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Resistance in Arthropods of Medical and Veterinary Importance—1946-58

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ABSTRACT

Resistance to insecticides among arthropods of public health importance has shown a steady increase since the initial report of resistant *Musca domestica* L. and *Culex molestus* Forskål in 1947. In the 1946–58 period, the total number of species reported as physiologically resistant to one or more pesticides was 46. Thirty of this number represented confirmed cases, including 20 species of mosquitoes (9 malaria vectors, 2 transmitters of encephalitis, one transmitter of yellow fever, and one vector of filariasis). In 1958, dieldrin resistance was reported for the initial time in *Anopheles albimanus* Wiedemann (El Salvador, Guatemala, Nicaragua), *A. pseudopunctipennis* Theobald (Mexico), and *A. aquasalis* Curry (Trinidad). In certain parts of El Salvador and Nicaragua, *A. albimanus* also is resistant to DDT. Except for resistance in *Chrysomya putoria* (Wied.) in the Belgian Congo, and in *Phaenicia caprina* (Wied.) in Australia, blow fly species continue to remain susceptible to chlorinated hydrocarbon insecticides. Other species in which physiologic resistance has been confirmed are *Pediculus humanus humanus* L., *Blattella germanica* (L.), *Cimex lectularius* L., *C. hemipterus* (F.), *Glyptotendipes paripes* Edwards, and *Culicoides furens* (Poey). Behavioristic resistance to DDT is evident in *A. albimanus* (Panama), and in the United States, *M. domestica* has displayed similar resistance to malathion bait in a few localities. Resistance to both organophosphorus and chlorinated hydrocarbon insecticides has been demonstrated in *M. domestica*, *C. putoria*, *G. paripes*, *Culex tarsalis* Coq., and *Aedes nigromaculis* (Ludlow). Despite the increase in the magnitude of the resistance problem, many species continue to remain susceptible to DDT and other chlorinated hydrocarbon compounds even though under repeated exposure to these toxicants for periods of 5 to 10 years.

The resistance problem in arthropods of medical and veterinary importance has become one of increasing significance to all individuals engaged in the control of pests of man or animals. When DDT first appeared in public use in 1946, it was hailed as a panacea for insect control, some optimistic scientists even proclaiming the day had come when normal preventive measures such as screens and sanitation could be abandoned. Unfortunately, but in some ways fortunate for the entomologist, our arthropod enemies did not panic at the first sign of this atomic age attack. Instead, the survivors regrouped as a nucleus of future populations which could propagate despite the presence of a residual insecticide. Once such populations occupied a major role in an area, control difficulties ensued.

At first, such difficulties were blandly explained as the result of inferior formulations, poor spray techniques, and other operational errors; the thought that the lowly "bug" could withstand the miracle insecticide was difficult to comprehend. For example, in the United States, the residual house spraying program for malaria control won complete acceptance by rural families in 1946, partly because of its effect on house fly (*Musca domestica* L.) populations. Although only the dwelling and sometimes the privy were treated, no distinction was made between the fly and mosquito control obtained. In 1947, when recurrent reports claimed that the treatments were not so effective as in 1946, the quick explanation followed that successful fly control was not to be expected from house applications alone, and that the program was directed toward the mosquito vector only. Thus the issue of resistance in the fly population was avoided. Fortunately, the malaria incidence in United States at that time had declined to such a low level that incomplete acceptance of the program no longer endangered the disease situation.

From the initial occurrence of resistance in *Musca domestica* (Weismann 1947) and *Culex pipiens molestus* Forskål (Mosna 1947) in 1947, the problem has grown steadily during the ensuing 11 years. The number of resistant species has gradually increased until today more than 46 have lost their susceptibility to certain insecticides. In addition, the geographic area occupied by a given resistant species has expanded, as has the ability of various species to cope with a number of pesticides.

Before continuing with this discussion, it is desirable to define the term "resistance." As interpreted here, it is the ability of an arthropod population to survive exposure to dosages of a toxicant to which it formerly was highly susceptible. This definition excludes a population which never displayed a susceptibility to an insecticide. Such strains or populations have been considered by some authors to be naturally resistant or refractory to the chemical involved. Although it is true that any resistant population originally contained a naturally resistant element, the development of this element to the point where it becomes the dominant component of the population is the result of insecticide selection.

Two distinct types of resistance have been encountered:

Physiologic: The ability through physiologic

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processes to withstand a toxicant after it has entered the body.

Behavioristic: The ability through protective habits or behavior to avoid lethal contact with a toxicant.

When the resistance problem is considered *in toto*, it is obvious that, with few exceptions, the difficulties experienced in vector control have been the result of physiologic resistance. Consequently, the major portion of the discussion relates to that phase.

PHYSIOLOGIC RESISTANCE.—The growth of physiologic resistance in arthropods of medical importance during the period 1946–58 is depicted in figure 1. It is apparent that each year indicts one or more new species, in some instances species which had been under insecticide treatment for many years without evidence of any loss in susceptibility. Thus, in 1958, the cumulative total of 46 species was reported as resistant; of this number, 30 represented species in which the resistance was confirmed by laboratory or field tests. When confirmed cases of resistance are related to geographic area, it is found that 16 resistant species occur in North America, twice as many as in any other region. All of these species occur in the United States, a reflection presumably of the increased emphasis placed on chemical measures in this country, as well as the greater effort expended in the detection of resistance.

Mosquitoes.—Of the 30 species in which resistance has been confirmed, 20 of these are mosquitoes, 9 being malaria vectors, 2 transmitters of encephalitis, 1 the transmitter of yellow fever, and 1 a vector of filariasis. On an overall basis, the problem among malaria vectors has been of the greatest concern to medical entomologists.

UNITED STATES: The resistant species in the United States are *Aedes dorsalis* (Meigen) and *Aedes nigromaculis* (Ludlow) (California); *Aedes sollicitans* (Walker) (Florida), *Aedes taeniorhynchus* (Wied.) (Florida, Georgia); *Anopheles quadrimaculatus* Say (Mississippi); *Culex pipiens* L. (Massachusetts); *Culex tarsalis* Coq. (California, Oregon); *Psorophora confinnis* (Lynch Arribálzaga); and *Psorophora discolor* Coq. (Mississippi).

As early as 1948, control difficulties with DDT were experienced in California with *C. tarsalis*, *Aedes dorsalis*, and *A. nigromaculis*, and in Florida with the two salt-marsh pest species *A. sollicitans* and *A. taeniorhynchus*. As a result a

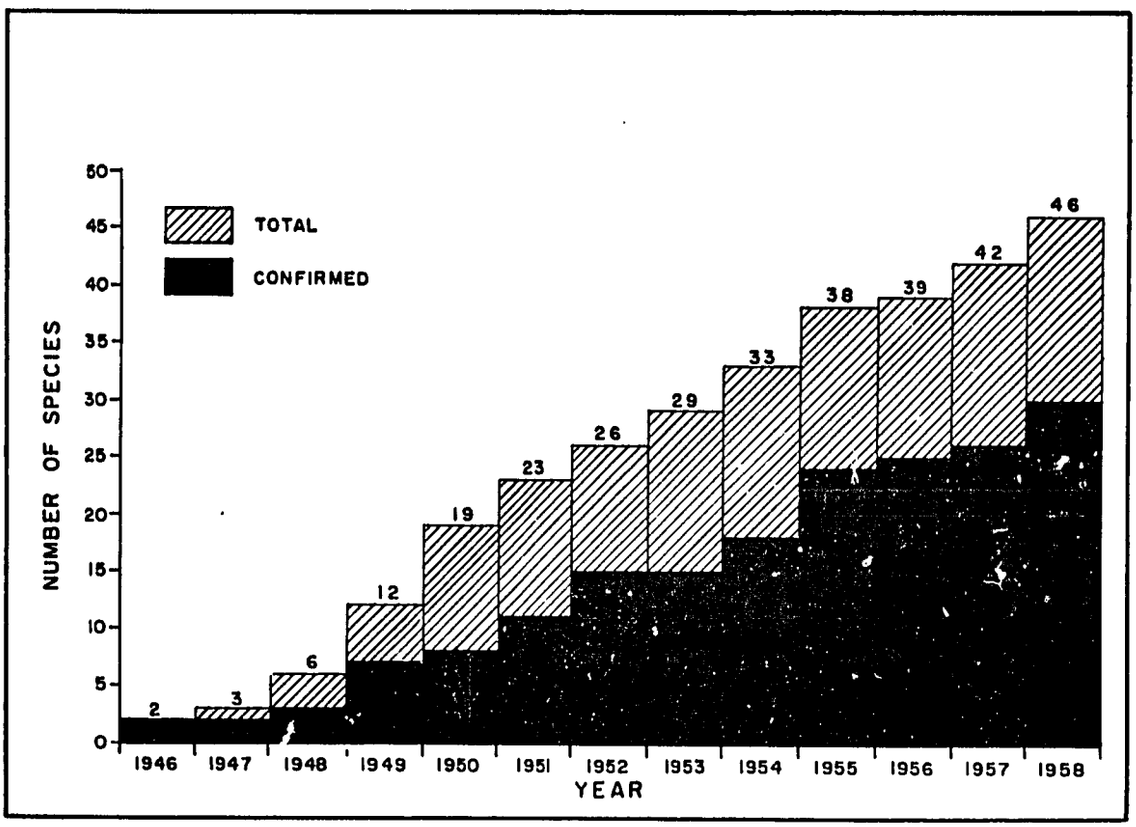

FIG. 1.—Cumulative number of arthropods of public health importance physiologically resistant to insecticides, 1946–58.

shift was made to the use of other chlorinated-hydrocarbon insecticides such as toxaphene, dieldrin, and BHC. In California, resistance to these materials readily developed in certain areas, so that organophosphorus materials such as EPN, malathion, and parathion were utilized in many abatement districts for larvicidal purposes. Up to 1957, little change was noted in the susceptibility of *C. tarsalis* to malathion application. However, in that year Gjullin & Isaak (1957) reported *C. tarsalis* larvae and adults from the Fresno area as highly resistant to malathion. In other areas where the same chemical and parathion had been used extensively, no change in susceptibility was noted. In 1958, in the King's Mosquito Abatement District where parathion has been used for 6 years, control failures against *A. nigromaculis* became apparent. Preliminary tests indicated a definite difference in the response to parathion of mosquitoes from this area as compared with that of larvae from Fresno (Lewallen & Brawley 1958).

In Florida, the replacement of DDT by other chlorinated-hydrocarbon insecticides gradually led to the development of resistance to these compounds in *A. sollicitans* and *A. taeniorhynchus*. As in California, the degree of resistance varied in different sections of the state, the intensity in part being a reflection of the type and amount of larviciding practiced. However, the introduction of organophosphorus compounds as larvicides was relatively minor as compared with that in California. As an adulticide, malathion is the chief toxicant employed, Rogers & Rathburn (1958) having shown that space applications of malathion formulations were far more effective against *A. taeniorhynchus* than were DDT treatments.

Other than Florida, the only southern area where resistant populations of salt marsh mosquitoes have been detected is a small focus in Chatham County, Georgia. Prior to 1958, *Aedes taeniorhynchus* in that county had been found to be susceptible to DDT and dieldrin. No organized abatement program existed until July 1957, when sporadic fog applications of 5 percent DDT were begun in the urbanized areas. In early 1958, adult tests with *A. taeniorhynchus* reared from sod at one localized site (Cockspur Island) indicated the species to have little response to either dieldrin or DDT residues (Mathis 1958, unpublished). When detailed comparison of the susceptibility to dieldrin of adults from Cockspur Island with that of adults from adjacent areas (3 to 7 miles) was made, the data showed clearly that the resistance was limited to Cockspur Island (table 1). The results with DDT were similar but at a lower level of resistance. The apparent explanation for the dieldrin resistance at Cockspur Island lies in the fact that in September 1957 the area was treated with dieldrin at a rate of 4 lbs./acre for white fringed beetle control. Why the population is resistant also to DDT is puzzling, in view of the general lack of such cross resistance in other mosquitoes.

Other resistant culicine species in United States are *Culex pipiens*, *Psorophora confinnis* and *Psorophora discolor*. *Culex pipiens* has been suspected of being resistant to DDT in Ohio, but the confirmed evidence relates to Armstrong's studies in Massachusetts (1955). Two species of *Psorophora*, *confinnis* (Mathis et al. 1955) and *discolor* (Quarterman & Schoof 1958), were shown to be resistant to dieldrin in Bolivar County, Mississippi, in 1954.

Table 1.—Susceptibility response of *Aedes taeniorhynchus* (Wied.) females to dieldrin-Risella deposits, 60-minute exposure.[a]

LOCALITY	24-HOUR PER CENT MORTALITY FOR DIELDRIN CONCENTRATIONS (%) OF:			
	0.2	0.4	0.8	1.6
Tybee Island	7	12	78	100
Whitmarsh Island	0	9	33	93
Causton Bluff	0	3	35	97
Cockspur Island	—	5	1	18

[a] From Mathis, W., in manuscript.

Of the anopheline species of United States, the common malaria mosquito *Anopheles quadrimaculatus* has shown high resistance to dieldrin, BHC, and lindane in Mississippi (Mathis et al. 1956) although continuing to be susceptible to DDT. Although originally the resistance was considered a reflection of the heavy aerial cotton dusting practiced in the Bolivar County area, subsequent tests have revealed low susceptibility to dieldrin in specimens collected as far as 50 miles from that general area. Another point of interest with the dieldrin-resistant strain from Mississippi is the fact that exposure of specimens to water-wettable dieldrin residues (50 mg./sq. ft.) in animal-baited huts for periods of 8 to 12 hours produces mortalities of 40 to 60%.

On a plantation (Lynah) near Savannah, Georgia, where dieldrin treatments for agricultural purposes are minimal,[2] *A. quadrimaculatus* populations show a partial resistance to dieldrin. Exposure for 90 minutes to dieldrin-Risella oil residues at concentrations of 0.1, 0.2, 0.4, 0.8, 1.6, 3.2 and 4.0% produced mortalities of the "Lynah" *A. quadrimaculatus* of 44, 64, 75, 78, 80,

[2] The past history of insecticidal use in the specific area is vague, but it is known that at least one limited treatment of dieldrin for agricultural purpose was made in 1957.

87, and 94%, respectively. With similar exposure, the susceptible strain yielded 0, 36, 97 and 100% kills at concentrations of 0.2, 0.4, 0.8 and 1.6%. The response of the "Lynah" *A. quadrimaculatus* shows the plateau effect which is characteristic of resistant populations.

Anopheles quadrimaculatus continues to remain susceptible to DDT residues despite the widespread use of this chemical in agriculture and as a residual spray for malaria control. In addition, laboratory efforts to select DDT-resistant populations have shown little success.

REGIONS OUTSIDE UNITED STATES: On a global scale, resistant malaria vectors occur in all major land areas except South America, (table 2). Four

Table 2.—Malaria vectors resistant (confirmed) to DDT and/or dieldrin.

SPECIES	AREA	RESISTANT TO:
A. albimanus Wied.	El Salvador[a]	Dld/DDT
	Nicaragua[a]	Dld/DDT
	Guatemala	Dld
A. aquasalis Curry	Trinidad, BWI	Dld
A. gambiae Giles	French West Africa	Dld
	Liberia	Dld
	Nigeria	Dld
A. pseudopunctipennis Theobald	Mexico	Dld
A. quadrimaculatus Say	U. S.	Dld
A. sacharovi Favre	Greece	Dld/DDT
	Lebanon	DDT
A. stephensi Liston	India	DDT
	Iran	DDT
	Iraq	DDT
	Saudi Arabia	DDT
A. subpictus Grassi	Indonesia	Dld
A. sundaicus (Rodenwaldt)	Burma	DDT
	Indonesia	DDT

[a] DDT resistance less severe than dieldrin and absent in certain areas

aspects of these data are of particular significance. The first is that, except for *A. sacharovi* Favre and *A. albimanus* Wied., resistance in a species is confined to either DDT or dieldrin. Consequently, with all other species the continuation of successful control or eradication has been made possible by shifting from one toxicant to the other. In Indonesia, dieldrin has served effectively against the DDT-resistant *A. sundacius* (Rodenwaldt); in Nigeria, dieldrin-resistant *A. gambiae* Giles are susceptible to DDT. The second point concerns the recent detection of dieldrin resistance in *A. albimanus* in El Salvador by Duret (1958a) followed by reports of similar resistance in Guatemala and in Nicaragua and possibly Jamaica. In El Salvador, Duret's tests extended to a number of localities, all of which indicated a high level of dieldrin resistance.

One-hour exposure to dieldrin-Risella oil residues (1.6%) produced mortalities of 3 to 15% in five of six villages (Metalio, Acajutla, La Libertad, Olomega, Sirama, and Tecomatal) distributed along the entire coastal area (Duret 1958b). Two inland towns (Nueva Concepcion, Belem Guijat) also showed similar levels of dieldrin resistance (Heredia 1958). In addition, the *A. albimanus* from three areas in southeastern El Salvador were definitely less susceptible to DDT than were those from towns northwest of that sector. LD-50 concentrations of DDT-Risella oil papers from the southeast sector were greater than 6.5%, while those from the northwest sector ranged from 1.3 to 1.8% (Duret 1958b). Prior to the use of dieldrin in 1957, DDT had been used as a residual treatment in coastal El Salvador. Except for the two inland towns, the villages lie in a cotton growing region where extensive aerial treatments of chlorinated-hydrocarbon and organophosphorus insecticides have been made.

The third element of interest is the resistance of *A. aquasalis* Curry to dieldrin in Trinidad. Here unpublished studies by Omardeen (1958) have shown the species to be resistant in a DDT-sprayed (10 years) area which had received, in part, its initial treatment with dieldrin at the time these tests were made. These reports on *A. aquasalis* and on *A. albimanus* again suggest that populations normally exist which may have a relatively large proportion of individuals with low susceptibility to dieldrin.

The fourth point is the detection of dieldrin-resistant populations of *A. pseudopunctipennis* Theobald in two areas in Mexico (Morelos, Michoacan) by Palacios Martinez (1958). At Temixco, Morelos, high levels of resistance were apparent, adult females yielded mortalities of 10% or less when exposed for 1 hour to papers impregnated with dieldrin-Risella oil concentration of 0.2 to 1.6%[3]. Houses in this area received their initial application of dieldrin in January-March 1958, after being sprayed with DDT twice in 1957 and periodically between 1945 and that year. To date, resistant populations have appeared only in areas which have rice field breeding sources. In the areas tested where only DDT or only dieldrin has been employed, *A. pseudopunctipennis* remains highly susceptible to both toxicants. Whether the association of DDT treatments followed by dieldrin applications with the occurrence of resistant *A. pseudopunctipennis*, as in Temixco, is a factor in the resistance picture awaits further study. The rapid appearance of dieldrin resistance in *A. pseudopunctipennis* within such a period, after the initial residual application of that toxicant in the area, is unusual

[3] In 1957, mosquitoes from Temixco showed mortality levels of 76, 95, 99, and 100% at dieldrin concentrations of 0.1, 0.2, 0.4, and 0.8%.

Tests to delineate the extent of *A. pseudopunctipennis* resistance in Mexico are now in progress by the National Commission for the Eradication of Malaria in that country.

Aedes aegypti (L.), the vector of yellow fever, has developed resistance to DDT in several parts of South America and in the Caribbean area. Initial detection of such resistance was in mosquitoes from Trinidad. This strain was readily susceptible to dieldrin, BHC, and malathion but required a dosage of 4.0 p. p. m. of DDT for an LD-50 kill of the larvae, even though 0.004 p. p. m. yielded that level of mortality against a laboratory strain (Fay, unpublished). The present distribution of DDT-resistant populations (confirmed) includes Haiti, Venezuela, Trinidad, Colombia and Dominican Republic.

Table 3.—Mortality of adult female *Culex quinquefasciatus* on 2-hour exposure to dieldrin- or DDT-Risella oil-impregnated papers.[a]

	PER CENT MORTALITY AT CONCENTRATIONS (%) OF									
	DIELDRIN						DDT			
STATE[b]	0.2	0.4	0.8	1.6	3.2	4.0	1.0	2.0	4.0	8.0
California	0	14	89	100	—	—	0	20	64	—
Alabama	0	58	36	50	63	83	13	46	85	83
Georgia	—	—	14	24	46	65	—	32	66	—
Florida	—	—	—	—	65	—	—	—	79	—
Illinois	—	—	—	54	—	—	—	—	28	—

[a] Unpublished data (Mathis, W.)
[b] Adults from Mississippi exposed for 1 hour to 4% DDT- and dieldrin-Risella oil papers showed kills of 0 and 9% respectively.

Culex quinquefasciatus Say is a species which has shown resistance to DDT, dieldrin, and BHC in various parts of the world. DDT resistance was confirmed in larval populations of the species in Venezuela, Taiwan, Okinawa, Reunion, and Puerto Rico; BHC- and or dieldrin-resistance, in strains in Malaya, Reunion, Puerto Rico, Okinawa, and India (Brown 1958, Quarterman & Schoof 1958). Adult *C. quinquefasciatus* apparently possess a relatively low natural susceptibility to DDT although they are relatively susceptible to deposits of BHC or dieldrin. Development of DDT-resistance was established in India, where it was shown by Pal et al. (1952) that only 9% kill was obtained with females from a DDT-treated village (6 years) as compared with 90% mortality of specimens from an untreated town. Dieldrin resistance also has been found in adult populations in Malaya and in French West Africa where residual treatments with this insecticide had been applied for several years. The low susceptibility of adult *C. quinquefasciatus* to chlorinated-hydrocarbon deposits is exemplified further by the difficulties encountered in obtaining *C. quinquefasciatus* of high susceptibility to both DDT and dieldrin in the United States. Tests with strains received from various parts of this country (table 3) indicate they are resistant to dieldrin and/or DDT, particularly to the former even though exposure to insecticide was absent or questionable. Only a strain from California showed high susceptibility to either toxicant; complete kills were obtained at the 1.6% dieldrin concentration. Of particular interest are the data for the Illinois strain, since the latter is a laboratory culture maintained since 1940 without exposure to insecticides.

House Flies and Other Diptera.—On the basis of distribution and resistance studies, the house fly, is the most extensively documented public health arthropod. Because of its biotic potential and versatility in breeding habits, this species has been foremost in coping with new chemical measures designed by man. Resistance in *M. domestica* has been more widespread than in other insects, there being few localities in the United States where populations susceptible to chlorinated-hydrocarbon pesticides exist. In *M. d. vicina* Macquart, resistance to this group of compounds also has been established.

The successful introduction and continued effectiveness of organophosphorus compounds in the control of multiresistant house fly populations led to an early but forlorn hope that this species would be unable to cope with this group of toxicants. In Denmark, where parathion and Diazinon® (*O,O*-diethyl *O*-(2-isopropyl-4-methyl-6-pyrimidinyl) phosphorothioate) were employed (Duret 1958b) prior to the use of such toxicants and malathion for fly control in the United States, resistance to Diazinon and Bayer 21 199 (*O*-(3-chloro-4-methylumbelliferone) *O,O*-diethyl phosphorothioate) was demonstrated by Keiding (1956). No reports of loss of susceptibility to malathion appeared in the United States prior to 1956 when *M. domestica* at a dairy barn in Savannah, Georgia, treated with malathion residual applications in 1954 and 1955, developed a physiologic and behavioristic resistance to poison baits (Kilpatrick & Schoof 1958). Two malathion-resistant strains also were detected in Florida the same year (LaBrecque & Wilson 1957). Since then, house fly populations resistant to malathion, Diazinon, and/or other organophosphorus compounds also have been detected in Arizona (Schoof & Kilpatrick 1958), Florida (LaBrecque et al. 1958), and New Jersey (Hansens 1958). Certain of these resistant strains

likewise exhibit lowered susceptibility to parathion and Bayer L13/59 (*O,O*-dimethyl 2,2,2-trichloro-1-hydroxyethylphosphonate). Resistance to organophosphorus compounds also has been shown in *M. domestica* from Italy (Sacca 1957) and Switzerland (Brown 1958).

One of the apparent anomalies among domestic flies has been the absence of resistance in the blow fly groups, *Phormia*, *Phaenicia* and *Calliroga*. Although this state still endures in North America, there are two instances abroad where blow flies have lost their susceptibility to insecticides formerly effective against them. In the Belgian Congo, the blow fly, *Chrysomya putoria* (Wied.), which breeds in human excrement in bored hole latrines, has developed resistance to BHC, Diazinon, and malathion larvicides (Bervoets et al. 1957). Since insecticidal treatment of all latrines in Leopoldville is scheduled on a routine 12-day cycle and the species is wholly an excrement breeder, it essentially was a case of the insect becoming resistant or facing extinction in that area. The second case occurred in Australia where *Phaenicia cuprina dorsalis* (Wied.), a cause of fly strike in sheep (in the U.S.A. a subspecies of the same species (*P. cuprina cuprina*) breeds in garbage), exhibited resistance to dieldrin in certain areas after 3 years of use (Shanahan 1958). After effective prevention of breech strike for periods of 6 to 10 weeks, strike was occurring within 1 to 2 weeks. The LD-50 level of susceptible *P. cuprina* was 0.025 microgram of dieldrin per fly as compared with LD-50's of 1.3 and 2.5 micrograms per fly for two resistant strains.

Two pest species, *Glyptotendipes paripes* Edwards and *Culicoides furens* (Poey), are the last members of Diptera in which resistance has been established. Control of larvae of *Glyptotendipes* in lakes in Florida by BHC or EPN applications was successful initially but poor control eventually occurred. Tests confirmed that the larvae from the treated lake were much more resistant to these toxicants than larvae from untreated lakes. (Lieux & Mulrennan 1956). Smith et al. (in press) recently showed that larvae of *C. furens*, after being readily controlled by dieldrin in Florida, developed resistance to that compound, heptachlor, and lindane.

Lice, Cockroaches and Bed Bugs.—The human body louse, *Pediculus humanus humanus* L., originally was shown to have developed resistance to DDT in Korea in 1951 (Hurlbut et al. 1952). Similar resistance also has been found in Japan, France, and Egypt (Quarterman & Schoof 1958). Recently, a comprehensive global appraisal of louse-resistance was accomplished by the World Health Organization. In this study, louse populations in 27 countries were tested against DDT, BHC, and pyrethrins (Wright & Brown 1957). The results indicated DDT-resistance in only 1 of 27 localities checked in Europe, but resistant strains were detected in Iran, Syria, Turkey, Jordan, China, Hong Kong, Mexico, Peru, Chile, and numerous parts of Africa. In Norway, South Africa, and Japan, strains were collected which showed mortalities of 0 to 12% for dosages of BHC which ordinarily yielded 100% kills of body lice from most of the other survey towns. In Japan particularly, the body lice had low susceptibility to pyrethrum dusts.

Recent studies by the Division of Foreign Quarantine of the Public Health Service (Anon. 1958) at migrant labor reception centers along the U. S.-Mexico border indicate that the body lice on these laborers also are resistant to DDT.

The bed bug *Cimex lectularius* L., another insect usually controlled readily by DDT, has shown the ability in several areas to develop resistance to DDT and in a few instances to BHC. In the United States, resistance was confirmed in specimens from Ohio, but, aside from several unconfirmed reports of control failure, such resistance appears to be limited. Outside of the U. S., DDT resistance has occurred in Hawaii, Italy, Israel, and Iran (Quarterman & Schoof 1958). In Israel, a BHC-resistant strain was found in one locality (Cwilich et al. 1957).

On Taiwan, *Cimex hemipterus* (Fab.) after 3 years of being successfully controlled by DDT, displayed a marked resistance to that toxicant but was readily susceptible to BHC (Chen et al. 1956). The same species was reported slightly resistant to DDT residues in the Hong Kong area (Quarterman & Schoof 1958). Rao & Halgeri (1956) also showed it to be resistant in Bombay State, India. There are unconfirmed reports of BHC and dieldrin resistance in this species in India and in Tanganyika. In Trinidad, British West Indies, *C. hemipterus* is reported to be resistant to DDT but not to dieldrin or BHC (Anon. 1957). Hamon et al. (1957) also recorded dieldrin resistance in *Cimex rotundatus* Sign. (a synonym of *hemipterus*) in French West Africa.

Among the cockroaches, several species (*Periplaneta americana* (L.), *Blattella germanica* (L.), and *Blatta orientalis* L.) have been reported as being resistant to the chlorinated hydrocarbon insecticides, but only for *B. germanica* is there definite proof of such resistance. Specimens from Corpus Christi, Texas, where chlordane had become relatively ineffective as a field treatment, were found to be highly resistant to that toxi-

cant. This strain subsequently was shown to have lowered susceptibility to BHC, dieldrin, and heptachlor (Brown 1958). Since that time populations of chlordane-resistant *B. germanica* have been reported from a number of areas in the southern and eastern United States. Resistance to DDT also has been established for *B. germanica*, but this toxicant never was exceptionally effective against the species, chlordane being the insecticide of choice.

The resistant species previously reported represent those in which the resistance has been confirmed by laboratory and/or field tests. In addition to these species, there are 16 other species and/or genera that have been reported as being resistant from control failures or observation. In some instances, such resistance undoubtedly is factual, but the lack of published confirmatory evidence places them in the "reported" category. Included in this group are seven species of fleas: *Nosophyllus fasciatus* (Bosc), *Nosophyllus londiniensis* (Roth.), *Ctenocephalides felis* (Bouché), *Polygenis* spp., *Pulex irritans* L., *Rhopalopsyllus claviculus*, and *Xenopsylla cheopis* (Roth.), *Anopheles maculipennis*, *A. superpictus* Grassi, *Rhipicephalus sanguineus* (Latr.), *Triatoma infestans* (Klug), *Psychoda alternata* (Say), *Stomoxys calcitrans* (L.), and *Musca nebulo* F. Probably the most frequently reported control failures have been those in which chlorinated-hydrocarbon insecticides were being employed against the common cat flea, *Ctenocephalides felis*. In numerous instances, DDT or chlordane applications failed to provide adequate control of field infestations. Despite the repeated occurrence of such reports, laboratory evidence has not confirmed this resistance.

Before discussing behavioristic resistance, it would be well to mention the resistance to chlorinated-hydrocarbon insecticides exhibited by two livestock pests, the blue tick, *Boophilus decoloratus* (Koch), and the Australian cattle tick, *Boophilus microplus* (Canestrini). The former, after years of successful control in South Africa by arsenical dips, developed resistance to sodium arsenite in 1937–45 (Omer-Cooper & Whitnall 1945). BHC proved effective against these resistant ticks, but within a year and a half control failures were encountered. In 1949, tests of ticks from these localities, and from areas where effective control still was being achieved, confirmed the BHC resistance (Whitnall et al. 1949). DDT resistance in the species occurred subsequently in 1956 (Whitehead 1956).

In Australia, *B. microplus*, which had displayed resistance to arsenicals as early as 1937, later proved readily susceptible to dips containing chlorinated-hydrocarbon toxicants. However, in southern Queensland, BHC failed after 2 years. Eventually, strains resistant to dieldrin, toxaphene, and DDT were detected in different parts of Australia (Hitchcock 1953, Legg et al. 1955, Stone & Meyers 1957). Resistance to BHC, dieldrin, and toxaphene also has been reported for this species in Brazil (Freire 1953).

BEHAVIORISTIC RESISTANCE.—Behavioristic resistance is an avoidance response of insects to pesticidal residues which has been frequently referred to in earlier reports of insect resistance. Much of the controversy on the existence of such resistance arises from the lack of pretreatment data on the normal habits or responses of the mosquitoes involved. Only when insecticide applications proved ineffective were observations made of mosquito behavior. Whether two races of mosquitoes were involved in a given area readily became a moot question. Theoretically, the possibility exists that the elimination of the dominant segment or race of a mosquito population which normally frequent households could readily lead to the remaining segments (outdoor resting mosquitoes) becoming the dominant element. However, the importance or unimportance of such a behavior shift in a vector population upon disease transmission would depend on the relative significance of each segment in spreading the disease.

One of the oftquoted instances of behavioristic resistance concerns *Anopheles gambiae* and *A. melas* Theobald in Africa. However, these species on their first exposure to DDT displayed irritation to the residues so that flight occurred shortly thereafter. Thus, it was not a progressive population change in response; merely a characteristic of the species with reference to DDT. Davidson (1953) showed that *A. gambiae* and *A. funestus* Giles had different responses to DDT, BHC, and dieldrin in regard to the resting time on each type of deposit.

The best evidence for behavioristic resistance in mosquitoes is that offered for *A. albimanus* in Panama. Trapido (1952) found that after 7 years of DDT treatment the number of mosquitoes in treated houses was at a level comparable to that in unsprayed houses of previous years. However, no change had occurred in the effectiveness of the treatment in reducing the number of specimens feeding on man. The mortality of the unengorged mosquitoes collected remained similar to that of unengorged mosquitoes of former years, but the kill of the engorged specimens was approximately 30 percentage points lower. Trapido (1954) later showed that the mosquito populations from the treated areas exhibited no differ-

ences in DDT susceptibility as compared with a laboratory strain. Thus, the data indicated that repeated exposure of successive generations to DDT treatments apparently resulted in populations that were hypersensitive to DDT residues; therefore such specimens had reduced contact (exposure) with the toxicant as compared with adults of earlier populations.

In house flies, a change in response to poison baits has been shown in regard to malathion (Kilpatrick & Schoof 1958). At Savannah, Georgia, after 12 weeks of effective control by use of periodic bait treatments, fly densities showed a steady climb. Despite increased applications and heavier dosages, control was not re-established; flies no longer congregated on the bait. The flies approached the bait but failed to rest or feed upon it. The same bait at other dairies was effective and baits containing other toxicants were attractive to the resistant strain. This difference in response was confirmed by laboratory tests (Fay et al. 1958). A similar behavior change also has been found in a population at a chicken ranch well removed from the dairy barn site.

DISCUSSION.—In any paper considering resistance on a global basis, it would be amiss to fail to give full recognition to the fact that the overall picture is not one of entire pessimism. Too often the mere fact that a species has shown resistance in one locality leads to the abortive conclusion that the particular chemical involved is a lost cause generally. Certain species are relatively limited as to the areas where resistant populations occur. In other instances, such as with the domestic blow flies of this country, there is, as yet, no evidence of a loss in susceptibility to the chlorinated-hydrocarbon insecticides. The disease vectors *Anopheles philippinensis* Ludlow, *A. minimus* Theobald, and *A. fluviatilis* James in India; *A. atroparvus* Van Thiel in Spain and Italy and *C. tarsalis* Coq. in Western U. S. (except California and Oregon) continue to succumb to residues of chlorinated-hydrocarbon insecticides despite the extensive use of such compounds in their control.

Of interest along these lines are data relating to *A. maculipennis* Meigen. Tests in Romania indicate little difference between the response of mosquitoes from villages sprayed for 8 years and of those from unsprayed towns (Brown 1958). In Albania, tests show specimens from two villages sprayed for 11 years with DDT to be highly susceptible to that toxicant (86% to 97% kill after 1-hour exposure to DDT-Risella oil papers, 4%), while adults from a third village with a similar treatment history were less susceptible (66% kill) but still not resistant (Ashta & Adham 1958). To complicate the picture further, adults of *A. maculipennis* from an unsprayed area of Iran showed marked differences in their dosage mortality response in the August versus the October period (Zulueta et al. 1957).

In our control of arthropods of medical and veterinary importance today, we are confronted with a resistance problem of ever increasing magnitude. To cope with this difficult situation, extensive research and investigation on a broad spectrum is an absolute necessity. Knowledge, persistence, and, to be frank, a certain amount of fortuity are the only means by which we can hope to solve the enigma facing us.

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