing anopheline within houses (99.1% of all captures), but that its incidence 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 anthropophile and endophile 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 incidence of A. darlingi in houses was confirmed by Ayrosa Galvan, Damasceno & Marques (1942). Deane Cursey & Deane (1948), however, in a wide series of observations conducted throughout Amazonia in the States of Para, 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 re-surveys were widely extended; attention was soon focused on the unexpectedly eclectic feeding habits of A. darlingi. Bustamante et alii (1949) 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, Bustamante & Guedes (1950), 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 Bustamante and his associates in 1949-1950, 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 Bustamante (1951) 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 with an average capture rate of 6.9 per hour in houses against 1.8 per hour on animal bait in the open; on the contrary 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, with an average capture rate of 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, Bustamante (1951) 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 Bustamante, 1950) observed A. darlingi resting on the outside walls of houses.

In British Guiana, Northern Venezuela and French Guiana, the reaction of A. darlingi to DDT has been dramatic with 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 (1953) 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 indices of zoophilic and anthropophilic adult specimens (mosquitos collected per man hour on animals/mosquitos collected per man hour in houses) was 4.7, which shows that zoophilism was their predominant characteristic. On the other hand these ratios were below one in the surrounding areas of dispersion: 0.51 to the North (Amazonia); 0.48 to the South (Paraná); 0.26 to the East (Litoral); and 0.34 to the West (Matto Grosso). In these zones, therefore, anthropophilism was predominant. (Data from Deane, Causey and Deane, 1948, for Amazonia and from Bustamante, 1951, for other regions.) Further North and West, in Venezuela, on the Coast of British and French Guiana and in Bolivia anthropophilism is still greater (Gabaldon 1952, Giglioli 1951, Floch 1952, Moscoso-Carrasco 1953)."

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 and 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 in the footsteps of 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, hitch-hiking on Indians along forest trails and in canoes; more recently we have seen it in launches, trains and planes. Antropophilia crescit eundo!

In British Guiana we have repeatedly observed evidence of penetration of A. darlingi into clean areas following the opening up of communication and increased human traffic: in the Rupununi Savannas about 1930; on the Pakaraima Plateau in 1947 (Giglioli 1948) and on the upper Corentyne Coast in 1951 (Giglioli & Charles, 1954). 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; 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 Savannas 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; not only adults disappeared inside the houses, but also larvae from suitable 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 as well as 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.
- (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) Further south, east, west and north, 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.
- (c) The quasi-complete disappearance of A. darlingi outside.

(4) In the extreme north of A. darlingi's distributional area, in Centro-Northern Venezuela and the coastlands of British Guiana, A. darlingi was strictly endophilic and anthropophilic and DDT application to the interior of houses has caused:

- (a) Malaria eradication.
- (b) A. darlingi eradication.

A. gambiae was for long accepted as the prototype of anthropophile and endophile mosquitos and the most dangerous and efficient of malaria vectors. It still holds its crown 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 (1930) 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 (1931). Symes also reported that in Kenya this species is prevalently anthropophilic (1932). 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 Aedes 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 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 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 those encountered at Mongiro and Mamirimiri, where over 30,000 (representing 93% of the total of all species) were taken in the 40 catches." (Haddow et al 1947). 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 mosquitos 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 visited 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." (Haddow, 1944)

These findings should be compared with Vinke's (1950) on A. gambiae and its reactions to DDT in Katanga, in the Belgian Congo, an area which like Bwamba belongs to the Central African Zoo-Geographical Region.

In this area endophilia and anthropophilia of A. gambiae was indicated by very high and habitual house infestation indices. This obviously is not in itself a sufficient proof of endo- and anthropophilia for the species as a whole; application 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.
- (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 endo- 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 (1949-1953) 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.

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 with a width ranging from 2,000 to 5,500 feet. As the surrounding area was not treated and heavily infested, outside influences were inevitable; however, the entirely parallel reduction 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 (1953), in a holoendemic area, in a valley in the Eastern Usambara Mountains, (some 40 miles 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 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 demonstrated that in some areas quite a considerable proportion of its population is naturally exophilic, zoophilic and is not thus affected by DDT.

In Mauritius (Dowling, 1951-1952) 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 habits 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 Italian Somaliland, the production of A. gambiae, in the areas watered by the Webi-Scebeli river, is distinctly intermittent. Suitable breeding conditions occur for only short periods: (1) after the peak of the bi-annual floods, in pools and ponds left along the banks by the receding waters; (2) 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 hyper-endemic intensity.

During 1955, the writer carried out a survey of the area with Drs C. Guttuso and 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 the 18th July, and in the following week they 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 refer to regions well within the distributional area of A. gambiae. Outside of this area, in Brazil and in South Egypt, A. gambiae became so well established as to cause disastrous malaria epidemics; in both countries it was distinctly endo-and anthropophilic and it was most successfully eradicated. We believe that it is the natural selection, for "export", of the more strictly endo-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 might then be possible 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 could envisage the possibility of DDT 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 South Egypt were obviously already evolved African export products; the same can be said for the highly domestic Aedes 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 resistance 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 is then the position with the exophilic A. gambiae of Mauritius and Madagascar?

SUMMARY

A remarkable range of variation has been demonstrated in the biting habits of A. darlingi, the most dangerous and widely diffused neo-tropical malaria vector. At the centre of its area of distribution on the Central Plateau of Brazil, the species A. darlingi comprises both anthropo-endophilic and zoo-exophilic individuals. DDT has controlled malaria and eliminated A. darlingi from houses, but the species continues to exist outside in abundance.

The antropophilic tendencies of A. darlingi increase progressively, on a well-defined geographical pattern, towards the periphery of its distributional area: in British Guiana and Centro-Northern Venezuela, the species is so specifically attached to man that it has been eradicated by DDT house spraying exclusively.

Conditions of travel and migration, imposed by the immense South American rain forest, have probably favoured the development of a specialized anthropophilic strain on a geographical pattern.

There is ample evidence of similar strain evolution in A. gambiae, but on a more confused pattern, probably in relation to the fundamentally different plan of African ecology. Aedes aegypti also presents an outstanding example of variation in biting habits, affecting practical control policies; the "export" strains that have followed man across the ocean to the Western Hemisphere and Mauritius are strictly domestic.

A proper understanding of the extent and significance of anthropophilic and zoo-philic tendencies, of the "fixity" or "lability" of these characteristics, is essential for the intelligent conduct of control campaigns; for the formulation of rational and economic long-term policies; for the proper evaluation of the probabilities of resistance to insecticides developing in the surviving, post-spraying exophile population of a former vector species.

The high index of domesticity of a vector species does not exclude the existence in the same locality of a zoophilic strain. In any preliminary malaria survey the zoophilic tendencies of the vector species should be fully investigated and measured.

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