RELATION OF THE SEX CHROMOSOME TO DDT RESISTANCE IN THE GERMAN COCKROACH

by

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Thesis submitted to the Graduate Faculty of the
Virginia Polytechnic Institute
in candidacy for the degree of

MASTER OF SCIENCE

in

Entomology

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1952

Blacksburg, Virginia.

160939

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INTRODUCTION

In recent years the development of insect resistance to insecticides has become an increasingly serious problem in the control of certain pests. Efforts to resolve this problem have lead to basic research in several fields outside the scope of economic entomology in which it was first encountered. Among the more important of these are physiology, biochemistry, and genetics. As a result of this research much progress has been made, but in all probability the final details will not be revealed until the physiological and biochemical processes of the insect body have been completely elucidated. At the present time this is being greatly handicapped by the lack of adequate techniques. In the ultimate sense the genetic aspects of this problem are also closely related to the physiology and biochemistry of the insect. Some aspects of resistance, however, can and are being studied by the usual techniques of genetics.

The present paper deals with this latter type of investigation. More specifically it is concerned with the inheritance of resistance to DDT in a certain strain of the German cockroach, Blatella germanica Linn. In the course of the development of this resistant strain there were indications that the inheritance is in some way related to sex. Such a relationship seemed likely because at the beginning of the study from 2 to 3 times as much DDT was required to kill female roaches as male roaches, and this difference became increasingly greater as resistance developed in the strain selected for survival to DDT treatments. The

research reported in this paper was undertaken in an endeavor to prove or disprove this relationship.

REVIEW OF LITERATURE

The reports of insects becoming resistant to insecticides began to appear in the literature very early. Melander's (12) "Can insects become resistant to sprays?" published in 1914, is probably among the first. In this work, however, he mentions that as early as 1908 the phenomenon was definitely recognized.

In spite of this early beginning the subject remained relatively unexplored until the extensive use of the newer organic insecticides brought it pointedly to the foreground. Since then the literature on the various aspects of resistance has become rather voluminous. Two critical reviews have been prepared and published by Babers (1) and Babers and Pratt (2).

Among the first suggestions as to how resistance arises in nature were those published by Painter (13) and Thorpe (15). Each discussed the presence of groups of individuals within a wild population which appear to differ from the main body of the population in one respect or another. Painter stated that sometimes two or more genetically distinct groups or strains may be present in the wild population. Dobzhansky (7) later elaborated upon this idea and suggested that it is an example of the gene variation typically existing in any population. Further, this variation constitutes the raw materials of evolution. Dobzhansky (7) also showed that genetic variation occurs as a result of gene mutation or chromosomal aberation. White (16) has stated that the former are far more frequent than the latter and

are, therefore, more important. Brown (4) stated that insects are heterozygous for many genes, and that this allows selection to occur for the more resistance individuals when a population is treated with an insecticide. He suggested further that it is also possible for a gene mutation for resistance to occur during the period in which chemical control is applied.

The mechanisms of inheritance of resistance are not well understood. Mendelian principles seem to be involved although the details vary in different insect species. The earliest investigations of this nature are those of Hough (10, 11) who made reciprocal crosses between strains of the codling moth, Carpocapsa pomonella (Linn.), which differed in their ability to enter apples that had been sprayed with lead arsenate. The progeny from these crosses proved to be intermediate between the two parental strains in their ability to enter sprayed fruit. The back crosses produced strains that were intermediate between the F_1 and the parental strain with which it was crossed. Hough reached no conclusions about the genetic mechanism involved, but Brown (4) interpreted it as indicating autosomal multiple-gene inheritance.

Dickson (6) proved that the resistance to HCN fumigation exhibited by the California red scale insect, Aonidiella aurantii (Mask.), is inherited as a simple sex-linked factor. This has been confirmed by Yust et al (18).

The literature on the inheritance of resistance to DDT in the

house fly, Musca domestica Linn., is somewhat contradictory. Bruce and Decker (5) found that a reciprocal cross between resistant and non-resistant strains resulted in the production of progeny whose resistance was intermediate between the two parental strains. This they conclude probably indicates autosomal multiple-gene inheritance. On the other hand, reciprocal crosses made by Harrison (9) resulted in the production of an F_1 generation which was slightly more resistant to DDT than the non-resistant parental strain. The F_2 generation from this cross produced a ratio of 3 non-resistant flies to 1 resistant fly. This would indicate a one-factor, autosomal inheritance with the factor for non-resistance incompletely dominant. There is some question about the validity of the toxicological criterion for resistance used by Harrison, but if her results are correct it would indicate that there are at least two genetic mechanisms involved in producing resistance in the house fly.

In addition to the investigations of the genetic mechanisms involved in the resistance of insects to insecticides there has been, in recent years, a very extensive investigation of the physiological mechanism for resistance. Perry and Hoskins (14) stated that there are three main physiological lines of defense involved. First, the resistant insect is able to convert considerable quantities of absorbed DDT into the relatively non-toxic ethylenic derivative of DDT, known as DDE. This occurs before DDT has time to do any damage. Secondly, a similar process of conversion to an unidentified compound

also occurs. Finally, resistant insects are capable of storing considerable quantities of DDT in certain tissues in their bodies and of disposing of it by degradation to non-toxic compounds at their leisure.

The physiological work has been carried out mainly on resistant house flies, and it is not known if the results can be generalized to other insects. In addition, the exact mechanism by which DDT is degradated is not known. Furthermore, the relationship between the physiological and the genetic mechanisms for resistance is not well understood. Perry and Hoskins (14) have theorized that perhaps resistant strains of house flies may arise by selection of those possessing an enzyme capable of dehydrohalogenation of DDT.

Wigglesworth (17) stated that there are several types of sex-determination mechanisms found in insects. Actually these seem to constitute only two basic types with some variations in them. The first type is that in which the females have two X sex chromosomes, and the males have one X and one Y sex chromosome; the second is that in which the females have two X sex chromosomes, but the males have only one X sex chromosome and no Y. This is referred to as the XO condition. No reference was found in the literature concerning the sex-determination mechanism present in the German cockroach. However, M. J. D. White* states that the German cockroach has males XO and females XX. This is in accord with the situation in most Orthoptera.

* Personal communication

The DDT-resistant strain of German cockroaches used in these experiments was developed in the laboratory by Grayson (8). The development of resistance proceeded very slowly through 5 generations of selection and then began to increase rapidly.* No other reference to a DDT-resistant strain of German cockroaches was found in the literature. Therefore, this is probably the first study of the inheritance of resistance to DDT in this insect species.

* Personal communication

MATERIALS AND METHODS

Materials:

The cockroaches used in these experiments were obtained from the stock cultures of DDT-resistant and non-resistant strains currently being maintained in the Entomology Section of the Virginia Agricultural Experiment Station.

In rearing the roaches the following materials were used: one gallon glass battery jars, ¼-inch pressboard, brown wrapping paper, cheese cloth, vaseline, and small strips of wood measuring ¼" x ¼" x 4." The roaches were fed dry commercial dog food which was occasionally supplemented with fresh lettuce leaves.

In testing the roaches for resistance the following equipment was used: a chainomatic, analytical balance equipped with magnetic damper and notched beam; a centigrade thermometer; an electrical blendor; an interval timer; and small mesh, cylindrical, screen wire cages measuring 1" in diameter and 4" in length. The form of DDT used was a wettable powder containing 75 percent DDT.

Methods:

I Rearing Technique:

Each of the 1-gallon glass battery jars used as rearing chambers contained approximately 20 pairs of adult roaches and the offspring they produced. In order to accommodate this large number of individuals in

each jar 4 or 5 layers of ¼-inch pressboard were arranged in tiers by placing small strips of wood between them. A six-inch band of brown wrapping paper was placed around the outside of each rearing jar to darken the interior and thus simulate natural conditions. Escape of the roaches was prevented by rubbing a thin film of vaseline in a 2-inch band on the inside top rim of the jars. In addition, the jars were covered with cheesecloth held in place with rubber bands.

The food was placed loose in the bottom of the rearing chambers so that the roaches had free access to it. Water was provided in petri dishes placed on top of the layers of pressboard and was available at all times.

A constant temperature room was not available for rearing purposes; hence, the roaches were reared at room temperature which varied from 70-80 degrees Fahrenheit. The relative humidity of the room was raised by keeping water in pans at various points in the laboratory.

II Genetic technique:

Reciprocal crosses were made between DDT-resistant and non-resistant strains of cockroaches. A reciprocal cross signifies, in this case, crossing females of the DDT-resistant strain with males of the non-resistant strain and females of the non-resistant strain with males of the DDT-resistant strain. In order to insure virgin females the sexes were separated within 24 hours after the adult stage was reached, and held separately until enough individuals were obtained to make the

desired crosses. Mating was not observed to occur within the first 24 hours following the last moult.

The experiments were conducted twice: First, when the DDT-resistant strain was in the ninth generation of selection for resistance and, secondly, when it was in the eleventh generation. The equivalent generation of the non-resistant strain was used in each case.

The parents involved in each cross were divided into four lots, and allowed to reproduce until a population of progeny sufficient for toxicological testing was obtained. Care was taken to remove parent roaches before any of the offspring reached the adult stage.

III Toxicological Technique:

The order of resistance to DDT of each F_1 strain, as well as the equivalent parental strains, was determined by treating known age adults from each strain with different concentrations of DDT. The method of toxicological assay consisted of dipping the roaches in a water suspension of the toxicant at 30 degrees centigrade. The samples of DDT were weighed on an analytical balance and the aqueous suspensions were processed in an electrical blendor for 15 seconds. The technique of testing was changed during the course of the two experiments because of the mechanical difficulties involved in putting enough DDT into suspension to kill the highly resistant females of the DDT-resistant strain. In the F_9 generation the roaches were dipped in the toxicant for 10 seconds and left in the treatment cages for 5 minutes, while in the F_{11}

generation they were dipped in the toxicant 15 seconds and left in the treatment cages 30 minutes before removal to recovery jars. For this reason the quantitative results from the two sets of experiments are not directly comparable, but all comparisons within each of the two experiments and the genetic trends indicated by both should be valid.

The sexes were treated separately in subsamples of approximately 30 insects each. Following treatment the roaches were placed in recovery jars which contained food and water. Observations for mortality were made at the end of three and six days with the criterion of mortality being failure to exhibit active locomotion.

IV Statistical Technique:

The data obtained by treating the various strains of roaches at different concentrations of DDT were plotted on logarithmic-probability paper and regression lines were fitted to the points by the method of least squares (Bliss, 3). Five or six points were used to establish each line. For each concentration from 50 to 150 insects, in subsamples of approximately 30, were used, and the tests were replicated from two to five times.

Ninty-five percent fiducial limits were placed on any lines that were considered close enough that they could be derived from identical populations. In addition, the difference between the LD_{50} values (concentration of DDT required to obtain 50 percent kill) of all lines were analyzed to further test whether or not any two lines were coming from identical populations.

RESULTS

The regression lines which resulted from plotting the toxicological data are shown in figures 1 to 6. The LD_{50} and LD_{90} points of these lines, as well as the order of resistance at LD_{50}, are shown in table 1. The F_1 males and females from the cross involving the DDT-resistant females and the non-resistant males are referred to as the A strain, and the F_1 males and females from the cross involving the non-resistant females and the DDT-resistant males are referred to as the B strain.

The data show that the A- and B-strain males and females from both the F_9 and F_{11} generation crosses are intermediate, with regard to resistance, between the two parental male and female types, respectively (table 1). The LD_{50} values of the F_1 regression lines were significantly different from those of all the parental lines.

The F_1 males and females from the A strain were more resistant to DDT at LD_{50} than the corresponding sex among the F_1 of the B strain (figures 3 and 6). An analysis of the LD_{50} values of all F_1 regression lines showed that there was a significant difference in all cases except between the A- and B-strain males of the F_9 cross. In that case the A-strain males were still more resistant at LD_{50} than the B-strain males, but the difference was not significant. The 95 percent fiducial limits indicate that these two lines could be coming from identical populations (figure 3). The data for the B-strain males, however, did not fit a straight line too well, as indicated by the CHI square test.

TABLE 1

Comparison of the effects of DDT on several strains of the German cockroach

	F_9 GENERATION			F_{11} GENERATION		
	Conc. of DDT in gm./l.		Times resistance at LD_{50}	Conc. of DDT in gm./l.		Times resistance at LD_{50}
	LD_{50}	LD_{90}		LD_{50}	LD_{90}	
Non-resistant males	.034	.066	0	.018	.038	0
B-strain males	.082	.230	2.4	.026	.046	1.4
A-strain males	.087	.170	2.5	.048	.140	2.7
Resistant males	.195	.670	5.7	.260	1.100	14.8
Non-resistant females	.093	.300	0	.036	.115	0
B-strain females	.290	1.200	3.1	.102	.400	2.8
A-strain females	.600	9.000	6.4	.195	.700	5.4
Resistant females	6.200	32.000	66.6	12.000	230.000	333.3

EXPLANATION OF FIGURE I

Figure 1 - Toxicity of DDT to the various strains of the German cockroach involved in the F_9 generation B-strain cross.

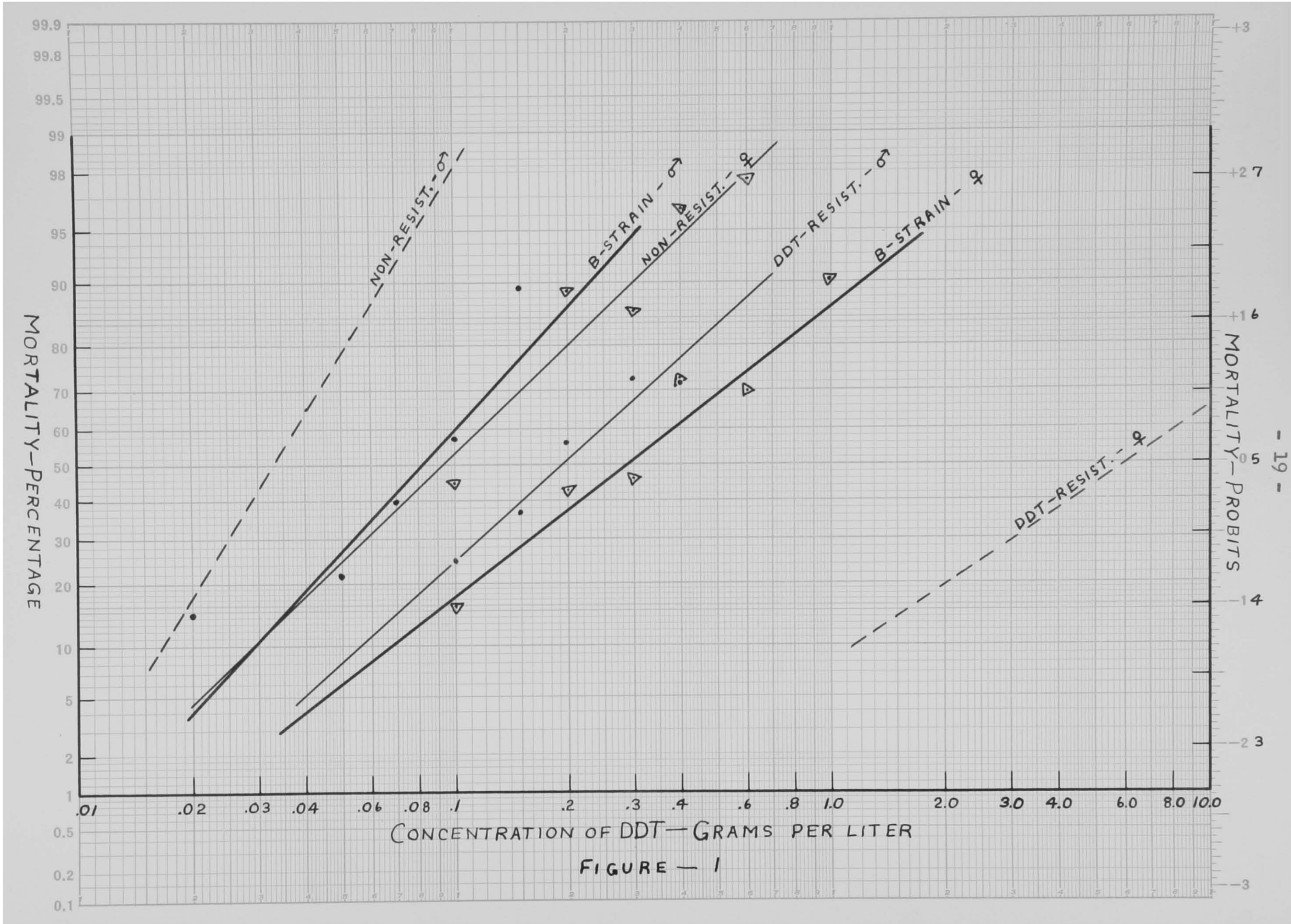
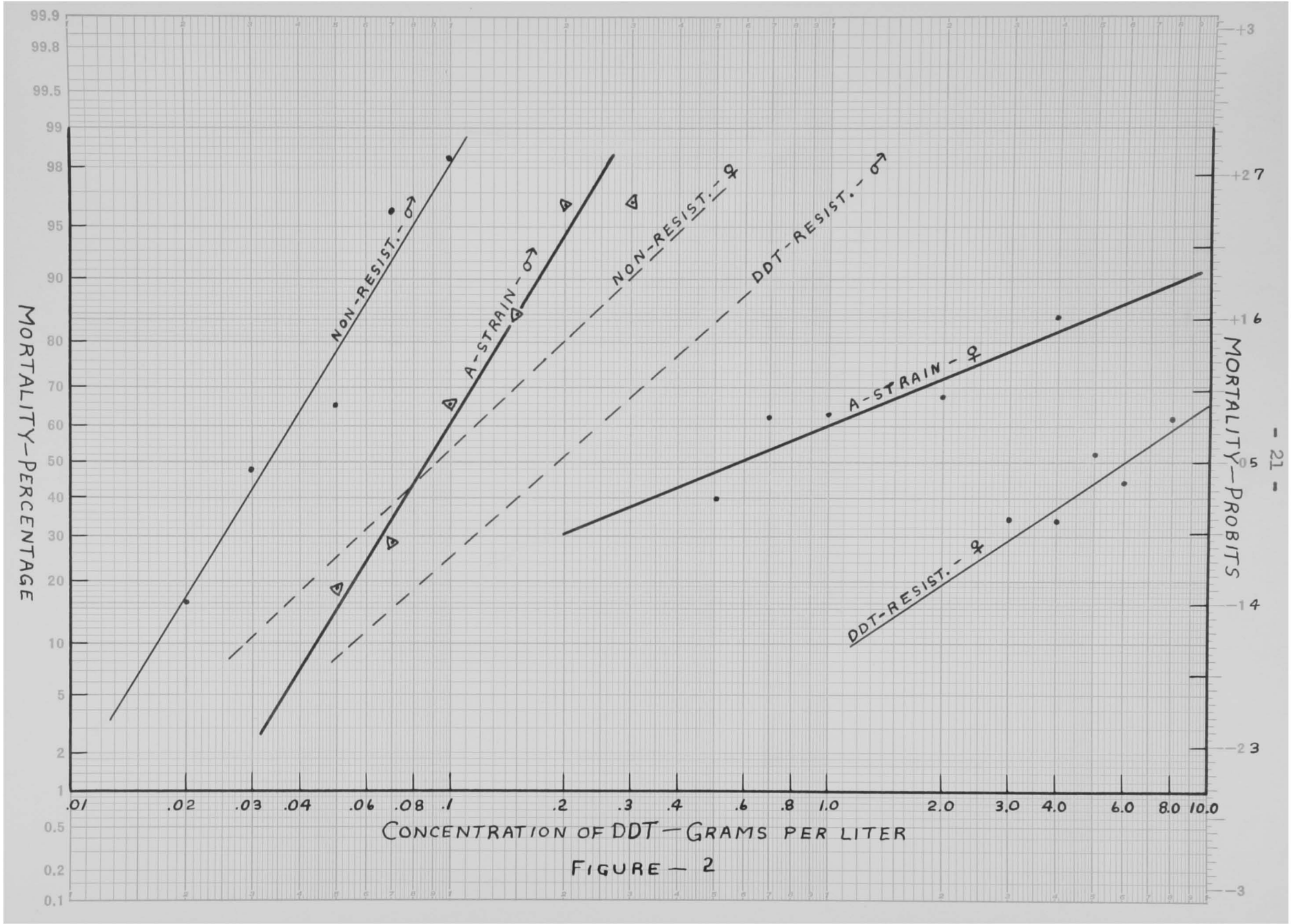

MORTALITY—PERCENTAGE
99.9
99.8
99.5
99
98
95
90
80
70
60
50
40
30
20
10
5
2
1
0.5
0.2
0.1
NON-RESIST. - ♂
B-STRAIN - ♂
NON-RESIST. - ♀
DDT-RESIST. - ♂
B-STRAIN - ♀
DDT-RESIST. - ♀
.01
.02
.03
.04
.06
.08
.1
.2
.3
.4
.6
.8
1.0
2.0
3.0
4.0
6.0
8.0
10.0
CONCENTRATION OF DDT — GRAMS PER LITER
MORTALITY—PROBITS
+3
+2 7
+1 6
0 5
-1 4
-2 3
-3

FIGURE — 1

EXPLANATION OF FIGURE II

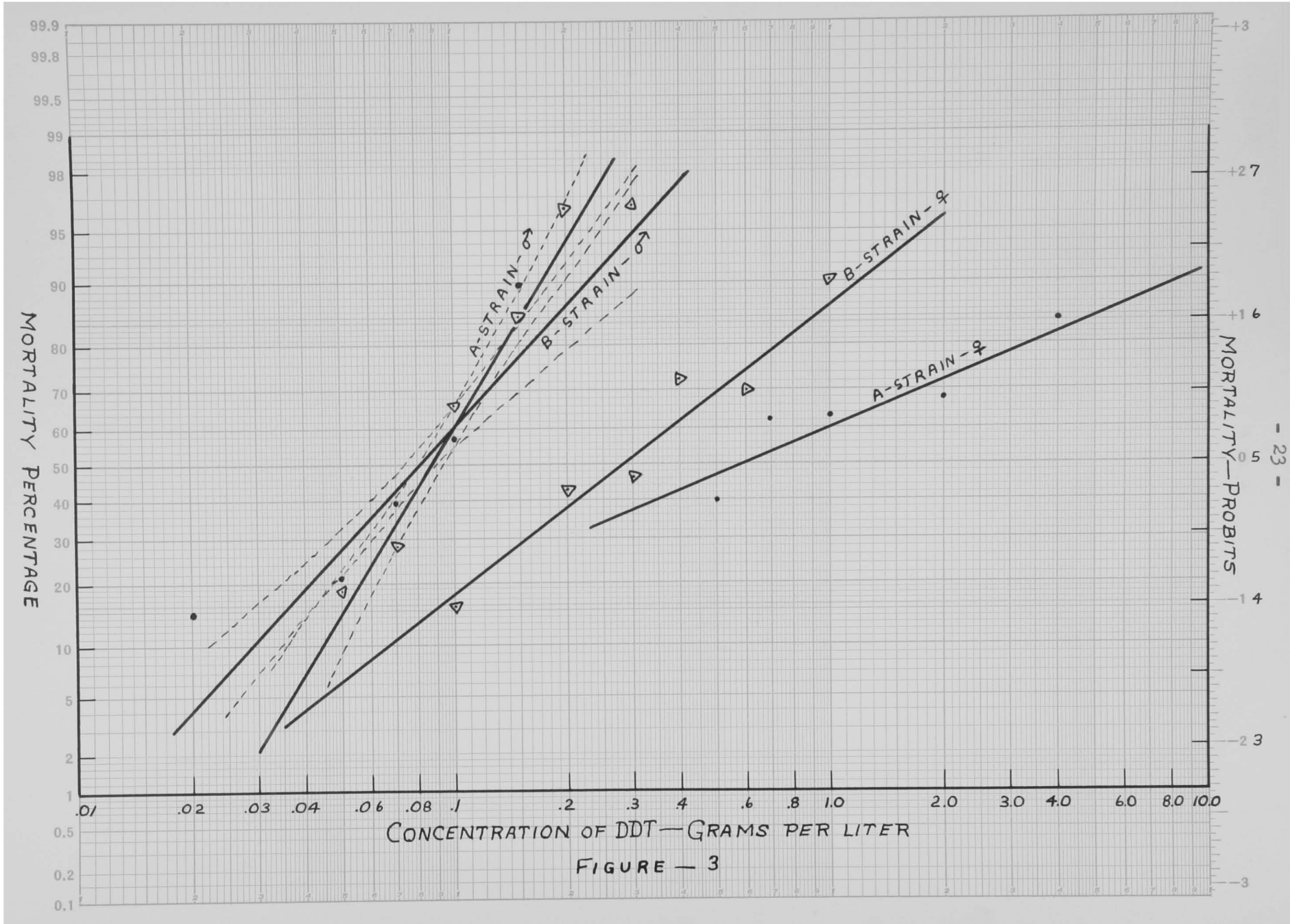
Figure 2 - Toxicity of DDT to the various strains of the German cockroach involved in the F_9 generation A-strain cross.


MORTALITY—PERCENTAGE
99.9
99.8
99.5
99
98
95
90
80
70
60
50
40
30
20
10
5
2
1
0.5
0.2
0.1
NON-RESIST.-♂
A-STRAIN-♂
NON-RESIST.-♀
DDT-RESIST.-♂
A-STRAIN-♀
DDT-RESIST.-♀
.01
.02
.03
.04
.06
.08
.1
.2
.3
.4
.6
.8
1.0
2.0
3.0
4.0
6.0
8.0
10.0
CONCENTRATION OF DDT—GRAMS PER LITER
MORTALITY—PROBITS
+3
+2 7
+1 6
5
1 4
2 3
-3

FIGURE— 2

EXPLANATION OF FIGURE III

Figure 3 - Toxicity of DDT to the F_9 generation A- and B-strain crosses.


MORTALITY PERCENTAGE
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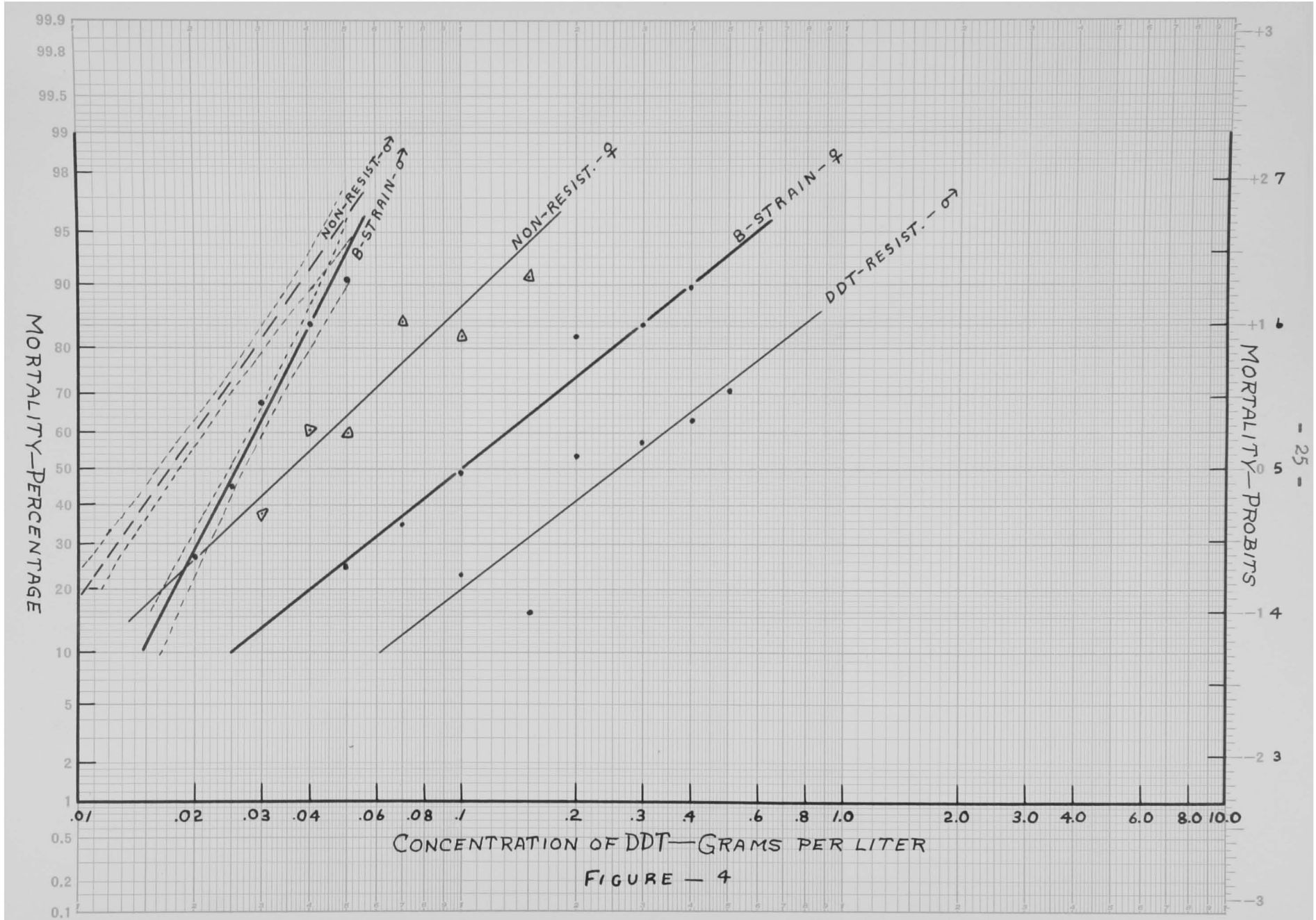
99.8
99.5
99
98
95
90
80
70
60
50
40
30
20
10
5
2
1
0.5
0.2
0.1
MORTALITY—PROBITS
+3
+2 7
+1 6
0 5
-1 4
-2 3
-3
A-STRAIN-♂
B-STRAIN-♂
B-STRAIN-♀
A-STRAIN-♀
.01
.02
.03
.04
.06
.08
.1
.2
.3
.4
.6
.8
1.0
2.0
3.0
4.0
6.0
8.0
10.0
CONCENTRATION OF DDT—GRAMS PER LITER

FIGURE — 3

EXPLANATION OF FIGURE IV

Figure 4 - Toxicity of DDT to the various strains of the German cockroach involved in the F_{11} generation B-strain cross.


NON-RESIST.-♂
B-STRAIN-♂
NON-RESIST.-♀
B-STRAIN-♀
DDT-RESIST.-♂
MORTALITY—PERCENTAGE
MORTALITY—PROBITS
99.9
99.8
99.5
99
98
95
90
80
70
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5
2
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0.5
0.2
0.1
+3
+2
7
+1
6
0
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-1
4
-2
3
-3
.01
.02
.03
.04
.06
.08
.1
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.4
.6
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2.0
3.0
4.0
6.0
8.0
10.0
CONCENTRATION OF DDT—GRAMS PER LITER

FIGURE — 4

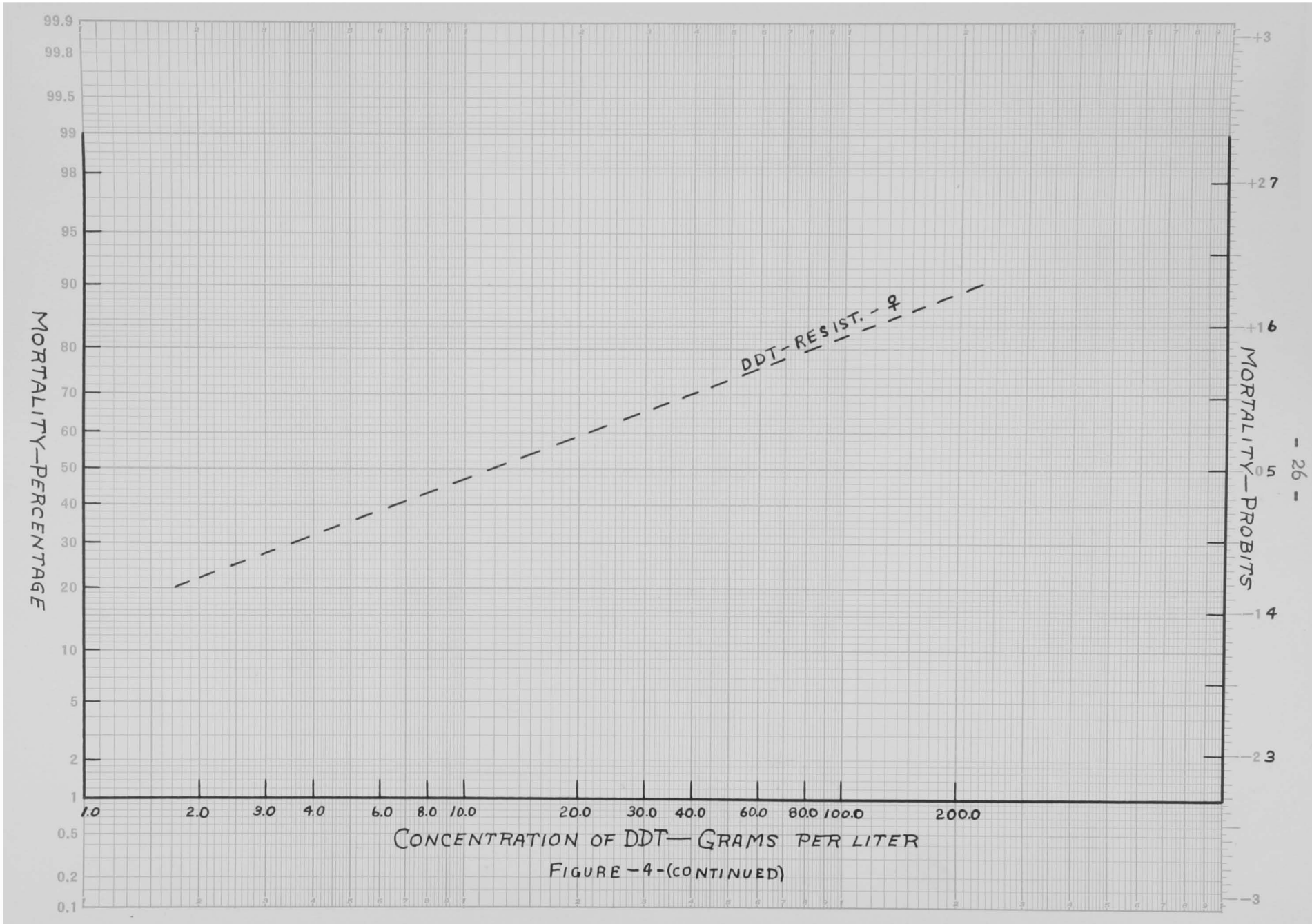
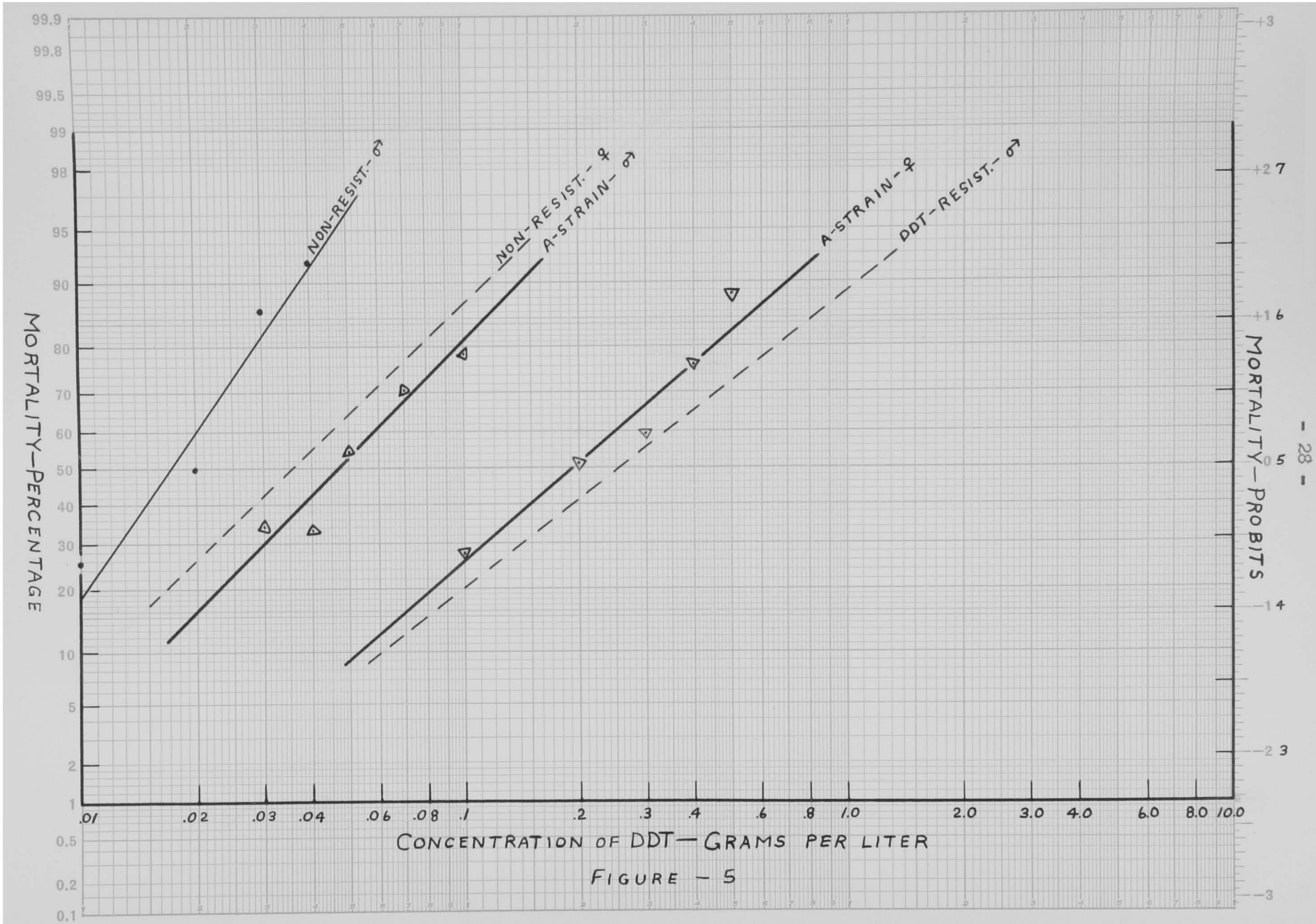


FIGURE-4-(CONTINUED)

EXPLANATION OF FIGURE V

Figure 5 - Toxicity of DDT to the various strains of the German cockroach involved in the F_{11} generation A-strain cross.


NON-RESIST.- ♂
NON-RESIST.- ♀
A-STRAIN- ♂
A-STRAIN- ♀
DDT-RESIST.- ♂
MORTALITY—PERCENTAGE
MORTALITY—PROBITS
99.9
99.8
99.5
99
98
95
90
80
70
60
50
40
30
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0.5
0.2
0.1
+3
+2 7
+1 6
0 5
−1 4
−2 3
−3
.01
.02
.03
.04
.06
.08
.1
.2
.3
.4
.6
.8
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3.0
4.0
6.0
8.0
10.0
CONCENTRATION OF DDT—GRAMS PER LITER

FIGURE – 5

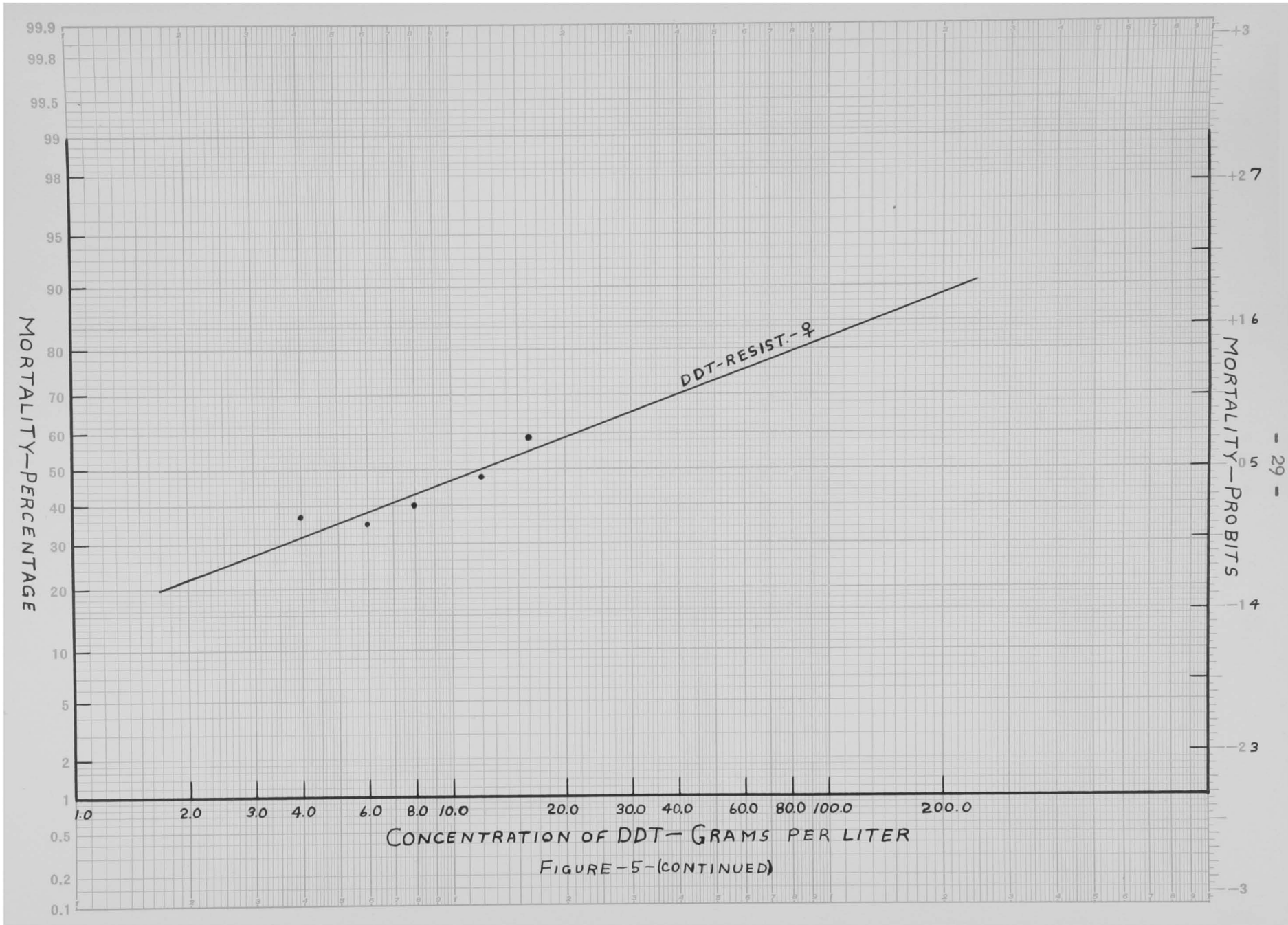
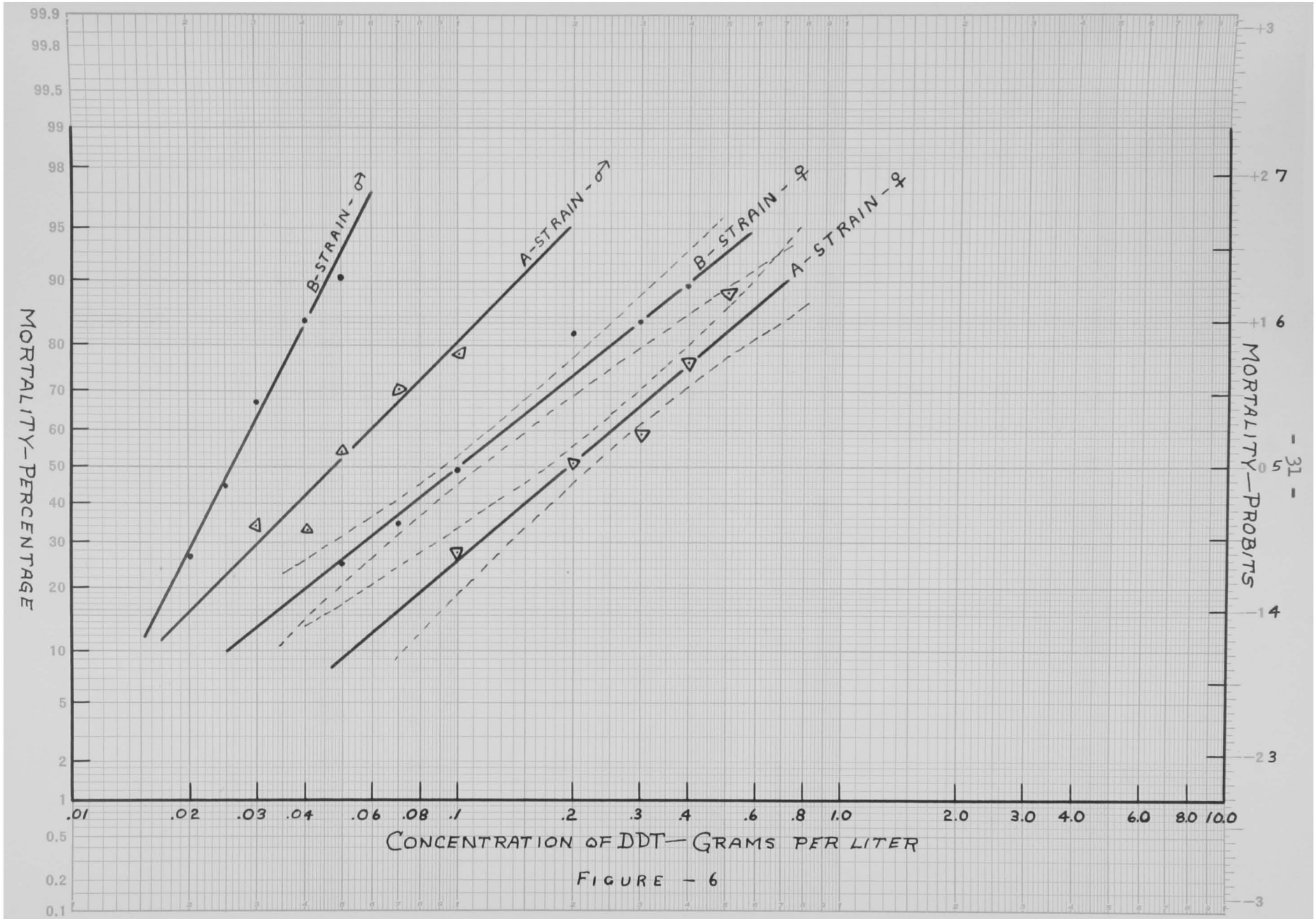


FIGURE-5-(CONTINUED)

EXPLANATION OF FIGURE VI

Figure 6 - Toxicity of DDT to the F_{11} generation A- and B-strain crosses.


B-STRAIN - ♂
A-STRAIN - ♂
B-STRAIN - ♀
A-STRAIN - ♀
MORTALITY—PERCENTAGE
99.9
99.8
99.5
99
98
95
90
80
70
60
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30
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2
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0.5
0.2
0.1
MORTALITY—PROBITS
+3
7
+2
6
+1
5
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4
-1
3
-2
-3
.01
.02
.03
.04
.06
.08
.1
.2
.3
.4
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2.0
3.0
4.0
6.0
8.0
10.0
CONCENTRATION OF DDT— GRAMS PER LITER

FIGURE – 6

DISCUSSION

The preliminary suggestion that inheritance of resistance is related to sex was based on the fact that the females always exhibited more resistance to DDT than did the males. This could be explained on the basis of sex-linkage because then the females would have two sets of these factors, one on each X chromosome, whereas the males would have only one. If this theory were correct the expected results would be F_1 females alike in resistance from both of the reciprocal crosses, and probably intermediate between the two parental female types, and F_1 males that resemble their respective maternal parent with regard to resistance. Since males and females are different with respect to resistance, however, the F_1 males would be expected to resemble the males of the strain from which their maternal parent came. The results that were actually obtained show that the males as well as the females are intermediate between, and significantly different from, their respective parental types. This would indicate that resistance is not inherited as a simple sex-linked factor.

Another mechanism for the inheritance of resistance must, therefore, be sought. One clue presents itself in the data from the B-strain cross (figures 1 and 4). In this cross the only source of resistance is the paternal parent (DDT-resistant males). Any resistance possessed by the progeny above that of the non-resistant strain must come from this source. Furthermore, the B-strain males receive no sex chromosome from the paternal parent because male gametes containing X

chromosomes produce only females when united with female gametes. The B-strain males do, however, receive a full set of autosomal chromosomes from the paternal parent. Inasmuch as they were found to possess resistance significantly greater than that of the non-resistant males, it would appear that at least part of the resistance mechanism is located on the autosomal chromosomes.

The explanation of the difference between male and female resistance must also be sought elsewhere. It will be remembered that the non-resistant females are more resistant to DDT than are the non-resistant males (figures 1 and 4). The difference is highly significant at LD_{50}. From this it would appear that the females are physiologically capable of withstanding the effects of more DDT than are the males. This might also explain why the females have become increasingly more resistant to DDT than the males as the selection progressed.

The greater resistance of the A-strain individuals as opposed to the B-strain individuals, both male and female, suggests that besides the chromosomal factors there may be a maternal factor involved in this resistance. In every case the A-strain individuals were more resistant than the B-strain individuals at LD_{50} (figures 3 and 6). The difference was significant in all cases except the F_9 males. This lone exception may probably be disregarded because it was not substantiated in the F_{11} crosses; furthermore, the data for the F_9 B-strain males showed more variation than expected.

The nature of the proposed maternal factor is not evident from this investigation, but one possibility is a cytoplasmic factor present in the eggs of the DDT-resistant females and passed along to their A-strain offspring. Such a factor, if present, would be found in the apparently inactive state in the non-resistant female eggs and would, therefore, have no visible effect on the resistance of the B-strain individuals.

The explanation of the convergence present at the lower ends of the regression lines of the F_9 generation A- and B-strain females (figure 3), and also at the lower ends of the lines of the F_{11} generation A- and B-strain males (figure 6), is probably twofold. First, there is probably enough residual heterozygosity present in the resistant strain to produce some non-resistant F_1 individuals, and secondly, the slope of the various lines could readily be affected by random sampling errors.

CONCLUSIONS

On the basis of these experiments it appears that the following conclusions are justified:

1. That the resistance which the German cockroach has developed to DDT is not inherited as a simple sex-linked factor.

2. That this resistance to DDT is at least in part an autosomally linked factor.

3. That the females of the German cockroach are physiologically more vigorous than the males with regard to their ability to withstand the effects of DDT.

4. That besides the already mentioned difference between the males and females there is an additional maternal factor involved in the inheritance of resistance to DDT.

SUMMARY

1. Reciprocal crosses were made between a DDT-resistant and a non-resistant strain of the German cockroach.

2. The techniques employed in rearing the roaches and obtaining toxicological data on the different strains, as well as the genetical and statistical procedures, are described.

3. The toxicological data are presented in the form of regression lines with appropriate statistical analyses.

4. A table showing the relative resistance to DDT of the various strains involved in this study is included.

5. Several conclusions are drawn relative to inheritance of resistance to DDT in the German cockroach.

ACKNOWLEDGMENTS

The author wishes to express his deepest appreciation to Dr. J. M. Grayson without whose assistance and direction this work would not have been possible. Thanks are also due to Dr. Max Levitan for his help with the genetical problems involved, and to Dr. D. B. Duncan for his assistance with the statistical analyses.

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