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The Effect of the Development of Dieldrin Resistance on the Biotic Potential of House Flies in Liberia[1]

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I. Introduction

1. *Description of the problem*

Numerous reports have been made of apparent numerical increases in the populations of such insects as house flies and bedbugs following the use of certain insecticides, especially dieldrin, BHC and chlordane. These reports have usually followed upon the application of one of these persistant chlorinated hydrocarbon insecticides as a residual spray to the interior of houses as part of a malaria eradication campaign (PETERS, 1954; MSANGI, 1960). BROWN (1958) refers to reports of increased house fly production following spraying as having occurred in Liberia, Nepal, Saudi Arabia, Japan, Sicily, Sardinia, Egypt, Kenya and Tanganyika. MIZUTANI & HIRAKOSO (1962) sprayed two organo-phosphorus insecticides as well as dieldrin inside houses in several villages in Southern Japan. They noted that while there was a reduction of the fly population in one village there was an unusual increase after the treatment in the other five.

There have been some areas where the increases caused such annoyance to the inhabitants of the sprayed houses that the continuation of the anti-malaria campaigns have been jeopardized through the householders refusing entry to spray-men (BAGSTER-WILSON, 1959; DE MEILLON, 1959). PETERS (1959) noted during operations in a malaria-eradication pilot project in Liberia that there was an 'explosive increase' in the house fly population in the area previously sprayed with dieldrin although no such increase was observed in the DDT and BHC sprayed areas. In light of the persistant complaints from the field it was deemed important to investigate the reported population increases and to attempt to verify if such increases could actually occur following the development of resistance to dieldrin in a given strain or strains of house flies.

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[1] This paper is part of a Thesis submitted as partial fulfillment for the requirement of a PhD thesis in the Laboratoire de Zoologie générale of the Université de Genève.

2. *Previous studies relating to insecticide resistance and biotic potential*

The literature was reviewed before the field studies were started, to see the results of any previous work of the effect on insecticide exposure on the fecundity and length of life, i.e. the biotic potential of house flies.

The development of insecticide resistance in a strain of a given species of insect may or may not be accompanied by morphological, physiological or behaviouristic changes. The factors associated with DDT-resistance in the house fly have been reviewed by PERRY (1958). In examining the possible effect of resistance on biotic potential of house flies, PIMENTAL et al. (1951) did not find any significant differences in the number of eggs laid by 4 DDT-resistant strains and a susceptible strain, although they did note that there was an increase in the length of the larval period in the resistant strains. VARZANDEH et al. (1954) concluded that the inheritance of characteristics such as egg production, adult longevity, egg hatchibility, etc. were not connected with the development of resistance.

McKENZIE & HOSKINS (1954) investigated the relationship between the length of the larval period of *Musca domestica* and the resistance of the adult flies to several insecticides, among them DDT, dieldrin and lindane, and did not note any increase in the egg production of resistant flies over the susceptible.

METCALF (1955) reviewed the results of a number of investigations into possible relationships between the development of resistance to the chlorinated hydrocarbon insecticides—DDT, dieldrin, benzene hexachloride (BHC) and lindane, and changes in the biology of the resistant insect. He concluded 'that there is little evidence of positive correlation between the factors responsible for biotic potential or vigor and specific insecticide resistance'. The studies reviewed by METCALF were comparisons of the biology of several non-related strains which had developed resistance to various insecticides at different times and places. BROWN (1958) cites a number of cases where the development of insecticide resistance was actually accompanied by a reduction in numbers or dying-out of the resistant laboratory strains possibly due to a lethal gene which was linked to that for resistance. BARBESGAARD & KEIDING (1955) in back-crossing a DDT-resistant strain of house flies found that many adults failed to reproduce and suspected the presence of a lethal or otherwise unfavourable gene linked to that of resistance. BROWN concludes (ibid) 'if resistant strains as a whole are compared with susceptible strains, there is no consistent difference in their bionomics'. Other authors (MARCH, 1952, and MILANI, 1954) have also noted a reduction in the reproductive potential of strains newly resistant to one of several insecticides, the former in a lindane-resistant strain, the latter in a DDT-resistant strain.

In contrast to most of these studies, several other field and laboratory observations indicated that there is a substantial increase in numbers of adult flies and of egg production following the development of dieldrin resistance in at least one species of insect, the house fly, and several of these have already been referred to. KNUTSON (1955) exposed *Drosophila melanogaster* adults to dieldrin at a concentration sufficient to give 66% to 99% mortality. Pairs of survivors were compared with pairs of controls. A 7.6% increase was found in the number of eggs laid by survivors over control flies. This was recorded over the total egg-laying period of the female and was due to the fact that the dieldrin survivors lived longer and thus had more time in which to reproduce, i.e. to lay a greater number of eggs.

The United States Public Health Service, Communicable Disease Laboratories (1956) examined the effect of DDT and dieldrin upon the number of eggs laid by house flies treated with sub-lethal doses of insecticide, water only, and benzene only, all applied topically in a drop on the dorsum of the thorax. The results indicated that treatment of susceptible five-day-old flies with sub-lethal doses of either DDT in benzene or dieldrin in benzene resulted in a significant increase in the number of eggs subsequently laid by these flies. However, with a topical application of water only, DDT- and dieldrin-resistant flies produced more eggs than the control. Flies of a dieldrin-resistant strain produced more eggs following the treatment with dieldrin whereas no increase followed when DDT-resistant flies were treated with DDT.

AFIFI & KNUTSON (1956) examined the number of progeny produced, length of life and weight of house flies which had survived exposure to a concentration of dieldrin causing 60% to 90% mortality. They also compared the F_1 to F_3 progeny of these survivors with control groups. There was no significant difference between the number of progeny produced by the survivors and unexposed controls, but there was a significant increase of 69.2% in the F_1 generation of the treated. The length of life of the treated P flies and the F_1 to F_3 progeny was not significantly greater than that of the controls.

KNAPP & KNUTSON (1958) compared the biotic potential of two separate field populations of susceptible house flies and found considerable variation between them. As a result, they cautioned against drawing a correlation between any given biological variation and degree of insecticide resistance.

The effect of the application of dieldrin on the biotic potential of a field population of house flies was studied by KNUTSON et al. (1958); no increase in biotic potential was found which was concomitant with the increase in dieldrin resistance and the authors again emphasized that there exists a considerable variation in reproductive potential between different fly populations in the field.

HUNTER et al. (1958) applied sub-lethal doses of DDT and the organo-phosphorus diazinon to a DDT-resistant strain of house fly and found that this resulted in a substantially reduced fecundity, fertility and life-span as well as reduced survival among the offspring of the treated females as compared to untreated controls. However, treatment of females of a DDT-susceptible strain with DDT resulted in an 18% increase of potential adult offspring production above the controls but treatment of susceptible females with diazinon in only a 1% increase.

KNUTSON (1959) summarized the recorded data up to that time on the effect of dieldrin on the reproductive potential of house flies and, as above, again emphasized the considerable variation in normal reproductive capacity which occurs from strain to strain and pointed to the difficulty in correlating these variations with any changes in the resistance of a particular strain of house flies to dieldrin.

Of the studies reviewed, some indicated a relationship between the development of resistance to dieldrin, or treatment with dieldrin, and changes in the biotic potential; others failed to show any such relationship. Considering the persistant reports from the field that indicated that some such effect of dieldrin on the biotic potential of *M. domestica* existed and the conflicting results of the previous studies, it was decided to carry out a similar study again but actually in an area of West Africa from where many of the complaints had arisen.

II. The site of the study

In connection with reports of increased house fly populations after dieldrin spraying mentioned above, SCHOOF (1957) surveyed the extent of house fly breeding in several towns and villages in Liberia; he found that, although there were substantial fly populations in many localities, there was no evidence to correlate these heavy populations with areas in which dieldrin had been applied;

the densest populations existed in the areas of poorest sanitation. Nevertheless, he recommended that a survey and study be made to investigate what effect dieldrin might have had on the house fly populations in Liberia as well as to control the flies with insecticides or environmental sanitation. In accordance with this recommendation, a World Health Organization House Fly Investigation and Control Project was established headed by the author.

1. *Description of Liberia*

The Republic of Liberia lies on the West coast of Africa bounded by Sierra Leone on the north-west, Guinea to the north, the Ivory Coast on the south-east and the Atlantic ocean on the south. There are raffia palm groves and areas of mangrove swamps in the flat coastal belt, while further inland are large areas of secondary growth forest succeeded in the interior by the virgin rain forest. There are patches of savannah along the northern border of the country which stretch north into Guinea.

2. *Climate conditions in Liberia*

The climate is of a hot rainy equatorial type, 90% to 95% of the rain falling between May and October. The rains are amongst the heaviest in West Africa and annual total rainfall is often greater than 431.8 cm. Temperatures range from 21.1°C to 26.7°C during the rainy season, and from 21.1°C to 36.7°C in the dry season.

III. Flies and sanitation in Monrovia

A survey was carried out on sources of fly breeding in the capital city of Monrovia following the author's arrival. The fly problem was very serious. Immense numbers of flies of various species were clustered on any organic refuse, and fly breeding both at the refuse dump and at innumerable points throughout the city was tremendous. Breeding was found in collections of refuse in all parts of the city such as in backyards, in gutters and in the frames of abandoned buildings. The presence of such extremely large fly populations was especially interesting in the light of an observation made several years earlier (1948) by the head of the US Public Health Mission in Liberia, Dr. J. West: 'The first house spraying with DDT was done (in Monrovia) in March, 1945 . . . The fly population was considerably reduced by the DDT spraying. Latrines were also sprayed with DDT ... The fly population has practically disappeared in the last two years although the prevalence of the indigenous species of flies was tremendous in 1945.'

IV. Fly surveys

1. *Larval fly survey*

Since the fly conditions found in 1958, ten years after WEST's survey, were again at least as serious although treatment with insecticides (mostly dieldrin), was continuous, an attempt was made to elucidate the reason for this.

Inasmuch as privies or pit latrines have often been reported as a source of house flies, emergence traps were made and set up on eight pit privies in various neighbourhoods of Monrovia. This trap consisted of a circular screen cage 50 cm high, 15 cm in diameter, with a screen cone in the interior, the trap being placed over one of the two wooden seat holes in one of the common two section pit privies. Since one was only interested in the species of flies, sufficient flies (several hundred) were caught in almost each trap to give this information.

In all of the privies in which trappings were carried out, the overwhelming majority of the flies emerging were *Chrysomyia putoria,* the normal pit privy breeding fly in West and East Africa. A few specimens of *Hermetia illucens* were taken from two privies and only *Culex fatigans* from one privy, whose contents were entirely below the water table. Privies were, therefore, eliminated as a possible cause and source of increased housefly production.

The most common fly breeding in the refuse throughout the city and at the tipping site was *Musca domestica vicina;* following this species in relative density was *C. putoria,* especially in refuse containing dead animals, meat or fish wastes; occasional larvae of *H. illucens* were also found as were a few *Sarcophagidae;* if the refuse contained fruit or vegetables, large numbers of *Drosophila* spp. larvae were found. No other species of flies were found with any degree of frequency.

Most of the *Musca sorbens* breeding was found in sites commonly used for random defaecation such as along fallen logs, alongside of walls, etc.

2. *Adult fly survey*

Although the larval survey had shown that there was a plentitude of breeding sites, an adult fly survey was made in the city to ascertain, (1) if there were substantial numbers of any species of adult fly present whose breeding site had not been found, (2) if the proportion of different species of adult flies found was in accordance with those whose breeding sources had been found, (3) if the numbers of adults noted were unusually large in relation to breeding sources already discovered—which would indicate further undiscovered sources of breeding.

3. *Methods of adult fly survey*

Surveys were carried out by net catches and visual observation of adult flies over different types of attractants, e.g. at the tipping site, refuse collections on the streets, at the municipal market, near butchers' shops, etc. These collections covered most parts of the city.

4. *Results of adult fly survey*

Most of the adult collections consisted of *M. domestica vicina* and *C. putoria*, other species being found only as occasional individuals—aside from sporadic numbers of *Drosophila* spp. when collections were made on refuse containing fruit and vegetable wastes. It was, therefore, not felt that any specialized larval habitat with breeding of any additional species of flies not already found in the larval survey remained undiscovered. In addition, the enormous numbers of adult flies seen before control measures were introduced were in proportion to the widespread fly breeding found throughout the city.

V. Rural fly survey

1. *The domestic fly problem in rural areas*

Prior to the collection of flies for resistance tests and biotic potential studies, surveys were also carried out in a number of villages and towns in the interior of the country; the location of these places is described in detail in Section VI. 3 'Results of resistance tests'. Generally, fly breeding was far more limited in rural areas than in Monrovia; in the smallest villages of twenty to thirty huts there were very few collections of refuse or organic matter to support breeding of domestic flies; the only species of *Musca* to be found in such villages was *M. sorbens* whose breeding site was individual human and animal faecal deposits. In the small, primitive villages, random defaecation is the usual human habit, usually close to the outermost huts of the village alongside fallen trees. In the wet climate of the rain forest, such deposits remain moist long enough for a generation of *M. sorbens* to develop. It may be mentioned, parenthetically, that such habits also account for the extremely high incidence of human parasitic worm infestations which reach 100% incidence in the rural areas. As soon as a village has developed to the extent that pit privies or latrines are dug and used, *Chrysomyia putoria* breeding will be found in all of these privies and large numbers of adult *C. putoria* can be found clustered on exposed foodstuffs during the day. *M. domestica vicina* usually does not occur in substantial numbers in the villages until they have grown large enough to support shops and produce collections of domestic refuse, which are usually cast by the inhabitants into heaps at several points around the village or town depending on its size. In small villages, such as Dieke or Koindu, or in those very distant from any road, few domestic flies could be found and Scudder grill counts would rarely be above ten to twenty flies—mostly *M. sorbens* and *C. putoria.* In large market towns through which a main road passes, such as Kpain, grill counts would rise to two hundred flies of which the majority would be *M. domestica vicina* and *C. putoria.*

2. *Adult fly habits in rural areas*

During the day adult flies in the large villages or towns could be found clustered upon any available foodstuffs, *C. putoria* especially being found on meat or fish exhibited for sale on tables in roadside shops, while *M. domestica vicina* would be found feeding on cassava peelings, sugar cane wastes and similar vegetable food or refuse.

A search was made by flashlight to determine the night time resting places, particularly of *M. domestica vicina;* while a few would be found resting on vegetation around refuse deposits, extremely large numbers were found resting within the houses or huts, usually on the ceiling. House flies were found resting inside of both insecticide sprayed and unsprayed premises and the former were later found to be insecticide-resistant populations. This observation, of the favoured night time indoor resting place of the adult house fly, was important in that it explained the contact between the flies and the insecticide applied to the dwellings as a residual spray against *Anopheles* mosquitos, and would account for the very rapid selection for insecticide resistance which occurred. It was also noted that in those villages where dieldrin had already been applied some time previously and where the house fly populations had developed resistance to dieldrin, lizards and other predators on adult house flies, such as spiders, were still very common. Nowhere prior to spraying did they appear to be present in substantial enough numbers to seriously affect the overall house fly population. More important, refuse heaps and other sources of house fly were *not* sprayed with dieldrin and, therefore, any predators, e.g. ants, on the house fly larvae in these sites, would have remained in the same numbers before and after the spraying of the towns and villages.

VI. Housefly insecticide resistance tests

1. *Reasons for resistance tests*

The city of Monrovia had been sprayed with DDT as a residual insecticide from 1945 to 1950 as part of an anti-malaria campaign. In 1950 the campaign switched to the use of dieldrin until early 1959; at that time the development of dieldrin resistance in the local primary malaria vector—*Anopheles gambiae*—forced a reversion to DDT. In rural areas the picture of insecticide usage was even more confusing—DDT, dieldrin and benzene hexachloride (BHC)—all had been used as residual sprays at one time or another in the malaria control programme. It was thus necessary to carry out resistance tests over a wide area of the country in order to determine the levels of insecticide resistance in the house fly populations—particularly to dieldrin—and in an attempt to ascertain if there was any correlation between the degree of resistance to dieldrin and an increase or decrease in the house fly populations. These tests were done in order to locate and obtain susceptible populations on which it would be possible to carry out laboratory selection for dieldrin resistance.

2. *Methods of testing for resistance to insecticides*

The insecticide resistance tests were carried out by exposing the adult flies to insecticide deposits on the inner walls of shell vials with an outside diameter of 21 mm, a length of 71 mm and a narrowed neck of 16 mm diameter. A 1% stock solution of the desired insecticide was prepared by adding 0.1 ml of a solution of 95% naphthenic base oil and 5% Triton X-155 to 10 ml of acetone. 10 ml of this mixture was then added to 40 ml of acetone containing 500 mg of the pure insecticide for a total of 50 ml. Lower concentrations were prepared by serial dilution. 0.5 ml of the desired concentration was pipetted into the vial and the acetone evaporated by rotating the vial on a glass plate fixed 1 cm over a 100 w light bulb. Practice leaves an even film of crystals of the insecticide over the inside of the vial.

Aside from laboratory strains, flies for resistance tests were obtained either from those emerging from field-collected pupae or, when it was difficult to find sufficient pupae, from net-collected adults in the field. Females emerging from pupae in the laboratory were tested three days after emergence. Adult flies collected in the field were held in the laboratory for 24 hours in cages with sugar water prior to being tested.

20 females were placed into each vial and exposed for 30 minutes to dieldrin and for 15 to DDT. The end of the vials was covered by a square of lens tissue held in place by a small rubber band; every two minutes the tubes were tapped on the table to dislodge flies which might have settled on the tissue and the tubes given a half-turn. At the end of the exposure period the flies were transferred to net-covered paper cups, given sugar water and held to determine the final percentage mortality of the number of flies exposed at each concentration; this was recorded 72 hours after exposure to dieldrin and 48 hours after exposure to DDT.

After the percentage mortality resulting from exposure to each concentration of insecticide was recorded, it was then plotted on logarithmic probability paper. The percent mortality at each dosage concentration of the insecticide was indicated as a point on the graph and a straight line was fitted as closely as possible by eye from the highest through to the lowest mortalities. The 'LC_{50}' was determined by noting the point at which the line drawn through the percent mortalities at the ascending concentrations intersected the 50% mortality level. With few exceptions, a minimum of five concentrations were used for each test.

3. *Results of insecticide resistance tests*

Monrovia: Many collections of house fly pupae were made from all parts of the city and females emerging from these tested for resistance; no group showed a higher than 5% mortality at even a 2% concentration of dieldrin and were, therefore, highly resistant to this insecticide.

River Cess: A small, isolated coastal town with a population of some 3,000, which at the time of the first tests had not been sprayed by any insecticide. When exposed to the two lowest concentrations used for testing in the field, house fly mortalities following dieldrin exposure were: 0.0001% = 74% mortality, 0.0005% = 100% mortality. The flies were, therefore, highly susceptible. Most of the adult flies collected were *M. domestica vicina* with smaller numbers of *C. putoria* and *M. sorbens.* Following these tests, the town was sprayed with dieldrin and later visits made to determine if there was any effect on population numbers; by seven weeks after spraying the *M. domestica* population which had dropped abruptly after the spraying had returned to at least its previous level; inasmuch as no year round check could be made (the town being reached by aeroplane only), the increase could be a seasonal one or related to other temporary factors not connected with the spraying. Dieldrin resistance tests at this time showed there had been a rapid and manifold selection for resistance—0.05% = 5% mortality, 0.1% = 10% mortality.

Voinjama: A large town near the north-west border. It had not been sprayed up to the time of the collection and susceptibility tests; the LC_{50} ranged from 0.0008% to 0.0035% for different groups tested showing the population to be susceptible.

Kpain: A town near the northern border with Guinea; it had been sprayed at one time or another with DDT, BHC and dieldrin. *M. domestica vicina, M. sorbens,* and *C. putoria* were all common, the sanitation level being very low in the town. 78-hour mortality following one half hour exposure to 1% dieldrin was only 35%, the populations, therefore, being fairly resistant to dieldrin.

Kailahun, Sierra Leone: A large market town 20 miles from the border of Liberia; no insecticide had been sprayed in the town prior to the time of the visit. The fly population was not heavy. The LC_{50} for dieldrin was 0.002% established from a colony started with wild caught females.

Koindu, Sierra Leone: A small market town 5 miles from the Liberian border. At the time of the collection, the town had not been sprayed with any insecticide and the house flies were extremely susceptible to dieldrin, the LC_{50} being 0.00009%.

In all of the above towns the house fly population varied according to the degree of sanitation; the heaviest fly population was found in Kpain where the resistance to dieldrin was also the highest of all the rural areas and the number of breeding places, i.e. domestic refuse, also appeared to be greatest.

VII. Biotic potential studies

1. *Method of carrying out the studies*

Previous studies, already described, have shown that the average length of female life and the average number of eggs laid, i.e. the biotic potential, are likely to vary substantially between one population in the field and another; because of the likelihood of such variations no direct comparisons of biotic potential were made between dieldrin susceptible populations and populations from localities where dieldrin resistance had already developed. Instead, susceptible strains were collected in the field, one portion of the strain selected for dieldrin resistance and the other left unselected—susceptible; the biotic potential of the two strains of the same population, one normally susceptible to dieldrin and the other newly resistant, were then compared. In order to do this, large numbers of adult flies were collected from places which the resistance survey had shown to possess populations susceptible to dieldrin. The flies were then brought back to the laboratory and the females allowed to oviposit on dishes of cotton soaked in milk. The larvae emerging from the eggs were grown to maturity on a breeding medium developed in the absence of such usual constituants as alfalfa meal and bran. The mixture consisted of 1 kg of peeled, grated, cassava *(Manihot palmata),* 200 grams of full fat milk powder and 2 grams of powdered yeast plus water added to the point of dripping. 50 ml of liquid milk were mixed into the medium every morning. Each bowl of breeding medium was covered by a cloth to prevent contamination by flies of any other strains; the larvae would pupate between 4 and 5 days later on or near the surface of the mixture. Part of the emerging F_1 females were used for dieldrin susceptibility tests; part were allowed to mate and oviposit normally and the adults eventually emerging were designated the F_2 'unselected' substrain. Two groups of 50 females and 75 males were separated from the remaining flies and each placed into a cage the second day after emergence from the pupa and before any oviposition took place. Each morning a fresh petri dish containing a pad of cotton soaked in milk and wrapped in black bolting silk was placed into the cages. The flies were able to feed on milk through the pores of the bolting silk but the holes were too small for eggs laid on the surface to be passed through onto the cotton. Each morning the petri dish from the previous day was removed and the eggs which had been laid counted through a stereoscopic dissecting microscope, the dead flies in the cage were recorded by sex and a fresh petri dish

TABLE 1

	River Cess		Voinjama "I"		Voinjama "II"		Voinjama "III" (Monrovia strain)		Voinjama "III" (LITM replicate)		Koindu	
Generation	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days
F_1	*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*	
	—		20,916	610	23,666	793	18,419	872	23,821	960	17,097	713
					24,845	762	19,046	590	25,476	820	17,993	827
					24,255	777	18,732	731	24,648	890	11,244	818
											15,444	786
			LC_{50} = 0.0022%		LC_{50} = 0.015%		LC_{50} = 0.005%				LC_{50} = 0.00015%	
F_2	*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*	
	12,066	768	15,347	437	19,513	641	12,394	372	21,437	684	25,847	868
	11,798	562			16,263	573	11,259	322	7,582	391	19,687	853
	9,182	524			17,888	602	11,826	347	14,509	537	14,710	580
	11,015	618									20,079	767
	LC_{50} = 0.0008%		LC_{50} = 0.001%		LC_{50} = 0.015%		LC_{50} = 0.007%				LC_{50} = less than 0.0001%	
	Selected		*Selected*		*Selected*		*Selected*		*Selected*		*Selected*	
	—		26,490	649	23,967	652	30,394	590	23,345	771	18,816	796
			30,911	764	24,338	552	29,307	742	17,102	504	28,278	894
			28,700	711	24,152	602	29,850	666	20,223	637	24,718	733
											23,937	807
			10% mortality at 1% dieldrin		20% mortality at 1% dieldrin		50% mortality at 1% dieldrin				LC_{50} = 0.03%	

TABLE 1 a

	River Cess		Voinjama "I"		Voinjama "II"		Voinjama "III" (Monrovia strain)		Voinjama "III" (LITM replicate)		Koindu	
Gener-ation	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days	No. of eggs	Female fly days
F_3	*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*	
	9,597	394	23,700	621	18,530	679	10,905	494	16,747	684	10,008	592
	LC_{50} = 0.001%		LC_{50} = 0.009%		LC_{50} = 0.02%		12,098	440	26,850	748	10,260	514
							11,051	467	21,798	716	10,134	553
							LC_{50} = 0.007%				LC_{50} = less than 0.0001%	
					Selected		*Selected*		*Selected*		*Selected*	
					11,522	474	25,762	718	24,609	713	21,020	896
					14,055	473	20,747	570	26,943	831	23,286	824
					12,738	473	23,254	644	25,776	772	22,153	860
							50% mortality at 1% dieldrin				LC_{50} = 0.015%	
F_4	*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*		*Unselected*	
	13,556	648	34,104	779	6,411	484	23,345	706	12,106	643	20,200	780
	12,653	561			10,450	439	16,535	579	14,692	607	20,889	849
	13,104	604			8,430	461	19,940	642	13,399	625	20,544	814
	LC_{50} = 0.05%		40% mortality at 1% dieldrin								LC_{50} = 0.00015%	
					Selected		*Selected*		*Selected*		*Selected*	
					8,353	324	23,916	696	17,737	697	21,342	1037
					8,658	342	22,985	682	14,403	642	12,784	853
					8,505	333	23,450	689	16,070	669	17,063	945
							5% mortality at 1% dieldrin				LC_{50} = 0.01%	

TABLE 1 b

Generation	River Cess: No. of eggs	River Cess: Female fly days	Voinjama "I": No. of eggs	Voinjama "I": Female fly days	Voinjama "II": No. of eggs	Voinjama "II": Female fly days	Voinjama "III" (Monrovia strain): No. of eggs	Voinjama "III" (Monrovia strain): Female fly days	Voinjama "III" (LITM replicate): No. of eggs	Voinjama "III" (LITM replicate): Female fly days	Koindu: No. of eggs	Koindu: Female fly days
F_5	*Unselected*		*Unselected*				*Unselected*		Uncompleted		*Unselected*	
	12,500	547	30,731	706			12,013	569			13,282	806
	LC_{50} = 0.8%		LC_{50} = 0.55%				18,568	681				
			Selected				15,290	625			*Selected*	
			44,994	930			*Selected*				18,263	847
			32,669	702			19,554	568			18,527	942
			38,831	816			16,524	1098			18,395	894
			5% mortality at 1% dieldrin				18,039	833				
F_6	*Unselected*										*Unselected*	
	10,358	562									23,830	963
	30% mortality at 0.5% dieldrin										17,442	914
											22,713	1019
											21,148	965
											LC_{50} = 0.0001%	
											Selected "I"	
											20,482	926
											20,595	753
											20,538	839
											LC_{50} = 0.00035%	
											Selected "II"	
											19,718	732
											25,117	917
											22,417	824
											LC_{50} = 0.0035%	
											Selected "III"	
											29,705	906
											LC_{50} = 0.009%	

TABLE 1 c

Generation	River Cess No. of eggs	River Cess Female fly days	Koindu No. of eggs	Koindu Female fly days
F_7	*Selected*		*Unselected*	
	24,164	648	16,163	764
	15% mortality at 1% dieldrin		14,301	712
			15,232	738
			LC_{50} = 0.0001%	
			Selected "I"	
			19,095	813
			19,590	862
			19,342	837
			LC_{50} = 0.0001%	
			Selected "II"	
			22,122	803
			19,393	897
			20,757	850
			LC_{50} = 0.002%	
			Selected "III"	
			18,229	716
			13,033	979
			15,631	845
			LC_{50} = 0.006%	
F_8	*Unselected*			
	23,443	632		
	24% mortality at 1% dieldrin			
	Selected			
	27,067	767		
	24,750	666		
	25,908	716		
	0% mortality at 1% dieldrin			

placed into each cage. Finally, the total number of eggs laid between the 3rd and 30th day of life (after which very few, if any, eggs were laid) were added to give the total number of eggs laid by each group of the F_1 'unselected'; the total number of female flies remaining alive on each day was also totalled as the total number of 'female fly days' of life. Finally, all the remaining F_1 flies were separated by sex on the first day after emergence from the pupae and on the following day each sex was separately exposed to concentrations of dieldrin in glass vials sufficiently high to give a substantial but not complete mortality. The surviving flies were then allowed to mate and oviposit and the adult progeny eventually developing from these eggs was designated the F_2 'selected' substrain. At the F_2 generation two groupes of 50 females and 75 males were separated from each of the F_2 substrains, the 'selected' and the 'unselected', and the daily number of eggs laid and the length of female life determined as for the F_1. Susceptibility tests were carried out on part of the remaining flies and the stock then allowed to breed the F_3 and F_4 of the respective substrains. The same determinations were again carried out on these succeeding generations.

2. *Strains on which bio-metric studies were carried out*

Five susceptible strains were collected from the field and studied in the manner described above; four of the susceptible strains were collected in Liberia and the fifth from Koindu, Sierra Leone.

a) *River Cess strain*

As there was no road connection between Monrovia and this coastal town, several hundred house flies were collected in the field and brought back by passenger-cargo plane to Monrovia, the site of the author's laboratory. It was later discovered that the same aircraft had been used to transport drums of dieldrin into isolated towns in the interior of the country for the antimalaria campaign. Apparently as a result of this the strain was 'contaminated' by dieldrin *en route,* which caused a rapid, unintentional selection for resistance. Despite this a further dieldrin selection was carried out on F_6 and the results are discussed below.

Results of selection on egg production of River Cess strain

As was previously described, dieldrin contamination gave rise to an unintentional selection for resistance in this strain; as may be seen from the figures in Table 1, there was a gradual increase

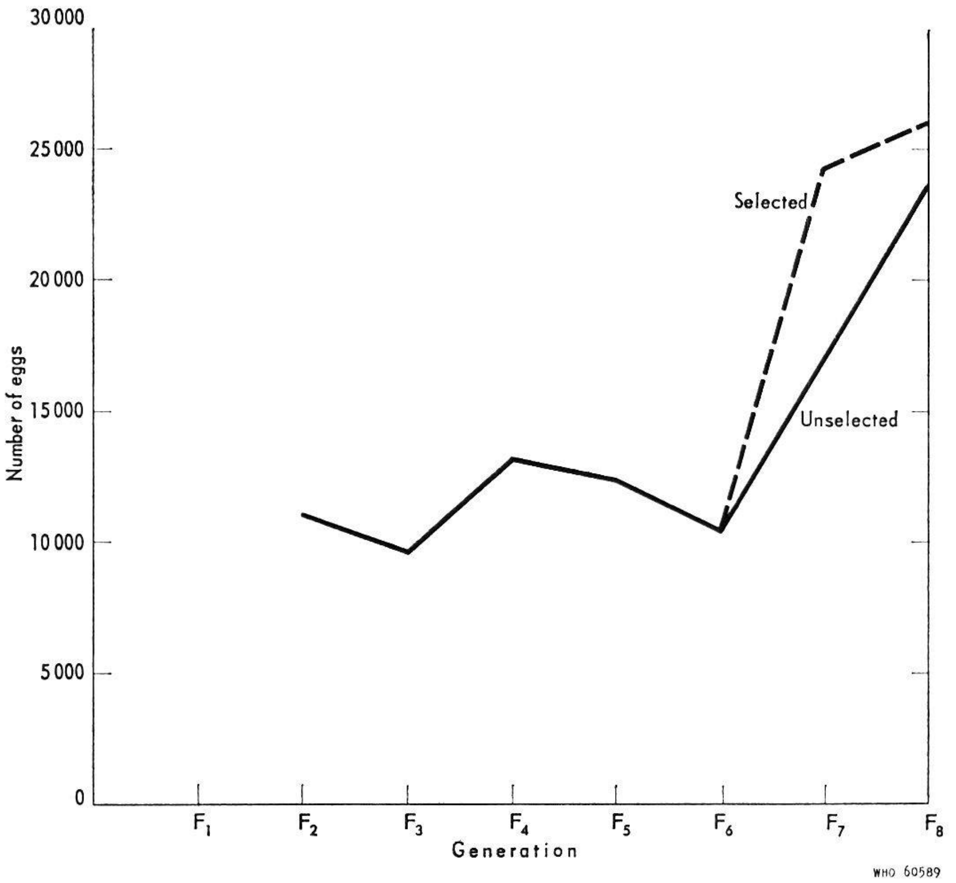

Fig. 1

in dieldrin resistance in the strain between the F_2 laboratory generation and the F_6; a selection for a still higher level of resistance was carried out on the F_6 and then on the F_7; while there was an increase in the number of eggs laid by the progeny of the survivors of this selection, as shown by the numbers of eggs for groups of 50 females in Table 1, the dieldrin resistance of the 'unselected' strains was by this time almost as great as that of the 'selected' and the number of eggs laid by the F_7 'selected' was statistically the same as that laid by the F_8 'unselected' and F_8 'selected'. In examining the results when expressed graphically, Fig. 1, the number of eggs per generation is seen to have increased along with the resistance to dieldrin.

b) *Voinjama strain*

The LC_{50} for dieldrin of the wild caught females used to establish the Voinjama 'I' strain was 0.0008%. F_1 virgin males and females were selected for dieldrin resistance by 30 minutes exposure to 0.05% dieldrin, and the survivors allowed to mate and lay eggs for the development of the F_2 selected i.e. resistant substrain. The LC_{50} of the F_2 unselected substrain was 0.001% as compared to only a 10% mortality in the F_2 selected substrain following 30 minutes exposure in tubes of 1% dieldrin concentration. This was replicated four months later by the collection of another strain from the same town, Voinjama 'II', which was selected as previously. Later a third replicate was made from a new collection in Voinjama, Voinjama 'III'; the wild caught parent flies were divided into two groups, one part being brought to the laboratory in Monrovia and the second to a laboratory at the Liberian Institute of Tropical Medicine, 30 miles from Monrovia, situated in an area never sprayed by any insecticide. Selection of the F_1 adults was done at a higher concentration of dieldrin than in the previous replicates, by exposing large numbers of females for 30 minutes to 1% dieldrin and the more susceptible males for 15 minutes to 0.1% dieldrin.

Results of selection on egg production of Voinjama strains

The various replicates examined have been described above; following selection by dieldrin on the Voinjama 'I' strain, the F_2 selected generation, i.e. the first generation progeny of survivors of selection, laid almost twice the number of eggs as the F_2 unselected, and significantly more than the F_1 unselected. The numbers are shown in the Table and graphically in Fig. 2. A further selection on the F_4 resulted in a significant increase in the progeny of the selected flies, i.e. the F_5 selected over both the F_5 unselected and F_4 unselected. The rise in the number of eggs in the unselected was again accompanied by a continual rise in the resistance of the unselected. The cause of this increased resistance was not determined although it may have been the use of cages used to bring the River Cess strain back from that town.

The next replicate, the Voinjama 'II', apparently was incompletely selected for dieldrin resistance as there was still a 20% mortality among the F_2 'selected' strain. There was no increase in the number of eggs laid by the F_2 'selected' as compared with the F_1 unselected but a small increase in the number of eggs as compared to the F_2 unselected. The figures for the number of eggs are shown in the Table and are presented graphically in Fig. 3.

Both the Voinjama 'III' substrain in Monrovia and that replicated at the Liberian Institute of Tropical Medicine were selected by higher levels of dieldrin and, as may be seen in the Table and Fig. 4, this gave rise to a much higher level of resistance in the F_2 selected; in the Monrovia substrain, at the same time, there was a much greater increase in the number of eggs laid by the F_2 selected over the F_2 unselected and F_1 unselected as well. In the LITM substrain there was a significantly greater number of eggs

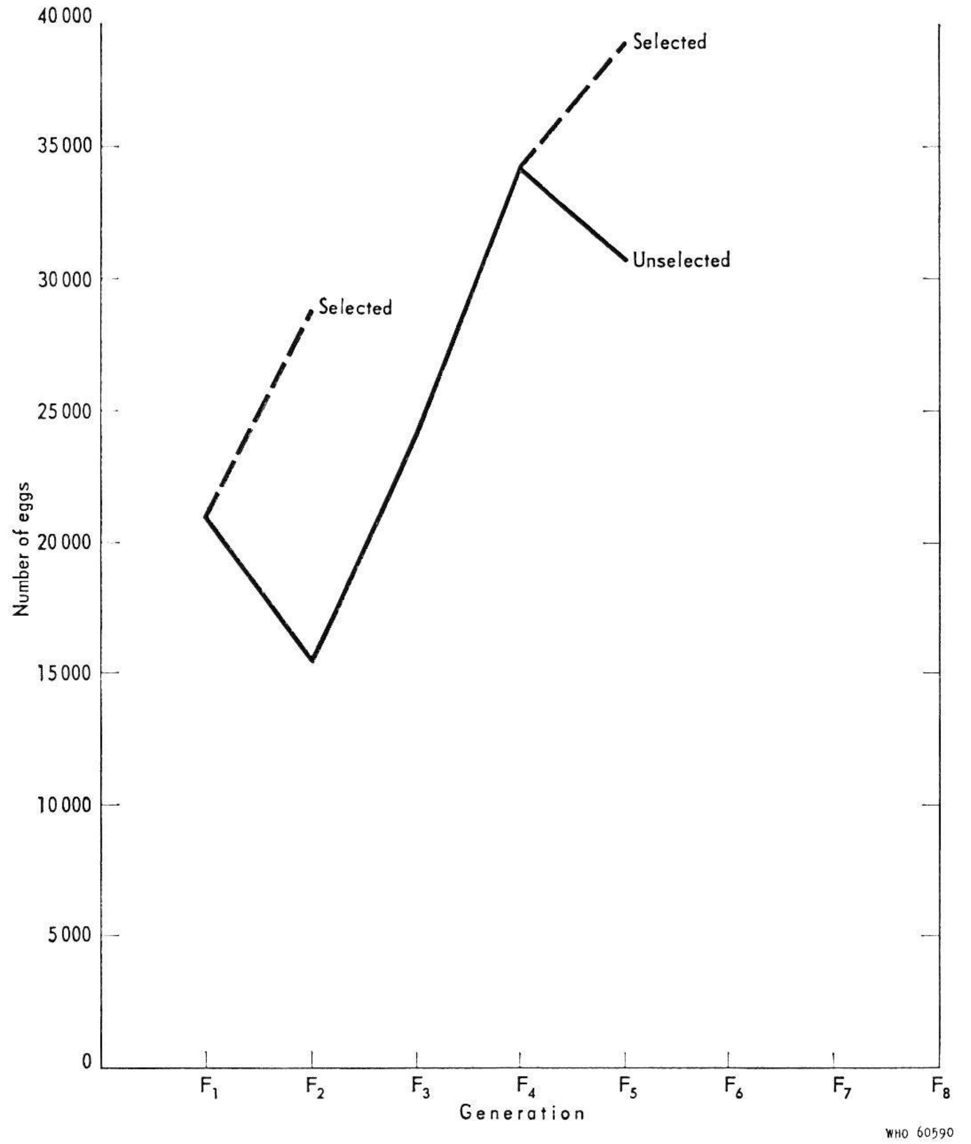

Fig. 2

laid by the F_2 selected than by the F_2 unselected but not significantly more than the F_1 unselected. By the F_5 in Monrovia and F_4 in LITM, the number of eggs laid by the selected groups was still greater than the unselected though the differences were smaller.

c) *Koindu strain*

A portion of the F_1 flies of this very susceptible strain was selected by exposing the females to 0.001% dieldrin for 30 minutes, which produced a 62% mortality and the males to 0.0001% dieldrin giving a 60% mortality and survivors being combined for mating, as usual, to give the F_2 selected substrain. The LC_{50} of the F_2 selected substrain increased to 0.03% while that of the F_2 unselected remained the same as the F_1 unselected, i.e. 0.0001%. A later re-selection was made on flies of the F_5 generation of the

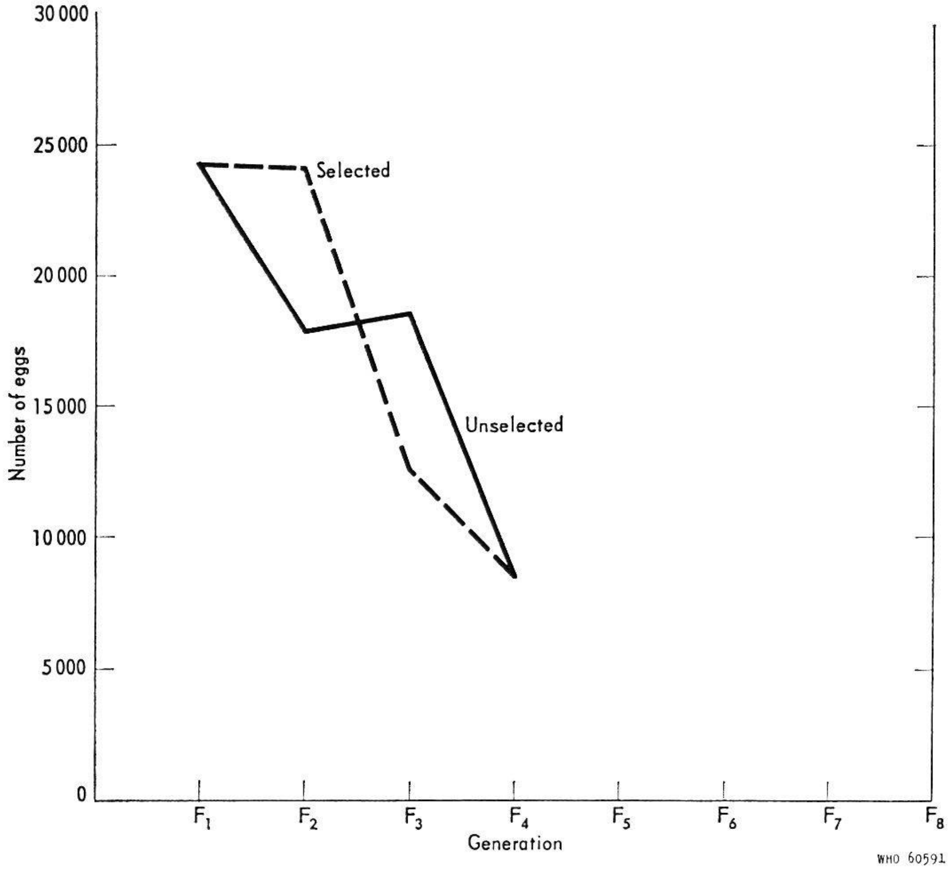
30 000
25 000
20 000
15 000
10 000
5 000
0
Number of eggs
Selected
Unselected
F1
F2
F3
F4
F5
F6
F7
F8
Generation
WHO 60591

Fig. 3

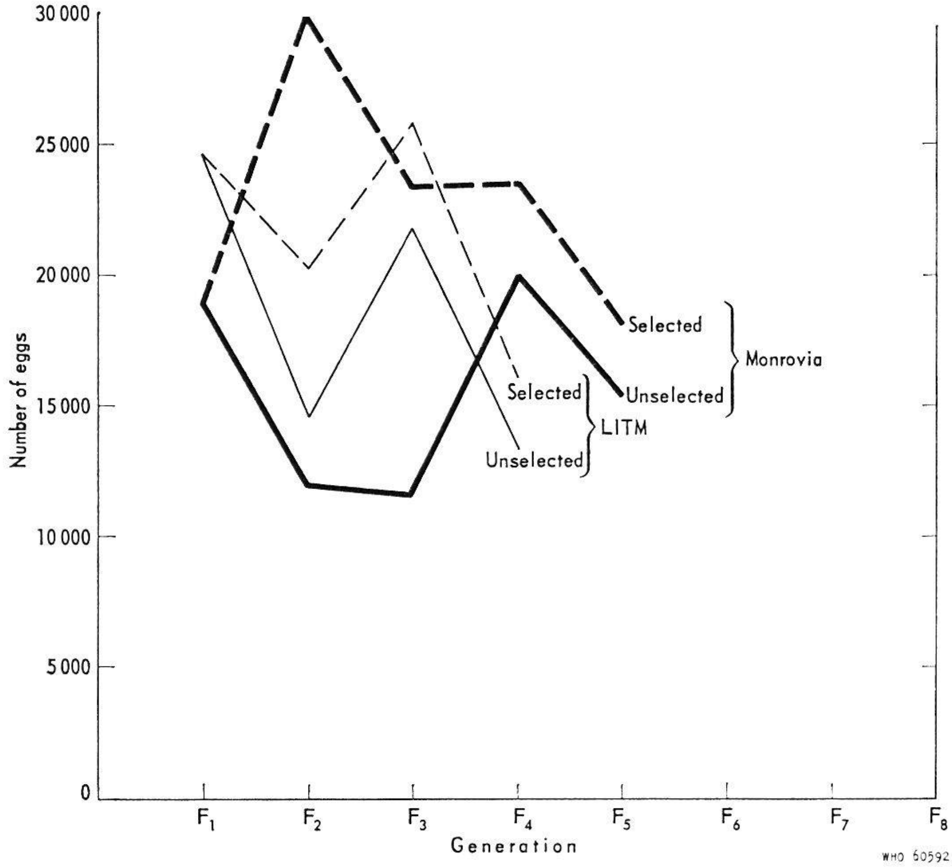
30 000
25 000
20 000
15 000
10 000
5 000
0
Number of eggs
Selected
Unselected
Monrovia
Selected
Unselected
LITM
F1
F2
F3
F4
F5
F6
F7
F8
Generation
WHO 60592

Fig. 4

Koindu strain; flies from the F_5 unselected substrain were selected by exposing the females to 0.005% dieldrin for 30 minutes and the males to 0.0005% dieldrin for 20 minutes producing a 69.3% and 61.6% mortality respectively; the progeny of the mated survivors of this exposure were termed the 'Selected II' substrain. Flies of the F_5 selected generation, i.e. the fourth generation progeny of F_1 survivors of exposures to lower dosages of dieldrin, were now exposed to higher selective dosages of the insecticide, the females to 1% dieldrin for 30 minutes and the males to 0.05% for 20 minutes, giving a 76.6% and 75.5% mortality, respectively.

The progeny of the mated survivors of this high level selection were termed the 'Selected III' substrain.

Results of selection on egg production of Koindu selected strain

Due to the degree of susceptibility of this strain to dieldrin, selection on the F_1 as noted above, had to be made with a much lower percentage of dieldrin lest practically all the exposed flies were killed. Despite this, as can be seen in the Table and Fig. 4, the number of eggs laid by the F_2 selected significantly exceeded both those laid by the F_2 unselected and the F_1 unselected. Two generations later, i.e. in the F_4, this difference disappeared. Unselected and selected flies of the F_5 were exposed to varying concentrations of dieldrin as described above.

Three groups of Koindu F_6 unselected, two groups of F_6 'Selected I' (the 5th generation progeny of F_1 survivors), two groups of F_6 'Selected II' and one group of F_6 'Selected III' were examined; the results of the biometric studies are presented in the Table. There was a 40.4% increase in the number of eggs laid by the F_6 'Selected III' over the F_6 unselected and a 61.4% increase over the F_5 probability level although there was also a 59.2% increase in the number of eggs laid by the F_6 susceptible over the single group of F_5 unselected. The increased number of eggs laid by the F_6 'Selected II' over the F_5 unselected and the F_6 unselected and 'Selected I' was not significant. These results are expressed graphically in Fig. 5.

d) *Lagos strain*

Following the completion of the above work, an additional experiment was performed in which a highly resistant 5th generation laboratory strain of flies in Lagos, Nigeria, was exposed in vials to a concentration of 2% dieldrin for 30 minutes. Mortality was low, only 4% to 5% in all batches of flies exposed. While there was an increase in the number of eggs laid by the progeny of the

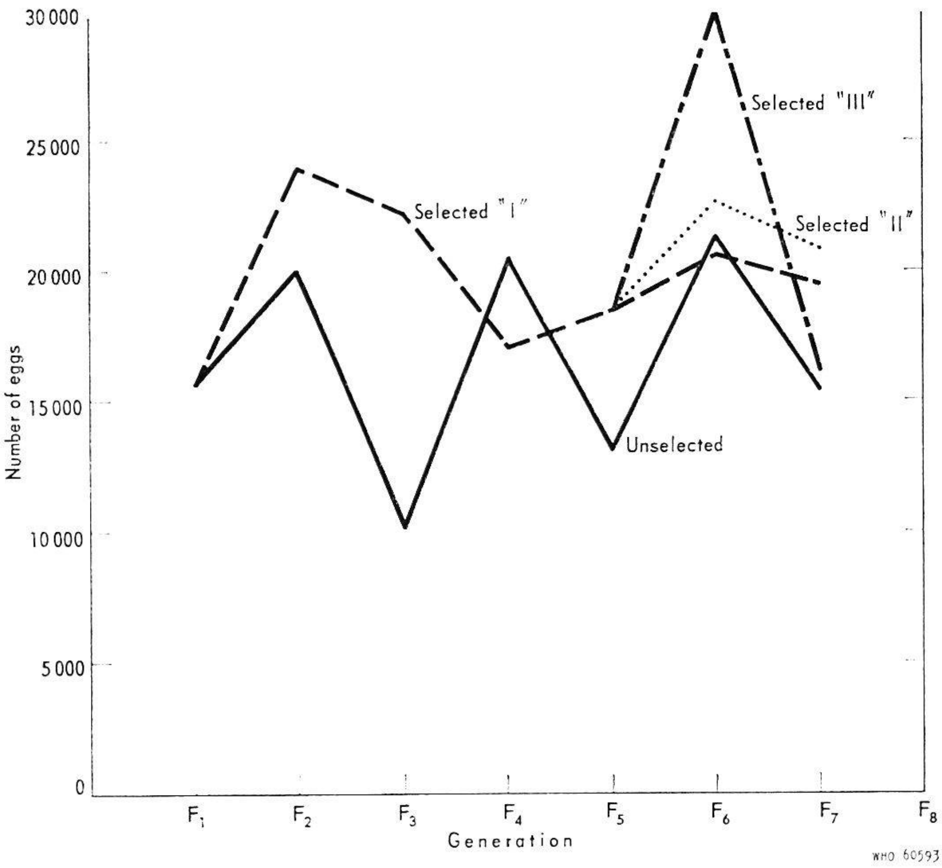

Fig. 5

survivors of the dieldrin exposure as compared to the same generation of unexposed flies, it did not appear to be significant. Inasmuch as the geographical origin of the strain is far distant to that of the Liberian strains, nothing conclusive can be said of this latter comparison, other than that the re-exposure of a single group of a single strain of already dieldrin-resistant *M. domestica vicina* did not cause an unusual increase in the fecundity of either the survivors or their progeny.

VIII. Discussions of results of biometric tests

Of the five strains presented in the Table and Figs. 1 to 5, selection for dieldrin resistance resulted in an increase in the number of eggs laid by the selected F_2 over both the unselected F_2 and unselected F_1 in three instances: Voinjama I, Voinjama III (Monrovia replicate) and Koindu; in two instances there was an increase of selected F_2 over unselected F_2 but not over unselected F_1 and in both instances where a higher level of dieldrin selection was done on a later generation—Voinjama 'I', F_5 and Koindu III,

F_6, there was an increase in the number of eggs laid by the progeny of the selected flies over both the unselected flies of the preceding generation and the unselected flies of the same generation.

In only two cases was an increase in number of female fly days of the F_2 selected over both the F_1 and F_2 unselected, in Voinjama I and Koindu.

IX. Statistical analysis [2]

An extensive statistical analysis was carried out on the data resulting from the biometric tests. This was done in order to determine the significance of the increases in both the number of eggs laid, and the length of life, after selection of the various strains for dieldrin resistance. The tests specifically analyzed the number of eggs laid by groups of 50 female flies and the number of 'fly days' lived by them.

Prior to proceeding further with the statistical analysis, the bio-metric results of all the strains tested were examined in order to determine whether or not there were any significant differences at all between the different groups tested and within the groups resulting from selections. Obviously, should the results of these tests be negative, there would be no further need to proceed with a detailed analysis. A technique of analysis of variance was applied to each of the types of biotic measurements, separately for each strain, each group consisting of either selected or unselected flies of one generation. In statistical terms this was to compare the variance 'between the groups' with the variance observed 'between repetitions within each group'. The following mathematical model was applied:

$$x_{ij} = m + a_i + e_{ij}$$

where x_{ij} denotes the measurement (number of eggs or female fly days) taken to the 'j-th' observation of the 'i-th' generation and/or selection group, 'm' denotes the grand mean, 'a_i' denotes the mean for the 'i-th' group and 'e_{ij}' denotes the random fluctuation occurring. The results of the analysis of variance showed that for the number of eggs laid by groups of 50 females, the differences among groups are statistically significant in four out of the five strains tested. On the other hand, for the female fly days, a statistically significant difference was detected in one strain only.

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[2] The detailed statistical analysis of all the following material is available upon request to the author.

It is apparent that the number of eggs varied considerably from generation to generation or between selected and unselected substrains, but there was much less variation in the total number of female fly days.

Comparisons were made between selected and unselected groups of flies of the F_1 and F_2 generations. These comparisons were tested by the t test method for each strain by using the values of standard error with were computed in the above described analysis of variance. The results of t tests for all the strains were then combined by Fisher's method of combined probability. This enabled certain general conclusions to be drawn from the results which have greater significance than those based on any one strain alone:

1. *Number of eggs:* The unselected F_2 flies laid less eggs than the unselected F_1. The selected F_2 laid more eggs than the unselected F_1 and, therefore, more than the unselected F_2.
2. *Female fly days:* The unselected F_2 showed less female fly days than the unselected F_1. The selected F_2 showed no such general tendency, although a statistically significant decrease was observed in one strain.

The first of these two general conclusions demonstrates that in the strains examined, there is a significant increase in the number of eggs laid by first generation progeny of flies selected for dieldrin resistance. As reported in the introduction to this paper, so general were the complaints of increased numbers of house flies in the field following the spraying of dieldrin that it is quite likely that what has now been shown to occur in the laboratory also occurs, and quite widely, in the field.

The second conclusion demonstrates that the increased number of eggs is not merely due to the newly resistant female flies having lived longer and, therefore, having time to lay more eggs but that the increase occurs within the same average lifespan, or less, as that lived by the susceptible, i.e. unselected, substrains.

Some additional statistical comparisons were made between the F_1 and each subsequent generation and those between a given generation and the preceding one. They have been tested by the same t-test method as used for the comparisons between F_1 and F_2 generations. The results of these tests indicate that very frequently the number of eggs laid by subsequent generations was smaller than the number laid by the F_2, i.e. the increase which occurred in most cases in the selected F_2 generation was not sustained.

Possible causes for the increased biotic potential

The purpose of the study was only to determine if such a unique biological relationship between fecundity and insecticide resistance could occur, not to determine the cause of it. Nevertheless, certain speculations may be presented for further study.

Considerable research has been carried out in order to elucidate the cause of dieldrin resistance, so far with little success. Numerous comparisons have been made between the physiology and morphology of dieldrin-resistant and dieldrin-susceptible flies (PERRY, 1960). None of the observed differences, however, shows any consistency for a number of strains.

The selective doses to which the susceptible strains were exposed were apparently sufficiently discriminative to result in a strain which maintained a high level of dieldrin resistance for several generations without re-exposure to the insecticide, indicating a genetic control of dieldrin resistance. The increased biotic potential, as demonstrated by the increased number of eggs, lasted only 1 or 2 generations before reverting to normal, i.e. to the same number as the unselected substrain. It, therefore, would seem unlikely that the increase in biotic potential has a genetic base.

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Zusammenfassung

Zahlreiche Beobachtungen in vielen Teilen der Welt zeigten eine bedeutende Zunahme in Hausfliegenpopulationen in Gegenden, die mit Dieldrin — einem lange wirkenden chlorierten Carbohydrat-Insektizid — bestreut wurden. Diese lästige Zunahme der schädlichen Insekten hinderte die Fortsetzung der Malaria-Bekämpfung. Es schien deshalb wichtig, unter kontrollierbaren Bedingungen festzustellen, ob eine Zunahme des biotischen Potentials der Hausfliegen nach Kontakt mit und der darauffolgenden Entwicklung der Resistenz zu Dieldrin wirklich stattfand, und die Möglichkeit auszuschließen, daß die Zunahme auf andere Faktoren, z. B. das Vernichten von Dieldrin-empfindlichen Feinden der Hausfliegen, zurückzuführen sei.

Die Möglichkeit einer Zunahme der Fekundität oder der Lebensdauer von weiblichen Fliegen nach der Entwicklung der Resistenz zu Dieldrin wurde im Feld und im Laboratorium geprüft. Mehrere Fliegenstämme verschiedener Gegenden Liberias in West-Afrika wurden für diese Studien gebraucht. Daneben wurde Material von Sierra Leone und Nigerien geprüft. Ein Teil von jedem der mehreren Dieldrin-empfindlichen Stämme wurde für Dieldrin-Resistenz ausgewählt, indem sie einer stark diskriminierenden Dose des Insektizids ausgesetzt wurden. Das biotische Potential des Elternstammes, der selektionierten Unterstämme (Nachkommen der zu Dieldrin ausgesetzten überlebenden Fliegen) und der nicht selektionierten Unterstämme wurden verglichen in bezug auf die Fekundität, gemessen durch die Anzahl der von Gruppen von 50 Weibchen jedes Unterstammes gelegten Eier, und die totale Lebensdauer dieser Gruppen.

Die statistische Analyse der Resultate zeigte für die geprüften Stämme:

a) daß die erste Nachfolgegeneration der für Dieldrin-Resistenz ausgewählten Fliegen statistisch bedeutend mehr Eier legten als die Fliegen der nicht selektionierten Unterstämme,

b) daß die Zunahme der Eizahl nicht einer erhöhten Lebensdauer der selektionierten Unterstämme zuzuschreiben ist, aber eine absolute Zunahme der Anzahl der gelegten Eier darstellt,

c) daß die erhöhte Fekundität temporär ist; sie verschwindet in der zweiten oder dritten Generation nach Selektion, obschon die Resistenz zu Dieldrin hoch bleibt.

Die möglichen Grundlagen der Zunahme des biotischen Potentials werden besprochen.

Résumé

De nombreuses observations, dans beaucoup de régions du monde, ont permis de déceler des accroissements considérables des populations de mouches domestiques dans des localités traitées par des pulvérisations de dieldrine, hydrocarbure chloré à effet prolongé. Cette multiplication fâcheuse d'insectes nuisibles a gêné le déroulement des campagnes antipaludiques. Il a donc paru très utile d'entreprendre, dans des conditions contrôlées, une étude visant à déterminer s'il s'agit bien d'une augmentation du potentiel biotique des mouches domestiques à la suite de leur contact avec la dieldrine et de l'apparition ultérieure d'une résistance à ce produit, et non pas d'une multiplication due à quelqu'autre facteur, par exemple à la destruction, par les pulvérisations des prédateurs de la mouche domestique qui seraient sensibles à la dieldrine.

On a donc cherché à déceler la possibilité d'une augmentation de la fertilité ou de la vie moyenne des mouches femelles après l'apparition d'une résistance à la dieldrine, en étudiant sur le terrain et en laboratoire plusieurs souches capturées en diverses régions du Libéria, ainsi que des mouches provenant du Sierra Leone et du Nigeria. On a pour cela examiné plusieurs souches sensibles à la dieldrine en soumettant une fraction de chacune à une dose critique de cet insecticide et on a sélectionné ainsi un certain nombre d'insectes résistants. On a alors comparé le potentiel biotique de la souche mère, de la souche secondaire sélectionnée née des insectes qui avaient survécu à l'exposition à la dieldrine, et des souches secondaires non sélectionnées ; cette comparaison a porté sur la fertilité, mesurée par le nombre d'œufs pondus par des groupes de 50 femelles de chaque souche secondaire, et sur la durée de vie totale des groupes.

L'analyse statistique des résultats a montré que pour les souches soumise à l'épreuve :

a) Il y avait une augmentation significative du nombre d'œufs pondus par la première génération issue des mouches sélectionnées pour leur résistance à la dieldrine, par rapport à la ponte des souches secondaires non sélectionnées.

b) Cette augmentation n'est pas due à une prolongation de la durée de vie des souches secondaires sélectionnées, mais représente un accroissement absolu du nombre d'œufs pondus.

c) L'augmentation de la fertilité est temporaire et disparaît à la deuxième ou troisième génération après la sélection, bien que la résistance à la dieldrine reste forte.

L'article expose diverses conjectures sur les causes possibles de l'augmentation du potentiel biotique.