



a 66239

ETHOLOGICAL RESISTANCE IN MALARIA VECTORS  
Behavioural response to intradomestic residual insecticides

by

R. Elliott and J. de Zulueta



Introduction

In the thirty years since the introduction of synthetic residual insecticides for the interruption of malaria transmission, the effects on the disease and on the vectors have been very variable in the many different situations that occur in the widespread malarious areas of the world. On the disease, the effects have in every case been positive, ranging from complete arrest of transmission with consequent eradication, through situations where ancillary measures were required to achieve this end, to cases where transmission and incidence, although significantly reduced, continued at levels not compatible with early attainment of the goal. Similarly, the effects on the vectors have extended from local species eradication on the one hand to cases where no apparent reduction in general density or man biting rate can be shown, although the effects on the disease do indicate a reduction in vectorial capacity.

When it was found that the standard operational procedures were not giving the expected results in every situation and with every vector, the phenomenon of insecticide resistance assumed importance. Although resistance to chlorinated hydrocarbons by European malaria vectors was suspected in the late 1940s, the first insect to become uncontrollable by these agents was the housefly, and early attempts to explain resistance were naturally largely based on this insect. An early theoretical treatment was that of Hess (1952), who divided resistance into three classes, physiological, morphological and behaviouristic. These terms, regarded as applying to phenomena of potentially equal importance, applied to resistance as shown by populations; the term tolerance was applied only to the response of individuals.

Physiological resistance, in which a part or the whole of a population come to possess enzyme systems capable of breaking down and disposing of toxic substances introduced into the body, was later to become very important in a number of malaria vectors, although Knipling (1952) considered that it had not then been proved in any species of Anopheles. Morphological resistance was mainly supported by observations by Wiesmann (1947) and D'Alessandro (1949) on the pulvilli and tarsal hairs of DDT-resistant houseflies, which were seen to be more heavily chitinized than those of susceptible ones. The polymorphism of the Musca domestica over its worldwide distribution is quite sufficient to account for small morphological differences between strains that also coincidentally differ physiologically. Morphological resistance is therefore no longer regarded as a factor in enabling insects to survive chemical attack measures, and only two aspects of resistance are now considered, physiological and behaviouristic or ethological.

The chief case of behaviouristic resistance considered by Hess (1952) was the observation by Bruce & Decker (1950) of an apparently acquired preference of houseflies for resting on horizontal surfaces instead of sprayed walls. This behaviour pattern, however, is common in tropical houseflies (M. vicina), and so well within the observed range of variation of members of the complex. Moreover, the strains concerned were in fact physiologically resistant, so that the behavioural peculiarities may be regarded as coincidental rather than causal. Hess

1975

The issue of this document does not constitute formal publication. It should not be reviewed, abstracted or quoted without the agreement of the World Health Organization. Authors alone are responsible for views expressed in signed articles.

Ce document ne constitue pas une publication. Il ne doit faire l'objet d'aucun compte rendu ou résumé ni d'aucune citation sans l'autorisation de l'Organisation Mondiale de la Santé. Les opinions exprimées dans les articles signés n'engagent que leurs auteurs.

also stated that many examples existed of morphological and behavioural resistance in insects of agricultural importance, basing this on a review by Morrison (1951). Reference to the original, however, shows that the cases described were either of morphological and ethological variations found associated with physiological resistance, or of cross-resistance to different insecticides.

The evidence for the existence and possible importance of ethological resistance in vectors of malaria is based mainly on observations that suggest a diminution of the impact of attack measures after some years of application, owing to changes in behaviour, without the intervention of physiological resistance. Before the evidence can be evaluated, the rationale of malaria eradication has to be considered. This is based on the fact that malaria vectors are always more or less domestic; to become infected they must feed at or near the peak of infectivity of gametocytes, which entails entering houses, in the case of the commonest human behaviour patterns. Having done so, their next action is usually to rest indoors for a period that may cover much of the ensuing gonotrophic cycle, or may be much shorter. In spite of the early warning by Ross (1902) that the number of vectors found in a house in the morning was no indication of the numbers that may have fed inside during the night, the endophilic pattern of prolonged indoor resting has been often assumed to be characteristic of vectors and also essential to the attack upon them. As late as 1971, Bruce-Chwatt insisted that a period of 12-24 hours of vulnerability to insecticides inside the house was essential for interruption of transmission. This may be unduly pessimistic, but many authorities have considered, with de Meillon (1933), that the vector of malaria is always a house-haunter.

It is therefore worth examining the pre-DDT records of daytime resting places of vectors, the observed reactions of vectors to the introduction of DDT and of other insecticides, laboratory studies of behaviour in relation to insecticides, and also the few cases of observations of vector behaviour after withdrawal of insecticides, before considering the various theoretical treatments that have been proposed.

#### Daytime resting places of vectors before DDT

A review of the literature covering some 40 years produced over 70 pages giving fairly clear statements of daytime resting habits before introduction of residual insecticides to the area concerned (see Table 1). The number of species covered was 33, and the total of observations was 100, since many papers referred to more than one vector. Of the 100, 37 described endophilic behaviour, 37 exophilic, and 26 gave both types as shown by the same species at the same time and place. Only three (nine observations) were stated to be endophilic in each case; these were the A. maculipennis complex, A. pseudopunctipennis and A. sudaicus. It seems probable that some degree of exophily in fact may have existed before DDT, but was not considered important enough to justify special efforts to detect or report. Six more (12 observations) were only reported resting outdoors by day; these were the A. leucosphyrus complex, A. minimus flavirostris, A. plumbeus, A. punctimacula, A. sergenti and A. vestitipennis. A. punctimacula obviously appears in this list only through lack of reports, as it is well documented as partially endophilic in the post-DDT period, but the two South-East Asian vectors have always been found basically exophilic in the presence or absence of house-spraying. The remaining vectors ranged from casual indoor resters like A. hyrcanus to species only occasionally seen outdoors, such as A. stephensi.

It therefore seems reasonable to conclude that the daytime resting patterns of the great majority of malaria vectors included facultative daytime exophily, even before this habit came to confer significant advantage for survival.

#### Reactions to spraying of DDT

A survey of some 46 papers reporting the impact of DDT on different populations of some 15 vectors, as shown in Table 2, produced the following most frequent observations:

Effective control or reduced general population ...	9
Higher indoor kill .....	9
Reduced entry, or repellency .....	12
Reduced indoor biting .....	7
Reduced survival after leaving house .....	2
Reduced resting in house .....	6
Irritability or increased phototropism .....	10
High survival after leaving house .....	8
No reduction in entry .....	5
No reduction in indoor biting .....	6

These reactions vary from those conducive to reduction or cessation of malaria transmission to those militating against achievement of that goal, and include some compatible with either result.

Some other responses that do not fit under the above heads may be mentioned. The European vectors of the A. maculipennis complex were stated by Livadas et al. (1946) to be generally reduced in population density, with reduced entry and biting; on the other hand, Foy et al. (1948) pointed out that the reduction in malaria rates in different parts of Greece occurred equally in unsprayed and sprayed areas, indicating minimal effect of DDT on the vector. D'Alessandro (1954) held that after the introduction of DDT, an endophagic man-biting population became extinct, leaving an exophilic and zoophilic one. Belios (1960) thought that deviation towards exophily and exophagy had occurred, while Cefalu et al. (1961) thought that facultative exophily had always been inherent in the vector, and showed by mark/release/recapture studies that, after the cessation of use of DDT, separate strains with different behaviour patterns had not developed. Gotberk (1961) found that, after 10 years use of DDT, the vector had become less domestic, and that outdoor transmission had increased. Although the explanations suggested vary, there is therefore a strong suggestion that changes may have occurred between the pre-DDT period and the earliest period of its use, and possibly also after some years of use.

This latter point, a change in the pattern of behaviour after some years, has been twice noted in American vectors. The first case was pointed out by Trapido (1946, 1952) in A. albimanus in Panama. The first paper reported the effect of the first three applications of DDT, which reduced entry into sprayed houses, reduced the proportion of those entering that succeeded in obtaining a blood-meal, and severely reduced survival in those that did succeed. The second paper reported a parallel set of observations made after eight years of treatment; the numbers entering sprayed houses had recovered to pre-DDT density, as had the numbers biting, while differential mortality in the fed fraction no longer took place. Physiological resistance had not then appeared, and the control of malaria remained satisfactory, but a vector population with a tendency to fly restlessly in the house, showing activation and increased phototropism after non-lethal contact with DDT, had replaced that of the earlier period. Further work on wild and laboratory strains of A. albimanus from different areas in Panama by Brown (1958) and Duret (1961, 1964) showed that differences in response to DDT could be demonstrated in the laboratory, a cultivated strain being the least activated. However, comparison of field strains from treated and untreated areas did not show the expected difference; strains from untreated areas were the most active.

In Mexico also, it was possible to repeat observations on the entry and feeding of A. pseudopunctipennis in treated and untreated houses in 1963, virtually duplicating those made in 1950. Martinez-Palacios and de Zulueta (1964) found that ethological changes had occurred, especially a decrease in deterrency. Although Hamon et al. (1970) did not accept this conclusion, since the numbers observed were small, the former great preponderance of vectors in the unsprayed against the sprayed houses, compared with practically equal numbers in the later observation do suggest that a real change may have taken place.

In both the above cases, the ethological change in response to DDT has apparently not been sufficient to effectively remove selection pressure from the insecticide, since physiological resistance is now present in both species in the areas concerned.

Suggestions of similar changes in the behaviour of A. gambiae in different parts of Africa have been made, but since four separate but morphologically indistinguishable species are now recognized from inland sites, over and above the two salt-water members of the complex, changes in the proportions of each in mixed sympatric populations could produce the observed effects. The contribution of insecticides to the apparent changes would therefore be very difficult to determine.

In Asia, according to Sundaraman (1958), A. sondaicus rested on walls both before and after feeding in the period before introduction of DDT, and control was considered to be successful for three to four years thereafter. Subsequent failure of control was attributed to a population that avoided contact with treated surfaces, while remaining physiologically susceptible.

There exist in the literature numerous similar observations that suggest that changes in the behaviour of various vectors in the direction of reduced contact, by day or by night, with sprayed surfaces may possibly be more than the effect of the sum of the reactions of individuals to the irritant, excitant or locomotor-stimulant properties of DDT. However, there is great difficulty in proving any individual case by field observations alone.

#### Responses to other insecticides

Some field observations made where DDT and other insecticides were used simultaneously may be considered. Davidson (1953) found that dieldrin and BHC allowed less A. gambiae females to escape from sprayed houses than DDT, but Smith (1962) noticed that dieldrin caused earlier exit, and also inhibited biting more than DDT. Wharton (1951b) found that the biting rate of A. maculatus was reduced more by BHC than by DDT, and Reid & Wharton (1956), observing A. maculatus and A. sondaicus, saw DDT as highly irritant but often non-lethal, BHC as lethal with some irritant effect, and dieldrin as lethal but non-irritant. Downs & Bordas (1951) stated that mortality in A. pseudopunctipennis both inside houses and in exit traps was greater with BHC than DDT.

Although some observations are slightly contradictory inter se in detail, the general consensus is that the stimulation to activity from DDT is as great or greater than that of any other insecticide, when reaching the vectors at sub-lethal dosages.

#### Laboratory observations

An early observation by Metcalf et al. (1945) on A. quadrimaculatus indicated, after contact with DDT, not only irritation, but reversal of the normal daytime phototaxis from negative to positive. Kennedy (1947) and McInnes (1947) found that DDT was not repellent, in the sense of acting at a distance, but that contact led to excitation, followed by hyperactivity and later ataxia, with possible recovery. Reid (1951), also found that true repellency did not occur. Mariani et al. (1959), in comparing the WHO standard susceptibility test method with earlier procedures, found that the former gave some of the effects seen in the facultative contact devices used by the above authors, in that the mosquitos tended to leave the impregnated papers to rest on the untreated gauze ends of the tubes, thus giving misleading survival of the test. Coluzzi (1963) was able to show different degrees of natural activity and DDT-induced irritability in different laboratory strains, but after comparing the responses of four components of the A. gambiae complex found the results unstable, affected by environmental conditions, and inconstant. Hamon & Eyraud (1961) also found results too inconstant for sure interpretation. Elliott (1964) attempted to simplify measurement of activity by avoiding effects of light, and was able to show that sublethal exposures to DDT caused activity in a similar way to the repellent deet, and that other insecticides were much less locomotor-stimulant; differences between responses of species and strains appeared, but high variance impeded interpretation. In general, it may be said that the existence of hyper-sensitive strains, so often postulated by field observers, has been very difficult to confirm in the laboratory; although it has certainly not been disproved, the link between this and a state of ethological resistance cannot be established.

In a different approach, Gerolt & Laarman (1964), using a facultative contact apparatus to separate the more and less irritated members of a colony of A. atroparvus, formed a sub-colony from the former. This resulted in significant differences between the reactions of the irritable sub-colony and the original colony. This suggests that a basis exists for the selection of protective behaviour patterns giving minimal contact with insecticides.

#### Vector behaviour after cessation of spraying

In only a few cases have systematic observations been made after spraying with insecticides has been terminated, either after the cessation of transmission or for other reasons. Giglioli & Charles (1954) noted that A. darlingi, virtually eradicated from coastal Guyana during the campaign of the 1940s, reappeared after the withdrawal of DDT, and rested by day in the houses just as before. When an outbreak of malaria occurred, spraying was re-introduced, with the same success as in the original campaign. Chow & Soeparno (1956) found that A. sundaicus in Indonesia reappeared resting in houses by day after DDT was withdrawn following the appearance of physiological resistance; similarly in Swaziland A. gambiae returned to indoor daytime resting when BHC was discontinued after termination of transmission (Mastbaum, 1957).

In Sicily, Cefalu et al. (1961) decided that facultative exophily of A. labranchiae was not caused by DDT selection, and Valentino et al. (1965), four years after DDT spraying ceased, showed that females resting outdoors did not belong to a separate exophilic population. In Tanzania, also, Smith (1966) found that both A. gambiae and A. funestus returned to endophily after spraying of dieldrin was stopped. There seems to be no recorded case to the contrary, in which a habit of exophily acquired possibly as a response to insecticide continued after withdrawal of the chemical. This is in strong contrast with the case of physiological resistance, which may lose some of its penetrance in the vector population after selection by insecticide is removed, but does not disappear.

#### Theoretical treatments of ethological resistance

Muirhead Thomson (1947) believed, on the basis of results obtained with early formulations of DDT against A. gambiae in Nigeria, that the irritant effect of DDT protected the vector from the lethal effect; later, Muirhead Thomson et al. (1952) pointed out that field experiments with insecticides are subject to wide variations in conditions, listing 31 separate environmental factors that could materially affect results. Again (1960), he stated that the irritant effect of DDT might be actually advantageous for malaria eradication, by reducing man-vector contact, while protecting the vector. He used the term "behaviouristic avoidance" to describe the various ways by which a vector might escape lethal contact. This might be natural, in which case it could be termed "protective avoidance", or developed through selection, in which case it might be called "behaviouristic resistance".

This, with some difference in terminology, was the position of Hess (1952), who considered that the irritated and repelled behaviour pattern, either inherent or developed as a response to the use of DDT, could through natural selection become increasingly effective. Aside from the rather unconvincing cases of supposed behaviouristic resistance already mentioned, supporting evidence included the report by Bustamante et al. (1951) on a change of habit in A. darlingi in Brazil, from resting inside houses before and after biting to using only outside walls for this.

Buxton (1952), after pointing out the success of DDT against A. darlingi in Guyana, and against A. fluviatilis in Assam, speculated as to whether it would be equally effective against A. albimanus or A. maculatus, these being less endophilic than other species, and therefore protected by their habits and choice of resting places. In the event, DDT proved very effective against A. albimanus in the Caribbean, and against A. maculatus in Malaya (Wharton, 1951), and also against the highly exophilic A. balabacensis (leucosphyrus) (de Zulueta, 1956). These cases fully support the recommendation of Gabaldon (1949), who reacted to the early reports of high vector survival of DDT by stating that the effectiveness of an insecticide should only be measured in terms of its impact on malaria, and not deduced from entomological results.

A more complex system of ordering the data was put forward by Gillies (1956), distinguishing three kinds of exophily; obligatory in the absence of available houses, facultative where houses were available but not used, and deliberate. Deliberate exophily was divided into type "A", where the species fed indoors but left the house soon after (A. aquasalis and A. maculatus) and type "B", where the species seldom fed indoors (A. coustani and A. pharoensis).

Although many other attempts have been made to produce order in the confused situation wherein, apart entirely from the implications of physiological resistance, vectors apparently good candidates for control fail to respond, while others seemingly unsuitable respond satisfactorily, the attachment of labels to abstractions has not been very successful in explaining the facts.

### Conclusions

Before deciding whether the concept of ethological resistance is a valid and useful one, it is worth contrasting the ways in which it differs from physiological resistance to insecticides. The latter has appeared in a number of taxonomic groups of arthropods, which are protected against a wide range of chemicals. It is based on enzyme systems that are relatively well understood, and is inherited by simple monofactorial or oligofactorial processes. It is measurable in pure strains by the ratios of LD50s, and its penetrance in populations can be closely estimated. Ethological resistance, conversely, if it indeed exists, is confined to a single genus, protecting against one chemical, by systems whose operation and inheritance are unknown, and has proved almost impossible to measure accurately or reproducibly even when the behavioural features concerned are reduced to the simplest terms.

The main argument in favour of the concept of ethological resistance to insecticides is that it is a convenient label to apply to an unsatisfactory situation. The hopes developed in the 1950s of early worldwide malaria eradication have been disappointed over large areas that are not affected by physiological resistance of the vector. The main objection to this attempted explanation is that it implies that a change in vector habits is the exclusive explanation, whereas the problem of refractory malaria is almost certainly more complex, involving not only the vector but also the human element and probably also more general ecological conditions. Human conditions such as nomadism and pioneer settlement place people in shelters that are poor substrates for insecticides, and the general environment often provides micro-climates equally as suitable for vector development as the unsprayed house. While the term ethological resistance may therefore have a limited use in pinning down the contribution of the vector to this situation, its over-emphasis may be dangerous, by leading the unsophisticated to suppose that it is a concrete fact of nature like physiological resistance, with no remedy in sight. In fact the areas concerned offer opportunities for improvement of the malaria situation through economic development and amelioration of the human condition, especially housing.

TABLE 1. DAYTIME RESTING PLACES OF VECTORS BEFORE USE OF DDT

Species	Country	Resting places	Reference
<u>A. aconitus</u>	Java	Stream banks	133
	Burma	In houses	78
	Malaya	Not in houses	135
<u>A. albimanus</u>	Mexico	Some in houses	60
	"	In houses	65
	Puerto Rico	Few outdoors	96
	Venezuela	In houses	62
<u>A. amictus hilli</u>	New Guinea	In bush; few in houses	102
<u>A. culicifacies</u>	India	Some outdoors	91
	Pakistan	Common in houses	94
	Ceylon	Many outdoors	16
<u>A. darlingi</u>	Guyana	In houses	48
	Colombia	Near, not in, houses	142
	South America	Endophilic at centre, exophilic at periphery of distribution	51
	Venezuela	In houses	43
<u>A. farauti</u>	New Guinea	In bush	102
	"	Not in houses	92
	Papua	Often in houses	10
	New Hebrides	Many in houses	95
<u>A. fluviatilis</u>	India	Many outdoors	107
	"	Only indoors	9
<u>A. funestus</u>	Uganda	Only indoors	58
	Tanzania	Outdoors (and in)	125
	"	" "	52
<u>A. gambiae (complex)</u>	Sierra Leone	In hedges and shrubs	11
	Liberia	Almost exclusively in houses	139
	"	40% left houses by dawn	46
	Nigeria	40% left at dawn	123
	Kenya	Many in grass and bush	117
	Uganda	All gonotrophic stages in houses	58
	"	All gonotrophic stages outdoors	52
	Tanzania	Some left houses at dawn	125
	"	In bush	109
	Sudan	Mostly in houses	75
	Swaziland	Few in houses	84
Brazil	Exclusively in houses	5	
<u>A. hyrcanus (complex)</u>	USSR (Ussuri)	Meadows and ricefields	93
	" (Dnieper)	Left houses before dawn	54
	China (S)	In farm houses	56
	"	Outdoors	23
	"	"	74
	Afghanistan	Never in houses	41
	Malaya	" " "	135
<u>A. jeyporiensis</u>	Hainan	Not indoors	63
	China (S)	Indoors	22
	"	"	74
	Burma	"	78
<u>A. koliensis</u>	New Guinea		92

TABLE 1 (continued)

Species	Country	Resting places	Reference
<u>A. leucosphyrus</u> ( <u>A. balabacensis</u> )	Burma	Outdoors	78
	"	Few in tents and godowns	71
	Borneo	Normally outdoors	24
	Malaya	All members of complex outdoors	26
	Hainan	Not indoors	63
<u>A. maculatus</u>	Java	Some in houses, mainly outdoors	132
	Malaya	Outdoors	135
<u>A. maculipalpis</u>	Rhodesia	Seldom indoors	99
<u>A. maculipennis</u> (com- plex)	USSR (Black Sea)	In houses and animal shelters	106
	USSR (Azov Sea)	" " " " "	30
	Egypt	" " " " "	3
	Portugal	" " " " "	19
<u>A. melas</u>	Nigeria	Partly outdoors	123
	Liberia	90% outdoors	46
<u>A. merus</u>	Tanzania	One-third outdoors	125
<u>A. minimus minimus</u>	China (N)	Leaves houses before dawn	21
	China (S)	All gonotrophic stages in houses	22
	Burma	Outdoors	78
	India	Indoors throughout gonotrophic cycle	121
<u>A. minimus flavi- rostris</u>	Philippine Is.	Along stream banks	130
	"	" " "	67
	Java	" " "	133
<u>A. moucheti</u>	Upper Volta	Outdoors	73
	Zaire	Not completely domestic	31
<u>A. nili</u>	Upper Volta	Occasionally indoors	73
	Nigeria	A few in houses	119
	"	In houses	4
<u>A. pharoensis</u>	Sudan	Outdoors	75
	Tanzania	In long grass	109
	Kenya	In houses with cattle	115
<u>A. plumbeus</u>	USSR	Never in houses	106
<u>A. pseudopictus</u>	USSR	Few in houses, most in swamp reeds	30
<u>A. pseudopunctipennis</u>	Mexico	Shelter in houses	12
	"	In houses	60
	Argentina	" "	85
<u>A. punctimacula</u>	Colombia	Outdoors	103
	"	"	141
<u>A. punctulatus</u>	New Guinea	Outdoors	102
	" "	Indoors	92
<u>A. quadrimaculatus</u>	United States of America	Treeholes	112
	" " "	Barns	113
	" " "		
<u>A. sergenti</u>	Jordan	Highly exophilic	40
<u>A. stephensi</u>	Afghanistan	Seasonally in houses	41
	"	In houses and stables	66
	Pakistan	Common in houses	94
	India	In houses	1
	"	Some outdoors	91
	Iran	In stables	82

TABLE 1 (continued)

Species	Country	Resting places	Reference
<u>A. sundaicus</u>	Indonesia	In houses	114
	"	" "	134
<u>A. superpictus</u>	Afghanistan	In houses	41
	"	In houses and stables	66
	Egypt	In houses and stables	3
	India	Common outdoors	91
<u>A. vestitipennis</u>	Mexico	Never in houses	60

TABLE 2. IMPACT OF DDT ON VECTORS

Species	Country	Observation	Reference
<u>A. albimanus</u>	Panama	Reduced entry and biting; low survival fed	128
	"	Biting returned to pre-DDT level, with high survival	129
	Mexico	DDT very irritant; more than other insecticides	80
<u>A. darlingi</u>	Guyana	Entered houses, fed, escaped and rested in vegetation	117
	"	DDT effective; few escaped	49
	Colombia	Effect minimal, as no indoor resting	100
<u>A. farauti</u>	New Guinea	DDT/kerosene effective	6
	" "	80-100% mortality, but biting continued	120
	" "	DDT less effective than dieldrin	87
<u>A. funestus</u>	New Hebrides	DDT effective	140
	Tanzania	100% kill in experimental huts	138
	"	Near 100% mortality in houses	64
<u>A. gambiae</u>	Madagascar	Species eradicated	72
	Nigeria	DDT repellent; reduced entry	70
	Cameroons	DDT irritant; caused behavioural avoidance	90
<u>A. hyrcanus</u>	Ghana	Many dead in houses (4 g/m <sup>2</sup> )	37
	Nigeria	High survival low dosage; irritant effect	122
	Tanzania	Near 100% kill at 2 g/m <sup>2</sup> ; low kill at 0.5 g/m <sup>2</sup>	64
	"	As 122 at 4 g/m <sup>2</sup> ; BHC more effective	124
	"	Left DDT huts fed; sublethal doses increased phototaxis; more entered DDT huts than unsprayed huts	57
	Uganda	Strong "deterrent" effect	144
	"	Deterrent effect in 144 an artefact of hut construction	111
<u>A. hyrcanus</u>	Taiwan	High survival in exit traps; sublethal doses excito-repellent	74
	"	No reduction of entry or feeding	77

TABLE 2 (continued)

Species	Country	Observation	Reference
<u>A. jeyporiensis</u>	Taiwan	As <u>A. hyrcanus</u>	74
<u>A. leucosphyrus</u>	Borneo	DDT kerosene (and kerosene alone) reduced periods of rest; repellency or activation	25
	Sarawak	Good control; some indoor biting continued	143
<u>A. maculatus</u>	Malaya	High mortality, biting rate unaffected	136
	"	Reduced entry and biting; some mortality, but also non-lethal irritation	98
<u>A. maculipennis</u>	Greece	Reduced density of general population	76
	"	Doubt if DDT contributed to reduction of malaria	42
	Sicily	Dense exophilic population remained; endophilic population destroyed	29
	Morocco	High survival by avoidance of treated surfaces	105
	Greece	25% irritated from outset; deviation to exophagy and exophily	7
	Sicily	Facultative exophily inherent; no separate strains developed	20
	Turkey	Less domestic after 10 years DDT; outdoor transmission	55
<u>A. minimus minimus</u>	Assam	Races with different degrees exophily and exophagy	101
	"	22% survived 2 g/m <sup>2</sup> ; 88% escaped 0.4 g/m <sup>2</sup>	8
	Philippines	Reduced density and malaria	38
	Taiwan	No reduction entry; reduced feeding	77
<u>A. pseudopunctipennis</u>	Mexico	Increased phototropism	34
	"	Deterrent effect lost between 1950-1963	83
<u>A. punctimacula</u>	Colombia	DDT increased existing exophily	103
<u>A. quadrimaculatus</u>	United States of America	Not repelled; activated but killed	(45)
	" " "	No repellency; increased phototropism; 60-70% mortality in exit traps	(46)
	" " "	Reduced biting and indoor resting	108
<u>A. sergenti</u>	Jordan	Inherent exophily led to failure to control	118
<u>A. sundaicus</u>	Malaya	Reduced entry and biting	40
	Java	Changed behaviour to avoid contact	98
			114

REFERENCES

- Abraham, A. C. (1932) Rec. Mal. Surv. India, 30, 179
- Adam, J. P. (1956) Bull. Soc. Path. exot., 49, 210
- Abdel Malik, A. A. (1938) Bull. Soc. ent. Egypt, 42, 519
- Anderson, D. (1933) Trans. roy. Soc. trop. Med. Hyg., 26, 408
- Anon. (1940) Publ. Hlth Rep., 55, 1801
- Bang, F. B. et al. (1947) Trans. roy. Soc. trop. Med. Hyg., 40, 809
- Belios, G. D. (1960) Riv. Malar., 39, 1
- Bertram, D. S. (1950) Ann. trop. Med. Parasit., 44, 242
- Bhombore, S. R., Sitaraman, N. L. & Achuthan, C. (1956) Indian J. Malar., 6, 23
- Black, R. H. (1952) Tech. Pap. S. Pacif. Comm. No. 60
- Blacklock, D. B. & Wilson, C. (1941) Ann. trop. Med. Parasit., 35, 37
- Bordas, E. & Downs, W. G. (1951) Amer. J. Hyg., 53, 217
- Brown, A. W. A. (1958) Bull. Wld Hlth Org., 19, 1053
- Bruce, W. N. & Decker, G. C. (1950) Soap & Sanit. Chem., 26, 122 and 145
- Bruce-Chwatt, L. J. (1971) Bull. Wld Hlth Org., 44, 406
- Buttiker, W. (1958) ibid., 19, 1118
- Bustamante, F. M. et al. (1951) Rev. bras. Malar., 3, 122
- Buxton, P. A. (1952) Trans. roy. Soc. trop. Med. Hyg., 46, 216
- Cambournac, J. C. & Hill, R. B. (1938) Acta Conv. ter. Malar. Morb., 2, 178
- Cefalu, M., Oddo, F. & Sacca, G. (1961) Parassitologia, 3, 23
- Chang, T. L. (1940) Chin. med. J., 58, 218
- Che Lee (1960) Acta. ent. Sin., 10, 96
- Chow, C. Y. & Soeparano, H. T. (1956) Bull. Wld Hlth Org., 15, 785
- Colless, D. H. (1952) Med. J. Malaya, 6, 234
- Colless, D. H. (1953) Ann. trop. Med. Parasit., 47, 261
- Colless, D. H. (1956) Proc. R. ent. Soc. Lond. (B), 108, 37
- Coluzzi, M. (1963) Riv. Malar., 42, 189
- D'Alessandro, G. et al. (1949) Sicilia Medica, 6, 5

- D'Alessandro, G. et al. (1954) Riv. Parassit., 15, 361
- Danilova, M. I. & Buduinko, F. A. (1938) Med. Parasitol., 7, 467
- Davidson, G. (1950) Ann. trop. Med. Parasit., 43, 361 and 44, 1
- Davidson, G. (1953) Bull. ent. Res., 44, 231
- Dowling, M. A. C. (1953) Trans. roy. Soc. trop. Med. Hyg., 47, 177
- Downs, W. G. & Bordas, E. (1951) Amer. J. Hyg., 54, 150
- Duret, J. P. (1961) Bol. Ofic. sanit. panamer., 51, 285
- Duret, J. P. (1963) ibid., 57, 259
- Eddy, L. G. (1947) Trans. roy. Soc. trop. Med. Hyg., 40, 567
- Ejercito, A., Hess, A. D. & Willard, A. (1954) Amer. J. trop. Med. Hyg., 3, 971
- Elliott, R. (1964) Bull. Wld Hlth Org., 31, 657
- Farid, M. A. (1956) ibid., 15, 828
- Fischer, L. & Steinhart, W. (1957) Z. Tropenmed. Parasit., 8, 69
- Foy, H. et al. (1948) Ann. trop. Med. Parasit., 42, 153
- Gabaldon, A. (1949) Trans. roy. Soc. trop. Med. Hyg., 43, 113
- Gahan, J. B., Travis, B. V. & Mathis, F. A. (1945) J. econ. Ent., 38, 231
- Gahan, J. B. & Lindquist, A. W. (1945) ibid., 38, 223
- Gelfand, H. M. (1955) Trans. roy. Soc. trop. Med. Hyg., 49, 508
- Gerolt, J. L. & Laarman, J. J. (1964) Nature, 204, 500
- Giglioli, G. (1948a) Amer. J. trop. Med., 28, 43
- Giglioli, G. (1948b) Mosq. Cont. Serv. Med. Dept British Guiana
- Giglioli, G. & Charles, L. J. (1954) Amer. J. trop. Med. Hyg., 3, 808
- Giglioli, G. & Charles, L. J. (1956) Bull. Wld Hlth Org., 15, 461
- Gillies, M. T. (1954) Bull. ent. Res., 45, 361, 375
- Gillies, M. T. (1956) Bull. Wld Hlth Org., 15, 437
- Goritzkaya, V. V. (1939) Med. Parasitol., 8, 91
- Gotberk, C. (1961) Mosquito News, 21, 101
- Ha, S. M. K. (1940) Lingnan Sci. J., 19, 403
- Hadaway, A. B. (1950) Bull. ent. Res., 41, 63
- Haddow, A. J. (1942) ibid., 33, 91

- Hamon, J. & Eyraud, M. (1961) Riv. Malar., 40, 219
- Hecht, O. & Corso, J. H. (1957) Z. Tropenmed. Parasit., 8, 391
- Hess, A. D. (1952) Amer. J. trop. Med. Hyg., 1, 371
- Hill, R. B. (1934) Amer. J. trop. Med., 14, 425
- Ho Ch'i & Feng Lan-Chou (1958) Chin. med. J., 77, 533
- Hocking, K. S. (1947) Trans. roy. Soc. trop. Med. Hyg., 40, 589
- Hoffmann, C. C. (1934) Bol. Inst. Hyg. Mex., 2, 1
- Iyengar, M. O. T. (1954) Trans. roy. Soc. trop. Med. Hyg., 48, 319
- Jesus, P. I. de, Jao, S. G. & Garcia, E. Y. (1938) J. P. I. med. Ass., 18, 291
- Kennedy, J. S. (1947) Bull. ent. Res., 37, 593
- Knipling, E. F. (1952) Amer. J. trop. Med. Hyg., 1, 389
- Kuhlowl, F. (1959) Z. Tropenmed. Parasit., 10, 328
- Kuitert, L. C. & Hitchcock, J. D. (1948) Proc. ent. Soc. Wash., 50, 77
- Lacan, A. (1954) Mem. Inst. sci. Madagascar, 4, 503
- Langouillon, J. et al. (1956) Med. trop., 16, 347
- Lee, L. G. (1957) Acta ent. Sin., 7, 481
- Lewis, D. J. (1958) Bull. ent. Res., 49, 133
- Livadas, G. A., Belios, G. & Issaris, P. K. (1946) Athens Sch. Hyg.
- Luh, P. L. et al. (1963) Acta ent. Sin., 12, 149
- Macan, T. T. (1950) Parasitology, 40, 290
- McInnes, D. G. (1947) Bull. ent. Res., 38, 123
- Mancera, V. O. & Hernandez, C. J. (1960) CNEP Bol., 4, 82
- Mariani, M. et al. (1959) Riv. Parassit., 20, 191
- Marsh, F. (1933) Rep. med. Dep. Anglo-Persian Oil Co., 1932, 53
- Martinez-Palacios, A. & Zulueta, J. de (1964) Nature, 203, 940
- Mastbaum, O. (1957) J. trop. Med. Hyg., 60, 190
- Mazza, S. & Rickard, E. (1930) 5° Reunion Soc. argentina Pat. Reg. Norte, 707
- Meillon, B. de (1933) Ann. trop. Med. Parasit., 27, 83
- Metselaar, D. (1957) Acta Leidensa, 27, 1
- Metcalf, R. L. et al. (1945) Publ. Hlth Rep., 60, 27 and 753

- Morrison, F. O. (1951) 81st Ann. Rept ent. Soc. Ont., 41
- Mouchet, J. & Cavalie, P. (1961) Riv. Malar., 40, 191
- Mulligan, M. W. & Baily, J. D. (1936) Rec. Mal. Surv. India, 6, 289
- Peters, W. & Standfast, H. A. (1960) Trans. roy. Soc. trop. Med. Hyg., 54, 249
- Plyater-Plokhotskaya (1939) Med. Parasitol., 8, 71
- Rafi, S. M. (1956) Pak. J. Hlth, 5, 146
- Rageau, J. & Vervent, G. (1959) Tech. Pap. S. Pacif. Commun.
- Rehn, J. W. H., Maldonado, C. J. & Henderson, J. M. (1950) J. nat. Malar. Soc., 9, 268
- Reid, J. A. (1951) Bull. ent. Res., 41, 761
- Reid, J. A. & Wharton, R. H. (1956) Bull. ent. Res., 47, 433
- Reid, E. T. & Woods, R. W. (1957) Proc. Rhod. Sci. Ass., 45, 47
- Renjifo, S. & Zulueta, J. de (1952) Amer. J. trop. Med. Hyg., 1, 598
- Ribbands, C. R. (1947) Bull. ent. Res., 37, 567
- Roberts, F. H. S. & O'Sullivan, P. J. (1948) ibid., 39, 159
- Ronnefeld, F. (1957) Z. Tropenmed. Parasit., 8, 376
- Ross, R. (1902) Mosquito brigades and how to organise them, Philip, London
- Sacca, G. & Guy, Y. (1960) Bull. Wld Hlth Org., 22, 735
- Schlenova, M. F. (1938) Med. Parasitol., 7, 501
- Senior-White, R. (1941) J. Malar. Inst. India, 4, 57
- Simmons, S. W. et al. (1945) Publ. Hlth Rep., 60, 917
- Smith, A. (1961) Nature, 190, 1220
- Smith, A. (1962) Bull. Wld Hlth Org., 26, 120
- Smith, A. (1963) Nature, 200, 861
- Snow, W. E. (1949) J. nat. Malar. Soc., 8, 336
- Snow, W. E. & Smith, G. E. (1956) Mosquito News, 16, 294
- Sundaraman, S. (1958) Indian J. Malar., 12, 129
- Symes, C. B. (1932) Rec. Med. Res. Lab. Kenya, No. 4
- Symes, C. B. (1940-41) E. Afr. med. J., 17, 291, 332, 414, 445
- Symes, C. B. & Hadaway, A. B. (1947) Bull. ent. Res., 37, 399
- Tarzwell, C. M. & Fisk, F. W. (1947) Publ. Hlth Rep., 62, 84

- Taylor, A. W. (1930) Ann. trop. Med. Parasit., 24, 425
- Thiel, P. H. van & Metselaar, D. (1955) Docum. Med. geogr. trop. (Amst.), 7, 164
- Thomson, R. C. M. (1941) J. Malar. Inst. India, 4, 217
- Thomson, R. C. M. (1947) Bull. ent. Res., 38, 449
- Thomson, R. C. M. (1948) ibid., 38, 527
- Thomson, R. C. M. (1949) Nature, 163, 109
- Thomson, R. C. M. (1951) Bull. ent. Res., 41, 487
- Thomson, R. C. M. (1960) Bull. Wld Hlth Org., 22, 721
- Thomson, R. C. M., Gordon, R. M. & Davey, T. H. (1952) Trans. roy. Soc. trop. Med. Hyg., 46, 271
- Trapido, H. (1946) Amer. J. trop. Med., 26, 383
- Trapido, H. (1952) Amer. J. trop. Med. Hyg., 1, 853
- Urbino, C. M. (1938) Mth Bull. Bur. Hlth PI, 18, 301
- Valentino, L. & Bruno Smiraglia, C. (1965) Riv. Malar., 44, 191
- Venhuis, W. G. (1941) Geneesk. Tijdschr. Ned-Ind., 81, 2178
- Venhuis, W. G. (1942) ibid., 82, 99
- Walch, E. W. (1932) ibid., 72, 682
- Wharton, R. H. (1951a) Ann. trop. Med. Parasit., 45, 141
- Wharton, R. H. (1951b) Bull. ent. Res., 42, 1
- Wiesmann, R. (1947) Mitt. Schweiz. ent. Ges., 22, 484
- Wilkinson, P. R. (1951) Bull. ent. Res., 42, 45
- Young, M. D. & Johnson, T. H. jr (1949) J. nat. Malar. Soc., 8, 247
- Yust, H. R. (1947) J. econ. Ent., 40, 762
- Zulueta, J. de (1950) Amer. J. trop. Med.
- Zulueta, J. de (1952) Amer. J. trop. Med. Hyg., 1, 314
- Zulueta, J. de (1956) Bull. Wld Hlth Org., 15, 651
- Zulueta, J. de & Cullen, J. R. (1963) Nature, 200, 860