EXPERIMENTS ON THE EFFECTS OF HOMOZYGOSITY AND HETEROZYGOSITY ON THE RATE OF DEVELOPMENT IN DROSOPHILA MELANOGASTER

GERT BONNIER, ULLA B. JONSSON AND CLAES RAMEL

Institute of Genetics, University of Stockholm, Stockholm, Sweden

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IN 1956 the authors made preparations for and started experiments on the effect of selection pressures of different strengths on irradiated populations of *Drosophila melanogaster*. When planning these experiments several problems on the relative viabilities of homozygotes and heterozygotes presented themselves. One of these concerned comparisons of homozygotes and different heterozygotes in multiple allelic loci.

In the selection pressure experiments, the strength of the pressure was regulated by letting a given number of larvae compete for a standard amount of food: a large number in high selection pressure populations but a small number in low selection pressure populations (BONNIER, JONSSON and RAMEL 1958). When many larvae compete for a limited amount of food the variation in the time which it takes for the larvae to reach the adult stage is large. It seems obvious that, at least as a rule, those individuals who reach eclosion early are more viable than those who need a long time for their development. In other words, among the characters which may be used for defining and measuring viability and selective ability, rate of development may be taken as one. We decided, therefore, to use a technique for studying rate of development similar to that we already had worked out in our irradiation experiments.

At the end of 1956, preparations were made to produce suitable strains for the experiments and the experiments themselves were performed in 1957. However, with the experience gained and after studying the results it was found necessary to make further experiments. New preparations were, therefore, made in 1957 and a new set of experiments were performed in 1958.

Experiments of the 1957 series

Synthesis of strains: Five alleles of the white locus were used, *viz.* +, w^{co}, w^{a}, w^{t}, w. The wild type chromosome was taken from flies in our stock bottle labelled w^{sat}. The stock of this bottle had been propagated for many years without any check of its content. As we were unable to distinguish the eye color of this stock from that of wild type flies, and as it proved to be dominant over all of the w alleles tested, we symbolize it here by the sign +. In chart I the synthesis is shown diagrammatically.

Experimental technique: All experiments were performed as larval competition experiments. After 16 hours of oviposition (from 5 p.m. to 9 a.m. of the next

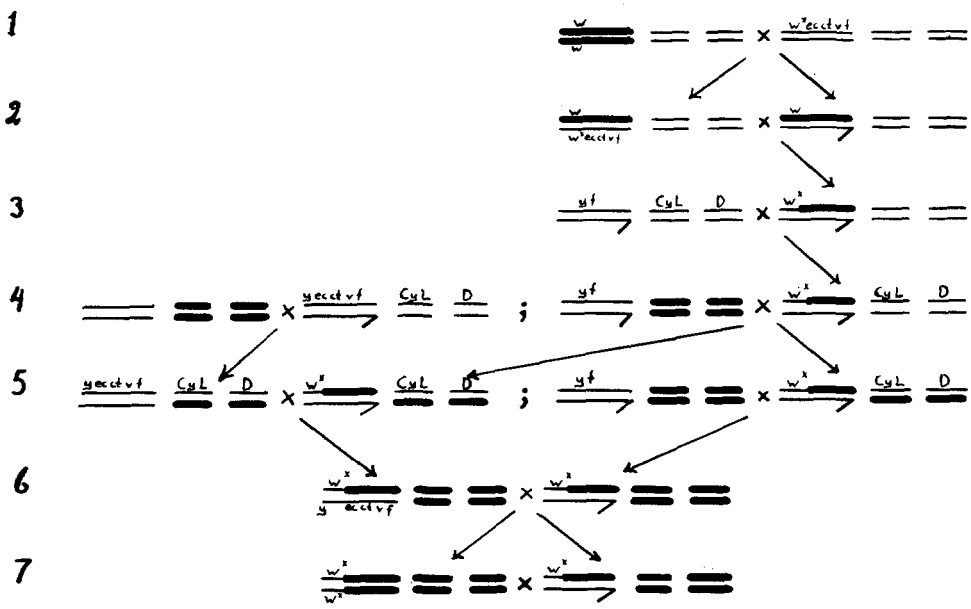


CHART I.—Synthesis of strains used in the 1957 series of experiments. Isolated chromosomes, with regard to which the strains were rendered isogenic, are drawn in heavy lines. Females were made homozygous for one *w* containing X chromosome as indicated in generation 1. Other females were made homozygous for a set of the two long autosomes containing wild type genes as indicated in generation 4. The chart shows how the gene *w* was substituted by other *w* alleles (collectively named w^x), and how these were combined with the set of isogenous autosomes. Apart from *w* (locus 1.5) and its alleles, the following sex-linked marker genes were used: *ec* (5.5), *ct* (20.0), *v* (33.0), *f* (56.7). The symbol *yf* refers to double attached XXY females homozygous for *y* and *f*. *M5*, *CyL*, and *D* are symbols for crossing over inhibiting dominant markers.

day) and a further 28 hours of incubation, freshly hatched larvae were collected and transferred to vials with food of standard type. The amount of food was in every vial about 12 ml, though no exact weighings or measurements were made. The number of larvae transferred to each separate vial was always 200—which means a strong competition between the larvae. Of these, 100 were taken from one of the prepared strains or cross between two of them, and 100 from another of these strains or cross between two other of them. All vials were incubated at 25°C in an incubator, not used for other purposes when these experiments took place.

Experiment 1957:1: Though the primary purpose for setting up the present series of experiments was to compare heterozygotes with homozygotes or with other kinds of heterozygotes it seemed appropriate to start with a larval competition experiment between the pure strains. As mentioned above we had produced five homozygous coisogenic strains. Ten different kinds of comparisons of two by two were, hence, possible to make. One of these, *viz.* that between w^t and *w*, could not be fulfilled because of the uncertainty in many individual cases in distinguish-

ing between these two eye colors. The nine remaining comparisons were, however, performed. Females were allowed to oviposit on four consecutive days (as mentioned above for 16 hours each time) and from each of these one vial with freshly hatched larvae was started for each of the nine comparisons. Table 1

TABLE 1

Experiment 1957:1

Results from competitions between pure strains. Figures show totals from four vials for each kind of comparison. Each vial started with 200 larvae of which 100 were taken from each of the two strains shown in the left margin of the table

Larvae from strains	Adults emerged up to 9 days 18 hours after beginning of mothers' ovipositions				Total number of adults emerged			
	Females		Males		Females		Males	
+ and w^{co}	74 +,	42 w^{co}	87 +,	29 w^{co}	161 +,	177 w^{co}	163 +,	149 w^{co}
+ and w^{a}	94 +,	12 w^{a}	67 +,	12 w^{a}	190 +,	181 w^{a}	160 +,	168 w^{a}
+ and w^{t}	85 +,	19 w^{t}	46 +,	14 w^{t}	202 +,	180 w^{t}	157 +,	136 w^{t}
+ and w	81 +,	31 w	95 +,	29 w	170 +,	161 w	189 +,	151 w
w^{co} and w^{a}	66 w^{co},	20 w^{a}	60 w^{co},	28 w^{a}	164 w^{co},	182 w^{a}	149 w^{co},	173 w^{a}
w^{co} and w^{t}	45 w^{co},	20 w^{t}	33 w^{co},	19 w^{t}	183 w^{co},	177 w^{t}	153 w^{co},	144 w^{t}
w^{co} and w	40 w^{co},	30 w	35 w^{co},	18 w	166 w^{co},	170 w	151 w^{co},	143 w
w^{a} and w^{t}	50 w^{a},	17 w^{t}	34 w^{a},	14 w^{t}	174 w^{a},	180 w^{t}	168 w^{a},	135 w^{t}
w^{a} and w	56 w^{a},	37 w	51 w^{a},	22 w	190 w^{a},	183 w	165 w^{a},	142 w

shows the results. The total number of observed adults was 5,987 or 83 percent of the 7,200 larvae. As an equal number (100) of larvae of each of the two competing types was collected one should expect that the adults should come out in a 1:1 proportion. As may be seen, the observed proportions after ceasing of eclosion are generally in good agreement with the expectations; among the 18 proportions for females and for males there were only two cases for which the probability of deviation was less than 0.10. From this point of view one would, therefore, be right in saying that the two competing types in all cases were of practically equal viability.

The vials with the emerging flies were emptied on several occasions before the eclosion ceased. The proportions between the two competing types were, at the early counts, very far from 1:1. Table 1 gives also the sums for the four vials with regard to the flies which had reached eclosion within nine days and 18 hours after the beginning of their mothers' ovipositions. When w^{co}, w^{a}, w^{t} or w competed with wild type, much more than 50 percent were wild type; when w^{a}, w^{t} or w competed with w^{co} much more than 50 percent were w^{co}; and when w^{t} or w competed with w^{a} much more than 50 percent were w^{a}. That the wild type larvae in the present material developed faster than any of the other types is thus obvious. Concerning the w^{co} larvae the absolute numbers of the adults were practically identical whether the larvae had to compete with +, w^{t} or w. The seriation of the percentages of w^{co} when competing with + (31%), w^{a} (72%), w^{t} (67%) or w (61%) must, therefore, be taken with some caution. The w^{a} larvae, on the other

hand, show the same kind of seriation whether one judges from the absolute figures or from the percentages. The total number of w^a in competition with +, w^{co}, w^t and w was respectively 24 (13%), 48 (28%), 84 (73%), 107 (64%). From this case one may conclude that the rate of development of larvae of Drosophila is determined, not only by the strength of selection pressure and by their own genotypes, but also by the genotypes of those other larvae with which they have to compete.

One finds the following seriation of competition ability: $+ > w^{co} > w^a > w^t$ and w. It seems, therefore, as if this seriation follows the degree of deviation from normality, in this case expressed as the deviation in eye color of the adults from the wild type red eye color. (Compare, however, experiment 1958:5, Table 9, Figures 13, 14).

Experiment 1957:3: From the five different genotypes, +, w^{co}, w^a, w^t and w one may get ten different heterozygotes, and these may be combined two by two in 45 different ways. Several of the genotypically different heterozygotes are phenotypically indistinguishable and, therefore, only 10 of the 45 comparisons were performed (Experiment 1957:2). As the results proved to be of no great interest, their description is omitted here.

In the hope of getting more information we decided, however, to make one more experiment, this time by always letting two kinds of wild type female larvae compete. However, to proceed in this way it is necessary to identify the genotypes of the observed females by progeny testing them individually. The experiment, as performed, included collection of 12,800 larvae, from which 5,428 females emerged; of these 4,818 or 88.8 percent could be identified by progeny tests.

Heterozygous females may be produced in two different ways, either by crossing wild type homozygous females with nonwild type males, or by making the reciprocal cross. The types of male larvae with which the female larvae have to compete depend thus upon the way in which the crosses are made. For instance, the production of $+/w^{co}$ and $+/w^a$ female larvae for a competition experiment may be made so as to have them compete with only + males, with + and w^{co} males, with + and w^a males, or with w^{co} and w^a males. To evaluate the competition abilities of the female larvae from these four types of crosses proved to be more difficult than we had expected. We confine, therefore, the present description to those four crosses in which the competition was between homozygotes +/+ and that kind of heterozygotes which themselves were produced by crossing wild type homozygous females +/+ to nonwild type males (Table 2). For each comparison one vial was raised on each of two consecutive days, and, as before, each vial contained 100 larvae from each of two crosses. The table shows the numbers of observed females and the genotypes and numbers of the identified ones. The percentages refer in this table to the number of observed females which could be identified by progeny tests.

Because of the fact that eclosion this time began somewhat later than in experiment 1957:1 we have, for the demonstration in the table, chosen ten days and 18 hours after beginning of oviposition as a suitable early stage for the comparisons.

TABLE 2

Experiment 1957:3

Results from competitions between wild type homozygous and heterozygous females, when the crosses were made in such a way that all males were wild type. The genotypes of the females were identified by individual progeny tests. Under the sign "%" the numbers of observed females which were possible to identify in this way are given as percents of the total number of females observed at the corresponding stage. Figures show totals from two vials for each kind of competition. Each vial started with 200 larvae of which 100 were taken from each of the two crosses shown in the table. The sign "w^x" means any of w^{co}, w^a, w^t, w

	Larvae from crosses shown below																			
	+/+ × + and +/+ × w^{co}				+/+ × + and +/+ × w^a				+/+ × + and +/+ × w^t				+/+ × + and +/+ × w				Total			
	Observed	Identified		%	Observed	Identified		%	Observed	Identified		%	Observed	Identified		%	Observed	Identified		
		+/+	+/w^{co}			+/+	+/w^a			+/+	+/w^t			+/+	+/w			+/+	+/w^x	
10 days 18 hours after beginning of mothers' oviposition	35	24	10	97	34	20	8	82	71	37	26	89	21	18	2	95	161	99	46	90
Total eclosion	160	75	75	94	149	70	61	88	181	78	78	86	176	84	77	91	666	307	291	90

TABLE 3

Experiment 1958:1

Total number of adults observed. Figures show totals from four vials per cross. Each vial started with 200 larvae. Autosomal homozygotes are a1/a1; *autosomal heterozygotes are from crosses* a1/a1 ♀♀ × a2/a2 ♂♂

	Larvae from X chromosome crosses shown below							
	+/+ × +		+/+ × w^{co}		+/+ × + w^a		+/+ × w	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Autosomal homozygotes	414	331	383	339	381	342	422	320
Autosomal heterozygotes	472	284	447	313	435	342	443	308

The results are of special interest as they show that in the present experiment the homozygous wild type females on an average reached eclosion earlier than the heterozygous ones; i.e. the homozygotes had a higher competing ability than the heterozygotes.

Experiments of the 1958 series

Experiment 1957:3 had indicated that homozygous wild type female larvae had a higher competing ability than heterozygous wild type female larvae. These results were, however, based on very little material and we decided, therefore, to take up this question for a more thorough investigation.

With the experiences gained from the 1957 series, we found several precautions desirable. These included *inter alia* (1) that all comparisons of competing wild type female larvae should be based on crosses producing males of only one kind, namely, wild type; (2) that temperature influences, as well as other environmental intervial influences, should be more thoroughly levelled out; and (3) that a new and still more careful procedure should be undertaken to make the strains coisogenic with regard to their X chromosomes.

Synthesis of strains: The strains were made coisogenic with regard to the long autosomes (chromosomes 2 and 3), in the conventional way, but this time we produced two different strains each of which was homozygous for chromosomes 2 and 3. These two strains will here be named *a1* and *a2*. The procedure of rendering the strains coisogenic with regard to their X chromosomes started now by isolating one single X chromosome from a wild type stock "Algeria" instead of, as in the 1957 series, from a stock of white. To simplify, we decided to drop w^t from our comparisons, which, therefore, came to include only four w alleles, *viz.* +, w^{co}, w^a, w. The synthesis is shown diagrammatically in chart II.

It should be mentioned that the simultaneous use of several eye color genes made it necessary to test the males of the different generations by crossing them to females homozygous for appropriate eye color genes. All such tests were performed. We had thus produced four X chromosomes containing respectively one of the four white alleles, +, w^{co}, w^a or w and which, at least with regard to the euchromatic region, were identical except for a segment ranging from a point between the loci of *pn* and w to a point between the loci of w and *ec*, i.e. for a segment, the maximal length of which is 4.7 map units. Each of these four X chromosomes were then combined, in one strain, with the autosomal set *a1*, and in a second strain, with the autosomal set *a2*. In all we had thus eight strains for use in the experiments.

Though we did not pay any special regard to the Y chromosome in the procedure of rendering the strains coisogenic, the Y chromosomes of all our final strains happened to have their origin from Y chromosomes in our stock of *pn*. This does not necessarily mean that the different strains got identical Y chromosomes, only that their origin was in a common stock which for many generations was mass propagated.

To chromosome 4 no regard was paid. The final strains might, therefore, have

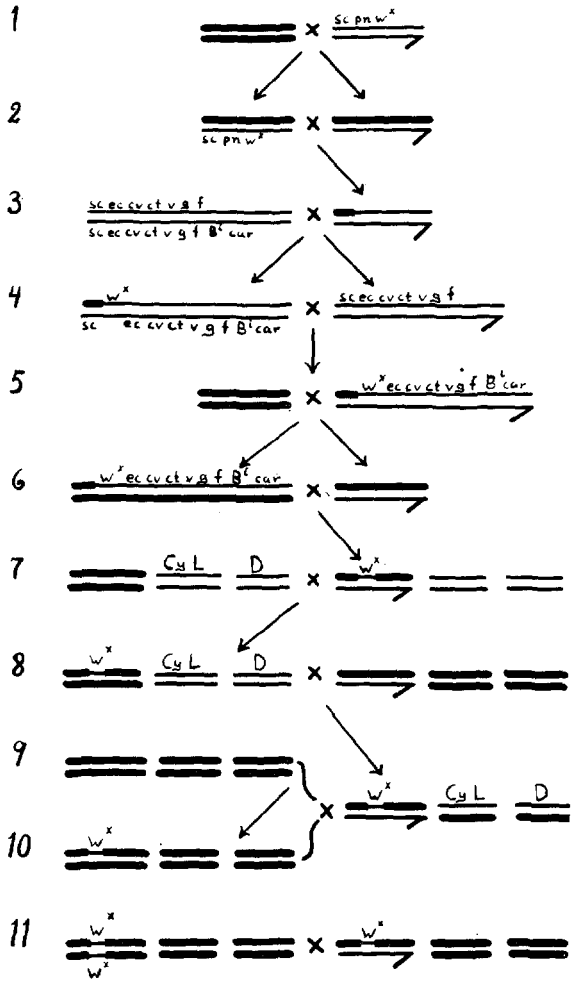


CHART II.—Synthesis of strains used in the 1958 series of experiments. Isolated chromosomes, with regard to which the strains were rendered isogenic, are drawn in heavy lines. The first six generations show the sex chromosomes only. Females were made homozygous for one wild type X chromosome (originating from a stock from Algeria) as indicated in generation 1. Other females were made homozygous for either the one or the other of two different sets of the long autosomes (containing wild type genes), as indicated in generation 8. These two sets are in the text named *a1* and *a2* respectively. The chart shows how the different *w* alleles (collectively named w^x) were combined with one of the autosomal sets. In this way each of the X chromosome were, in different strains, combined with either the set *a1* or the set *a2*. Apart from the sex-linked marker genes mentioned in the text to chart I the following were also used: *sc* (0.0), *pn* (0.8), *cv* (13.5), *g* (44.4), B^1 (57.0), *car* (62.5).

been homozygous or heterozygous for this chromosome; and they might also, *inter se*, have been coisogenic or not coisogenic.

Experimental technique: Not only from our experiences gained during the 1957 series of the present experiments but also from earlier studies (BONNIER and JONSSON 1957) we knew that larval growth rate is very sensitive even to small changes in temperature. As this rate possibly also is dependent on other environmental conditions we found it desirable to perform those experiments, the results of which were to be compared, simultaneously. But even with arrangements for a good temperature distribution, it is very difficult to get the variations between different vials to be due only to random causes. In the main experiments of the 1958 series, experiments 1958:1 and 1958:2, we proceeded, therefore, in the following way.

One of the ordinary rooms of the laboratory was equipped with thermo regulators for 25°C and fans circulated the air as evenly as possible. The whole of the development from oviposition to eclosion took place in this room. As will be described below, experiment 1958:1 included comparisons of larvae with four different X chromosomes and two different sets of autosomes. For each of the four X chromosomes, there were raised four cultures in vials containing food and freshly hatched larvae. These vials were put into two trays—one for each of the two autosomal compositions—and arranged within the trays in the way of a 4×4 latin square. The latin squares of the two trays were not identical but drawn at random from those described by FISHER and YATES (1949). Experiment 1958:2 included six X chromosomes, and two autosomal compositions. For each of the six X chromosomes there were raised six cultures in vials which were put into two trays—one for each of the two autosomal compositions—and arranged within the trays in the way of two 6×6 latin squares. It should be stressed that these arrangements in latin squares were not made with the purpose of partitioning the variances in the way such arrangements make possible. The reason was just to try to level out non random intervial environmental differences as much as possible.

After 16 hours of oviposition and a subsequent incubation in 25°C for 28 hours, freshly hatched larvae were transferred to the food in vials arranged in latin squares as just described where they remained undisturbed. From the beginning of eclosion the vials were emptied with four hour intervals, when the adults were counted. The earliest four hour period within which adults had emerged was that which ended 8 days, 14 hours after the beginning of the mothers' ovipositions. The vials were emptied and inspected with regard to eclosion in such four hour periods up to that which ended 12 days, 18 hours after beginning of oviposition. Thereafter the eclosions were checked at longer time intervals; only very few adults appeared in these late periods.

Symbols, diagrams and statistical treatments of the data: The symbols $+$, w^{co}, w^{a} and w refer to X chromosome constitutions and the symbols *a1* and *a2* to the autosomal sets. The maternal chromosomes are in the symbols placed on the left side, and the paternal chromosomes on the right side of the line. The symbol $+/w^{co}$

means, thus, a female the mother of which was wild type and the father of which was w^{co}; and the symbol *a1/a2* refers to flies which have inherited the autosomal set *a1* from their mother and the autosomal set *a2* from their father.

All diagrams are drawn on equal scales. The horizontal scale shows the numbers of days and hours which had elapsed from the beginning of the mothers' ovipositions to the emergence of the adults observed. The vertical scale shows averages referring either to the numbers of directly counted females or males, or —as in most cases all females were phenotypically wild type and hence indistinguishable *inter se*—to the number of females which could be identified with regard to their genotypes by progeny tests. The curves show the average number of adults which had emerged from the beginning of eclosion and up to the moment marked by the corresponding vertical lines (meridians); the points relating to two consecutive such moments are in the diagrams connected by straight lines.

In most of the diagrams a retardation in the rate of eclosion may be seen, e.g., in Figure 1 between 10 days, 2 hours and 10 days, 10 hours. This is due to the rhythm of eclosion: the emergence from the puparia is usually low during the early part of the night.

Comparisons of growth rates shown in Figure 17 are based on an analysis of variance of the usual kind. In all other cases the comparisons are based on t tests, in which the numbers of observed flies are used as variates and in which the number of variates is expressed by the number of vials. In noncompetition experiments the compared differences refer to differences between averages of variates from different vials; in competition experiments, the compared differences are differences of the numbers of the two competing types within the same vial.

The significance level, P, of the differences observed are, for each instance of observation, shown in the bottom of the diagrams by number of asterisks.

no asterisk	$P > 0.05$
one asterisk	$0.05 > P > 0.01$
two asterisks	$0.01 > P > 0.001$
three asterisks	$P < 0.001$

When the diagrams show the results for the two sexes separately the significance asterisks are also given separately for the two sexes or explained in the text to the figures.

A word of caution should be said with regard to biological evaluations and conclusions based on these tests. Competition ability and growth rate is a quantitative character, but when it is measured by *numbers* of flies, one is using a variate which can attain integral values only, i.e. a discontinuous variate. If the two types compared occur in different numbers, their difference cannot be smaller than one, and it is evident that such a difference has a relatively higher influence if the number of flies, or the difference between their numbers, is small than if it is large. This may, when the number mentioned is small, result in too small a difference between the averages compared; but it may also result in too small a sum of squares leading to too large a value of t with the consequence that the significance of a difference may be unduly overestimated. One should, therefore,

remember that in our tests (shown by asterisks in the figures) similar significance levels have, so to say, higher weights when the corresponding number of adults, or difference between their numbers, is large than when it is small.

Main experiments of the 1958 series

Experiment 1958:1: This experiment was a noncompetition experiment. With regard to the X chromosome four types were compared, *viz.* larvae from the following crosses $+/+ \times +$, $+/+ \times w^{co}$, $+/+ \times w^{a}$, $+/+ \times w$. Two hundred freshly hatched larvae from each of these crosses were transferred to each of four vials. All of the crosses were, with regard to the autosomes, made in two different ways: either, all parents were homozygous *a1/a1*, thus producing offspring, the whole of which also was homozygous *a1/a1*; or mothers were *a1/a1* and fathers *a2/a2*, thus producing offspring the whole of which was heterozygous *a1/a2*.

The final results after ceasing of eclosion are given in Table 3. Figures 1A, 1B, 1C show the averages—in the case of autosomal homozygosity *a1/a1*—of the numbers of adult females, which up to the times specified on the horizontal scale had reached eclosion. The solid lines are, in these three figures, identical, and refer to females which were homozygous +/+ in their X chromosomes. Figures 2A, 2B, 2C show the corresponding averages in the case of autosomal heterozygosity *a1/a2*.

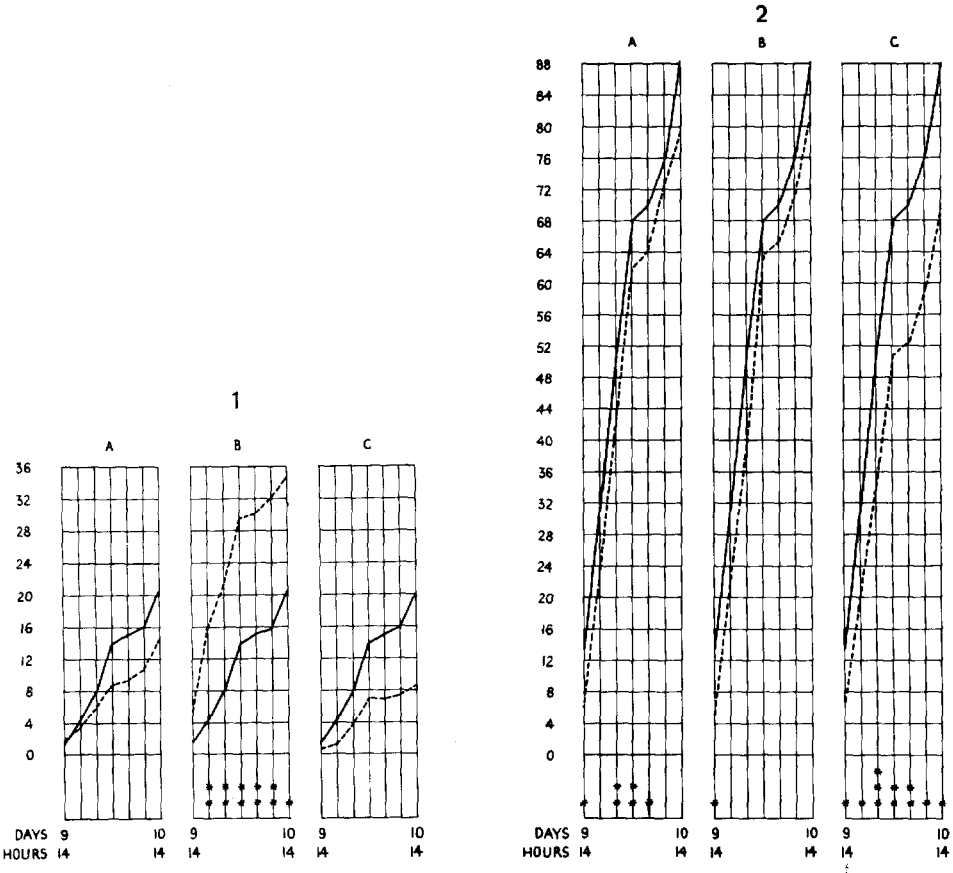
Experiment 1958:2: This experiment was a larval competition experiment. One hundred freshly hatched larvae from each of two crosses were transferred to a common vial. Six combinations of two by two crosses were made, which, with regard to the X chromosomes, were:

$+/+ \times +$ and $+/+ \times w^{co}$
$+/+ \times +$ and $+/+ \times w^{a}$
$+/+ \times +$ and $+/+ \times w$
$+/+ \times w^{co}$ and $+/+ \times w^{a}$
$+/+ \times w^{co}$ and $+/+ \times w$
$+/+ \times w^{a}$ and $+/+ \times w$

The total numbers of adults observed are given in Table 4.

For each of these six combinations six vials were started, and, as in experiment 1958:1, made in two different ways, corresponding to the two autosomal combinations. In one of these all parents of the crosses were autosomal homozygotes *a1/a1*, thus producing larvae which likewise were autosomal homozygotes *a1/a1*. In the second set all mothers were again autosomal homozygotes *a1/a1* but all fathers autosomal homozygotes *a2/a2*, thus producing larvae which were autosomal heterozygotes *a1/a2*.

As all mothers of the crosses in the present experiment were, with regard to the X chromosome, homozygous wild type, +/+, all offspring were also wild type. After eclosion the females were, in order to identify their X chromosome genotypes, individually progeny tested in vials, which were incubated at 25°C. If a female was a homozygote, +/+, she could produce only wild type sons but if she was a heterozygote, for instance $+/w^{co}$, she should produce two kinds of sons,



FIGURES 1 and 2.—Results from the noncompetition experiment 1958:1 with regard to early part of eclosion of females which were autosomal homozygotes *a1/a1* (Figure 1) and autosomal heterozygotes *a1/a2* (Figure 2). The solid lines are identical in A, B, and C and show eclosions of X chromosome homozygotes +/+. The broken lines show X chromosome heterozygotes: A, $+/w^{co}$; B, $+/w^{a}$; C, $+/w$. Each curve shows averages of four repeats. See also description in text.

wild type sons and w^{co} sons. In those comparisons where the purpose of the progeny test was to identify a female as being homozygous or as being heterozygous, the rule was followed that if, after 14 days of incubation, her male progeny consisted of only wild type males, she was classified as homozygous +/+, provided that the number of males was at least ten. In the few cases in which a female got only wild type sons and these were less than ten, she was excluded from those females which were recorded as "identified". This induces a small bias in favour of heterozygotes; a female producing, say six wild type sons and two w^{co} sons, could with certainty be identified as being a heterozygote $+/w^{co}$; whereas a female producing only eight sons all wild type was nonidentified. Such cases formed, however, a very small group and the bias is certainly of no importance.

TABLE 4

Experiment 1958:2

Total number of adults observed. Figures show totals from six vials per cross. Each vial started with 200 larvae of which 100 were taken from each of the two crosses shown in the table. Autosomal homozygotes are a1/a1; *autosomal heterozygotes are from crosses* a1/a1 ♀♀ × a2/a2 ♂♂. *All flies phenotypically wild type (except six nondisjunctional males not included in the table)*

	Larvae from X chromosome crosses shown below											
	+/+ × + and +/+ × w^{co}		+/+ × + and +/+ × w^{a}		+/+ × + and +/+ × w		+/+ × w^{co} and +/+ × w^{a}		+/+ × w^{co} and +/+ × w		+/+ × w^{a} and +/+ × w	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Autosomal homozygotes	581	573	548	547	600	487	553	522	555	541	522	544
Autosomal heterozygotes	676	467	691	458	668	471	624	524	649	498	672	470

TABLE 5

Experiment 1958:2

Identification of genotypes through progeny tests of individual females. The numbers of females which could be identified are in the table given as percents of the numbers of females actually observed. The stage, 10 days 14 hours from beginning of the mothers' ovipositions, correspond to the end stage of the curves in the diagrams, Figures 3 and 4

	Larvae from X chromosome crosses shown below						
	+/+ × + and +/+ × w^{co}	+/+ × + and +/+ × w^{a}	+/+ × + and +/+ × w	+/+ × w^{co} and +/+ × w^{a}	+/+ × w^{co} and +/+ × w	+/+ × w^{a} and +/+ × w	Total no. of females identified
Autosomal homozygotes: Up to 10 days, 14 hrs. from beginning of mothers' ovipositions	96	91	87	96	95	91	826
Total eclosion	72	78	70	75	67	77	2,457
Autosomal heterozygotes: Up to 10 days, 14 hrs. from beginning of mothers' ovipositions	90	96	94	97	95	95	2,525
Total eclosion	80	93	81	84	80	82	3,256

A rather large part of those females which reached eclosion within the period between 10 days, 18 hours and 11 days, 6 hours after beginning of oviposition died without any progeny for the progeny tests. This unfortunate fact, the reason of which is unknown, make comparisons rather worthless between the final numbers of the two competing types. Such comparisons are, however, still possible to make for females reaching eclosion not later than 10 days and 14 hours after beginning of oviposition, i.e. during periods which are of the greatest interest for the present

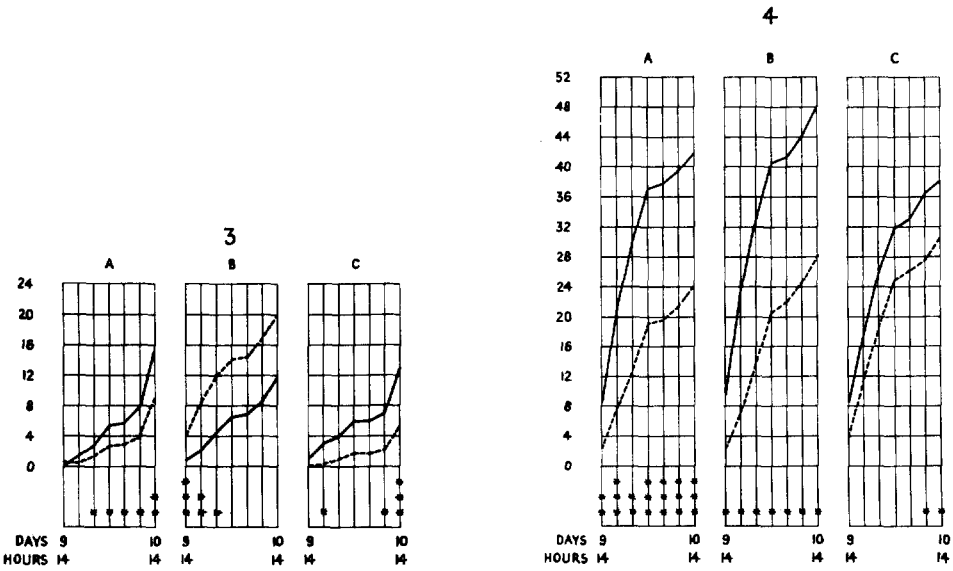
study. Table 4 shows the final results and Table 5 shows the percentages of females which could be identified through progeny tests. The numbers of (identified) females observed during the early part of eclosion are shown in the diagrams Figures 3, 4, 5, 6.

Additional experiments of the 1958 series

As may be seen from the diagrams Figures 1, 3, 5 there was in combination with autosomal homozygosity *a1/a1* a peculiar effect in descendants of w^a males. This "w^a effect", which was quite unforeseen, will be discussed later. It seemed, however, desirable to make some additional experiments to shed, if possible, more light on the causes underlying this effect.

In the 1957 series we had found a seriation of the rates of development of the pure strains *viz.* $+>w^{co}>w^a>w$. It was, hence, also of interest to try to find out if this seriation would hold with the strains used in the 1958 series, especially with regard to the w^a effect. It was, finally, of interest to repeat a part of experiment 1958:2, in the hope that we might identify through progeny tests that part of the wild type females which emerged as adults during the later stages of eclosion.

Experimental technique: Because of other works in our laboratory, these additional experiments could not be performed with all the precautions taken in the 1958:1 and 1958:2 experiments. The vials, standing in trays, were put into a

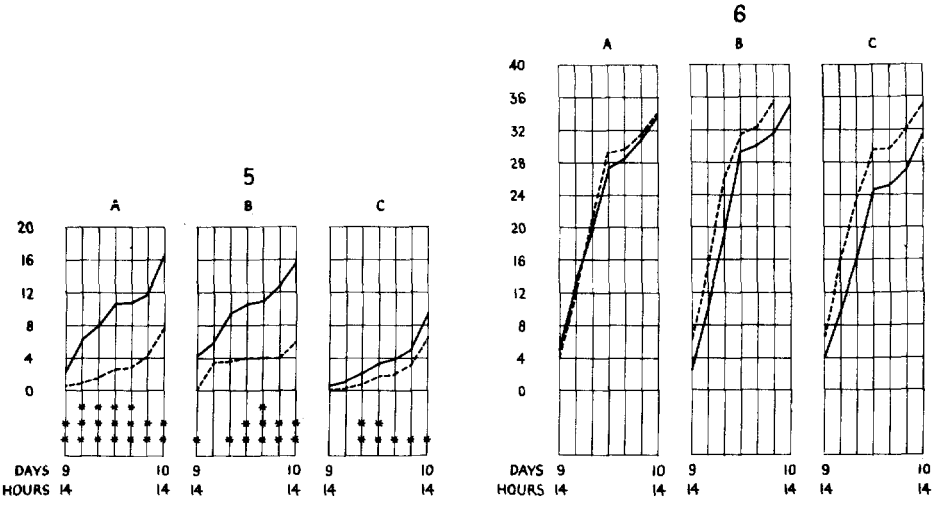


FIGURES 3 and 4.—Results from the competition experiment 1958:2, with regard to early part of eclosion of progeny tested females which were autosomal homozygotes *a1/a1* (Figure 3) and autosomal heterozygotes *a1/a2* (Figure 4). Concerning the X chromosomes the curves show: A, solid line $+/+$, broken line $+/w^{co}$; B, solid line $+/+$, broken line $+/w^a$, C, solid line $+/+$, broken line $+/w$. Each curve shows averages of six repeats. See also description in text.

small incubator at 25°C, and this incubator was not used for other simultaneous purposes. All of the experiments were made with three vials which were put rather randomly into the trays. The vials were emptied and the adults counted on a limited number of occasions. These experiments could not all be made simultaneously.

Experiment 1958:3: This was a competition experiment between pure X chromosome strains of autosomal homozygotes *a1/a1* as well as of autosomal heterozygotes *a1/a2*. The final results are given in Table 7 and the early part of the eclosions is shown on Figures 9 and 10.

Experiment 1958:4: This experiment was a competition experiment in which the females had to be identified through progeny tests as to their genotypes. It included three comparisons *viz.* between $+/+$ and $+/w^{co}$, $+/+$ and $+/w^{a}$, $+/+$ and $+/w$ and was made with autosomal homozygotes *a1/a1* as well as with autosomal heterozygotes *a1/a2*. It included also one comparison between $+/+$ and $+/w^{a}$, in which the autosomal homozygotes were *a2/a2* and the autosomal heterozygotes were *a2/a1*. As is shown in Table 6, a large proportion of the observed females could be identified from the whole of eclosion. The proportions between the total number of the two competing types are also in a good agreement with the expected 1:1 proportions. The probability of deviation, P, is in no case less than 0.2. As the purpose of this experiment was just to test the final proportions between competing types among identified females, only very few counts were made before eclosion had ceased. No counts were made between 9 days, 18 hours



FIGURES 5 and 6.—Results from the competition experiment 1958:2 with regard to early part of eclosion of progeny tested females which were autosomal homozygotes *a1/a1* (Figure 5), and autosomal heterozygotes *a1/a2* (Figure 6). Concerning the X chromosomes the curves show: A, solid line $+/w^{a}$, broken line $+/w^{co}$; B, solid line $+/w^{a}$, broken line $+/w$; C, solid line $+/w^{co}$, broken line $+/w$. Each curve shows averages of six repeats. See also description in text.

TABLE 6

Experiment 1958:4

Identification through progeny tests of individual females. Each vial started with 200 larvae of which 100 were taken from each of the two X chromosome crosses shown in the table. In all crosses except the rightmost one, autosomal homozygotes are a1/a1 *and autosomal heterozygotes from crosses* a1/a1 ♀ ♀ × a2/a2 ♂ ♂. *In the rightmost cross autosomal homozygotes are* a2/a2 *and autosomal heterozygotes from crosses* a2/a2 ♀ ♀ × a1/a1 ♂ ♂. *Figures show totals from three vials per cross.*

		Larvae from X chromosome crosses shown below							
		+/+ × + and +/+ × w^{co} +/+		+/+ × + and +/+ × w^a +/+		+/+ × + and +/+ × w +/+		+/+ × + and +/+ × w^a +/+	
			+/w^{co}		+/w^a		+/w		+/w^a
Autosomal homozygotes	Total identified females	143	139	114	105	116	117	160	143
	Numbers of identified females as percents of actually observed females:								
	10 days, 18 hours after beginning of mothers' ovipositions	98		99		97		98	
	end of eclosion	97		91		93		98	
Autosomal heterozygotes	Total identified females	153	150	145	139	159	162	141	124
	Numbers of identified females as percents of actually observed females:								
	10 days, 18 hours after beginning of mothers' ovipositions	95		98		99		98	
	end of eclosion	94		96		98		97	

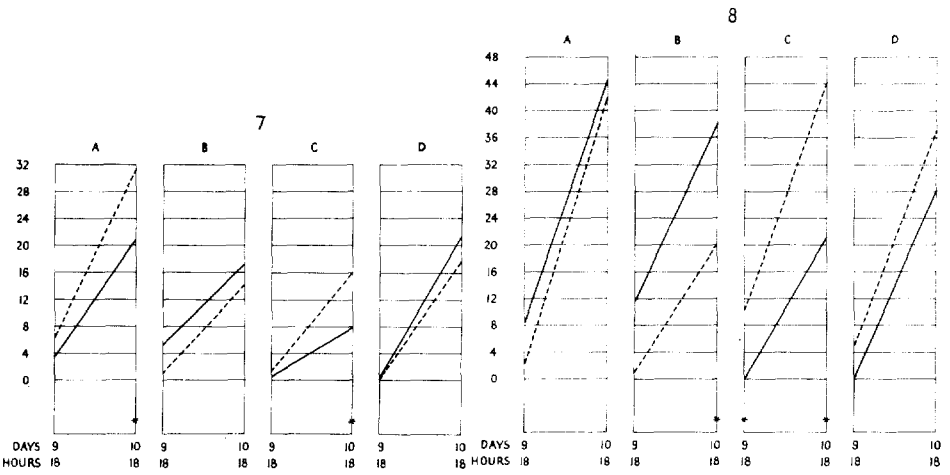
and 10 days, 18 hours after beginning of the mothers' ovipositions; each of the corresponding diagrams, Figures 7 and 8, has thus only two points connected by straight lines.

Experiment 1958:5: This experiment was a noncompetition experiment including X chromosome wild type homozygotes and different wild type heterozygotes. Autosomal homozygotes and heterozygotes were, in this case, *a2/a2* and *a2/a1* respectively. The results are given in Table 9 and Figures 13 and 14.

Experiment 1958:6: This was a competition experiment between pure X chromosome strains. The autosomal homozygotes were *a2/a2* and the autosomal heterozygotes *a2/a1*. The results are given in Table 8 and Figures 11 and 12.

DISCUSSION

The w^a *effect:* From experiments on larval competition between pure strains of the 1957 series (experiment 1957:1, Table 1) it could be shown, that the absolute growth rate of a certain strain depends, apart from environmental conditions, not



FIGURES 7 and 8.—Results from the competition experiment 1958:4 with regard to early part of eclosion of progeny tested females which were autosomal homozygotes *a1/a1* in A, B, and C, and autosomal homozygotes *a2/a2* in D (Figure 7) and autosomal heterozygotes *a1/a2* in A, B, C and autosomal heterozygotes *a2/a1* in D (Figure 8); Concerning the X chromosomes the lines show: A, solid line +/+, broken line $+/w^{co}$; B, solid line +/+, broken line $+/w^{a}$; C, solid line +/+, broken line $+/w$; D, solid line +/+, broken line $+/w^{a}$. Each curve shows averages of three repeats. See also description in text.

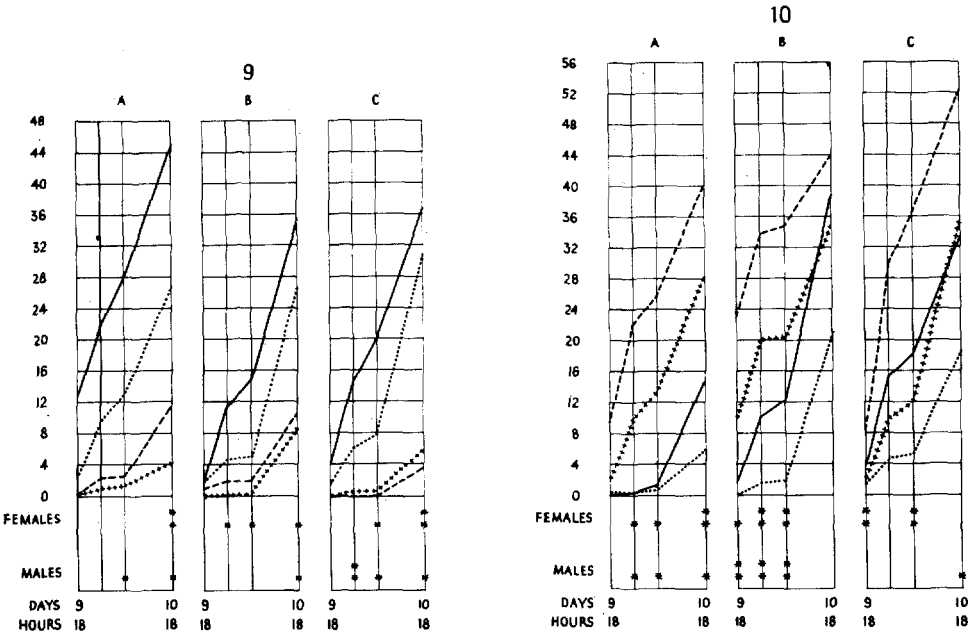
TABLE 7

Experiment 1958:3

Total number of adults observed. Figures show totals from three vials per competition. Each vial started with 200 larvae of which 100 were taken from each of the two strains shown in the table. Autosomal homozygotes are a1/a1, *autosomal heterozygotes are from crosses* a1/a1 ♀♀ × a2/a2 ♂♂

	Larvae from X chromosome strains shown below											
	w^a and +		+		w^a and w^{co}		w^{co}		w^a and w		w	
	♀♀	w^a ♂♂	♀♀	♂♂	♀♀	w^a ♂♂	♀♀	♂♂	♀♀	w^a ♂♂	♀♀	♂♂
Autosomal homozygotes	159	125	128	108	141	145	141	133	148	141	139	130
Autosomal heterozygotes	160	125	154	125	163	124	140	114	115	90	166	115

only on the genotype of the strain itself, but also on the genotypes of those individuals with which the individuals of the strain have to compete. A similar situation occurs also in other organisms, e.g. barley (HAGBERG, personal communication). From the point of view of larval competition ability, the 1957 strains showed a seriation which seemed to follow the degree of deviation of the eye color of the adults from wild type eye color $+ > w^{co} > w^{a} > w^{t} > w$. The strains of the 1958 series did not show this seriation, but this was to a certain extent due to what we have named the "w^a effect".



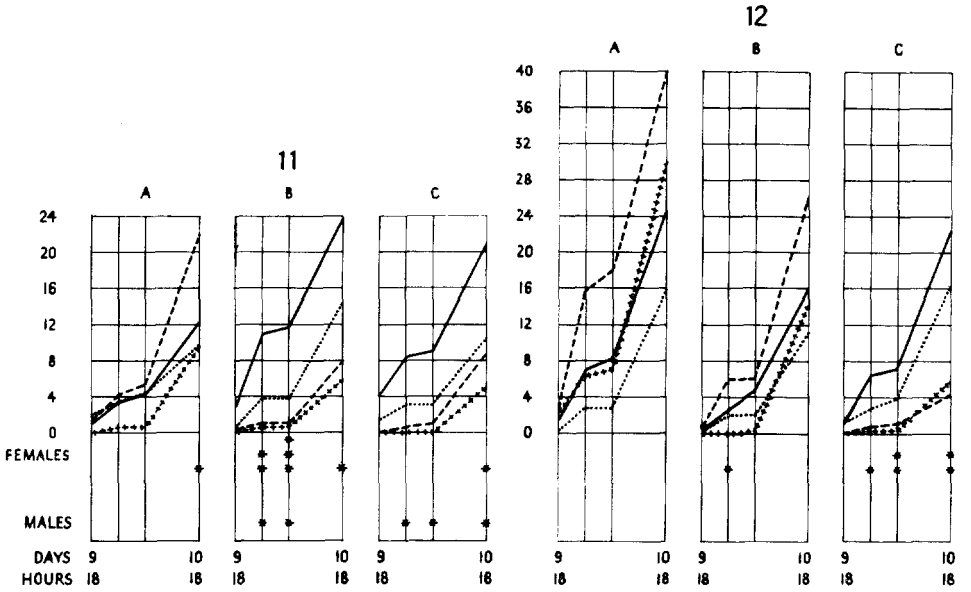
FIGURES 9 and 10.—Results from the competition experiment 1958:3 between pure strains with regard to early part of eclosion of flies which were autosomal homozygotes *a1/a1* (Figure 9) and autosomal heterozygotes *a1/a2* (Figure 10). Concerning the X chromosomes the curves show: A, solid line w^a females, broken line, wild type females, dotted line w^a males, cross-marked line wild type males; B, solid line w^a females, broken line w^{co} females, dotted line w^a males, cross-marked line w^{co} males; C, solid line w^a females, broken line w females, dotted line w^a males, cross-marked line w males. Each curve shows averages of three repeats. See also description in text.

TABLE 8

Experiment 1958:6

Total number of adults observed. Figures show totals from three vials per competition. Each vial started with 200 larvae of which 100 were taken from each of the two X chromosome strains shown in the table. Autosomal homozygotes are a2/a2; *autosomal heterozygotes are from crosses* a2/a2 ♀ ♀ × a1/a1 ♂ ♂

	Larvae from X chromosome strains shown below											
	w^a and +				w^a and w^{co}				w^a and w			
	w^a		+		w^a		w^{co}		w^a		w	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Autosomal homozygotes	133	98	148	117	138	102	152	119	131	99	159	115
Autosomal heterozygotes	118	124	142	142	108	122	149	131	129	105	160	120



FIGURES 11 and 12.—Results from the competition experiment 1958:6 between pure strains with regard to early part of eclosion of flies which were autosomal homozygotes *a2/a2* (Figure 11) and autosomal heterozygotes *a2/a1* (Figure 12). Concerning the X chromosomes the curves show: A, solid line w^a females, broken line wild type females, dotted line w^a males, cross-marked line wild type males; B, solid line w^a females, broken line w^{co} females, dotted line w^a males, cross-marked line w^{co} males; C, solid line w^a females, broken line w females, dotted line w^a males, cross-marked line w males. Each curve shows averages of three repeats. The asterisks in Figure 12 refer to females. See also description in text.

TABLE 9

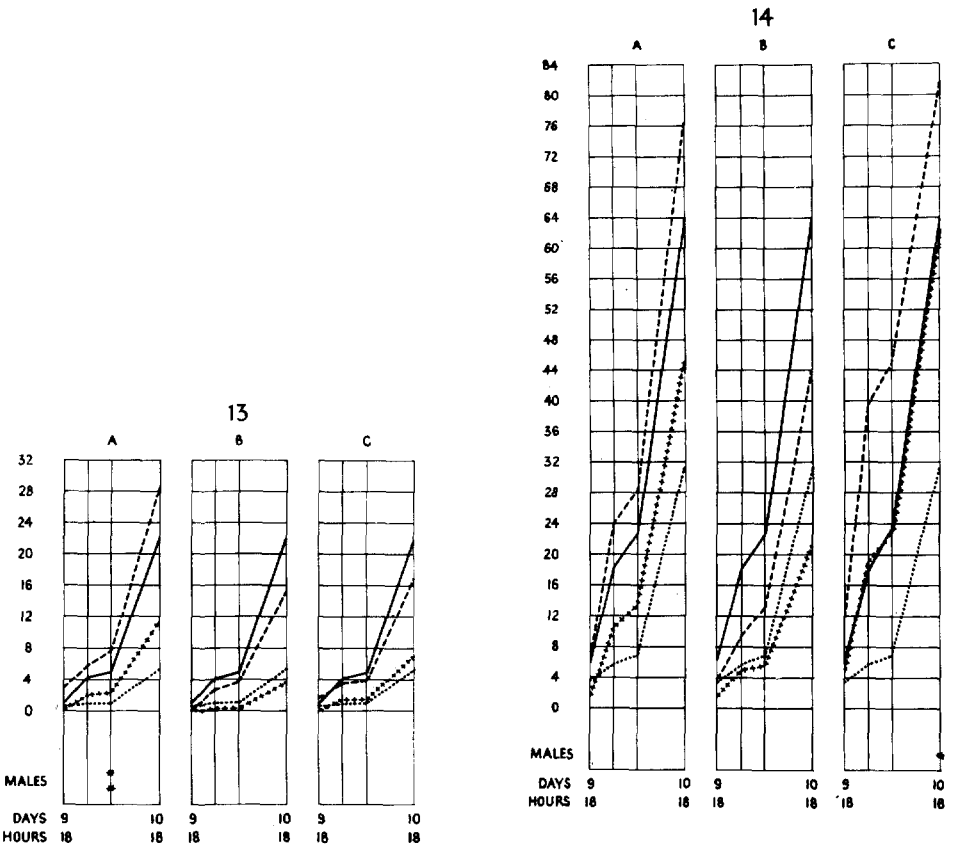
Experiment 1958:5

Total number of adults observed. Figures show totals from three vials with 200 larvae. Autosomal homozygotes are a2/a2; *autosomal heterozygotes are from crosses* a2/a2 ♀♀ × a1/a1 ♂♂

	Larvae from X chromosome crosses shown below							
	+/+ × +		+/+ × w^{co}		+/+ × w^a		+/+ × w	
	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂
Autosomal homozygotes	313	234	309	234	313	253	313	235
Autosomal heterozygotes	311	240	307	269	305	244	305	261

As the chief purpose of the experiments 1958:1 and 1958:2 was to compare the growth rates of females of different genotypes, these experiments were designed so as to always produce males of equal genotypical constitutions. This was done by always using X chromosome homozygous wild type females as mothers to the larvae, the growth rates of which were to be compared. By doing so all sons of these mothers were also wild type, and the sons were, hence, expected to be geno-

typically identical. However, very soon after the beginning of eclosion in experiment 1958:1, it was found that in the case of autosomal homozygosity, *a1/a1*, wild type males with w^a fathers grew at a higher rate than wild type males with fathers being +, w^{co} or w (Figure 15). At first it was believed that this was due to the Y chromosome: if so, we had, in the *a1/a1* strain of w^a, unintentionally isolated a special kind of Y chromosome. But we soon found that in the same experiment a corresponding thing also happened with the females: among the autosomal homozygotes, *a1/a1*, those females which, with regard to their X chromo-

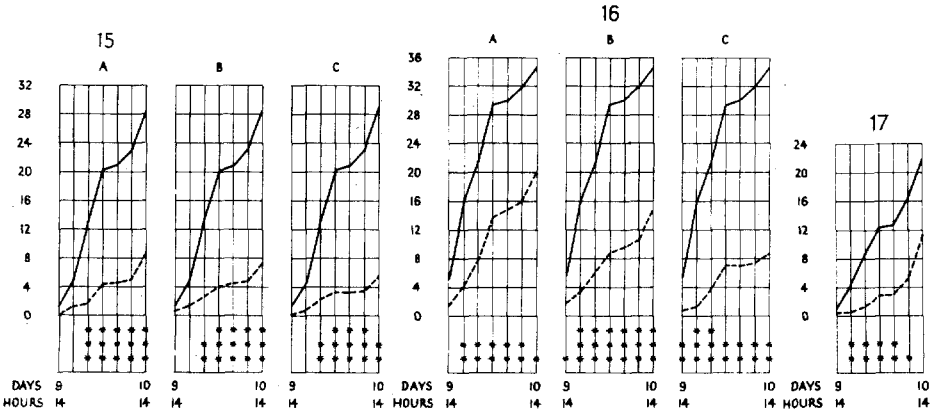


FIGURES 13 and 14.—Results from the noncompetition experiment 1958:5 with regard to early part of eclosion of flies which were autosomal homozygotes *a2/a2* (Figure 13) and autosomal heterozygotes *a2/a1* (Figure 14). Concerning the X chromosomes the curves show: A, solid line +/+ females, broken line $+/w^{co}$ females, dotted line wild type males from wild type fathers, cross-marked line wild type males from w^{co} fathers; B, solid line +/+ females, broken line $+/w^a$ females, dotted line wild type males from wild type fathers, cross-marked line wild type males from w^a fathers; C, solid line +/+ females, broken line $+/w$ females, dotted line wild type males from wild type fathers, cross-marked line wild type males from w fathers. Each curve shows averages of three repeats. See also description in text.

somes, were $+/w^a$, grew at a higher rate than any of $+/+$, $+/w^{co}$, or $+/w$ females (Figure 16).

When the identifications of the genotypes of the females in experiment 1958:2 were ready it was also found that *a1/a1* females which in their X chromosomes were $+/w^a$ grew at a higher speed in competition with any of the other types tested i.e. with any of $+/+$, $+/w^{co}$ or $+/w$ (Figures 3B, 5A, 5B). The wild type sons produced in experiment 1958:2 were always a mixture from fathers of two different kinds. Corresponding to the daughters shown in Figures 3 and 5 the fathers included w^a males in Figures 3B, 5A, and 5B but did not include w^a males in Figures 3A, 3C and 5C. The curves in Figure 17 show now the averages of the pooled number of males corresponding to these two groups of crosses respectively. As may be seen, here also male descendants of fathers including w^a males grew faster than descendants whose fathers did not include w^a males.

We have thus in experiments 1958:1 and 1958:2 found that, in combination with autosomal homozygosity *a1/a1* all descendants (female and male) of w^a males grew faster than descendants of $+$, w^{co} or w males. The w^a effect can consequently neither be believed to be located in the X, nor in the Y chromosome. As



FIGURES 15 and 16.—Results from the noncompetition experiment 1958:1 with regard to early part of eclosion of flies which were autosomal homozygotes *a1/a1*, Figure 15 males and Figure 16 females. The solid lines are in A, B, and C identical and show progeny from the X chromosome cross $+/+ \times w^a$; the broken lines show progenies from X chromosome crosses: A, $+/+ \times +$; B, $+/+ \times w^{co}$; C $+/+ \times w$. The curves of Figure 16 are the same as those shown in Figure 1, but arranged differently, so as to make other comparisons easier. Each curve shows averages of four repeats. See also description in text.

FIGURE 17.—Results from the competition experiment 1958:2 with regard to early part of eclosion of males which were autosomal homozygotes *a1/a1*. The solid line shows the pooled average number of males from three competitions, which, with regard to females, are shown in Figures 3 B, 5 A, 5 B, *viz.* progenies of $+/+ \times +$ and $+/+ \times w^a$; $+/+ \times w^{co}$ and $+/+ \times w^a$; $+/+ \times w$ and $+/+ \times w^a$. The broken line shows the pooled average number of males which, with regard to females, are shown in Figures 3A, 3C, 5C, *viz.* progenies of $+/+ \times +$ and $+/+ \times w^{co}$; $+/+ \times +$ and $+/+ \times w$; $+/+ \times w^{co}$ and $+/+ \times w$.

may be seen from Figures 2, 4, 6 no w^a effect was found in case of autosomal heterozygosity *a1/a2*. This also rules out the possibility of cytoplasmic inheritance as the cause of the w^a effect.

In the additional experiments with pure strains the w^a larvae of both sexes, which were autosomal homozygotes *a1/a1*, grew faster than other *a1/a1* larvae (experiment 3 Figure 9). But in the additional experiment with progeny testing of the females the X chromosome wild type homozygotes which were *a1/a1* grew at a higher rate than the $+/w^a$ females (experiment 4, Figure 7B); the difference was, however, of no statistical significance.

As mentioned earlier we have, in the synthesis of the strains, paid no attention to chromosome 4. It is thinkable that, by chance, one or several of the strains were rendered homozygous for chromosome 4 as well. Suppose now that that strain which was homozygous for the autosomal set *a1* and in its X chromosome contained the gene w^a, also was homozygous for a 4th chromosome dominant *A*, the effect of which was to accelerate larval growth rate. In such a case the progeny from all crosses within the *a1* strains—i.e., producing *a1/a1* homozygotes—in which the male parents were w^a, would carry the gene *A*, whereas the progeny from other kinds of males would not carry *A*. The hypothetical gene *A* would thus explain the results from experiments 1958:1 and 1958:2. A consequence of the existence of such a gene, *A*, would be that if the mothers were *a2/a2* a w^a effect would show up among the larvae, only if the fathers were *a1/a1* but not if they were *a2/a2*. The results from the additional experiments, however, do not speak in favour of the existence of such a dominant gene *A*, as may be seen from Figures 8D, 11B, 11C, 12A, 12B, 13, 14. But as we believe that the general background of growth rate is to be found in a great number of polygenes one must expect that the interaction between a major gene *A* and the polygenes is of a very complicated nature. As the purpose of making the present studies was of a quite different kind we did not find it worth while to inquire more into the causes of the w^a effect. We may thus content ourselves by saying that the w^a effect perhaps is due to a dominant gene in chromosome 4, but that we have not been able to prove that this is the case.

The main problem: Viability expresses itself, and may be measured, in a number of different ways. Likewise, selection acts on several different characters, and may exert its influence during many different stages of an animal's development. In most animals such characters as fertility and fecundity are of a high selectional importance. The same is the case with abilities for search for food in quantities enough for maintenance and growth. Most of that part of the food which is used for growth in holometabolic insects is consumed during the larval period. Now, it is known, that larval growth rate in Drosophila is to a large extent genetically determined (DOBZHANSKY, HOLZ and SPASSKY 1942; BONNIER and JONSSON 1957; MARIEN 1958). That this rate, besides external influences, must be strongly related to larval competition abilities seems, moreover, evident. We think, hence, that when we use larval growth rate and larval competition ability—measured

by the time which elapses from the mother's oviposition to the moment her offspring reaches eclosion—we have chosen a character which from the point of view of viability and selection is of a very high importance.

When, in the 1957 series, wild type homozygous females +/+ were crossed to +, w^{co}, w^a, w^t, or w males and thus made competitions possible between wild type homozygous female larvae +/+ and any of the wild type heterozygous larvae viz., $+/w^{co}$, $+/w^a$, $+/w^t$, or $+/w$ (in which cases the competing male larvae always were wild type) it was in all cases found that the homozygous female larvae grew at a higher rate than the heterozygous ones. These experiments (experiment 1957:3, Table 2) were, however, made on a very small scale. The chief reason for starting the 1958 series of the present study was the hope, thereby, to get some more knowledge of the influence of homozygosity and heterozygosity on the rate of larval development.

We have now results permitting two kinds of comparisons *viz.*, on the one hand, the effect of autosomal homozygosity and heterozygosity on the growth rate of larvae of both sexes; and, on the other hand, the effect on female larvae of homozygosity and heterozygosity in the X chromosome.

Autosomal homozygosity and heterozygosity: The difference in growth rate between autosomal homozygotes and autosomal heterozygotes is in most cases of the present study very conspicuous and does not make any statistical treatment necessary. Autosomal homozygotes *a1/a1* and heterozygotes *a1/a2* may be compared on several of the diagrams: Figure 1 versus Figure 2, Figure 3 versus Figure 4, Figure 5 versus Figure 6, Figure 7A, B, C, versus Figure 8A, B, C. The differences between the curves of the pure strains Figure 9 versus Figure 10 may seem less obvious, but if one disregards the w^a effect and only compares the curves relating to the non w^a larvae the difference is again found to be very conspicuous. Comparisons between *a2/a2* homozygotes and *a2/a1* heterozygotes may be made on diagrams, Figure 7D versus Figure 8D, Figure 13 versus Figure 14. The differences between the curves of the pure strains Figures 11 and 12 are less obvious, but if one again only compares the non w^a larvae one will find a higher growth rate in Figure 12A, B, than in Figure 11A, B. Only with regard to the w larvae one does not find a higher growth rate of the heterozygotes *a2/a1* than of the homozygotes *a2/a2* (Figures 11C and 12C).

We thus have in the great majority of our experiments found a higher viability —expressed as a higher larval growth rate—among autosomal heterozygotes than among autosomal homozygotes. Now, the synthesis of our homozygous strains has most probably also included the homozygotization of one or more detrimental genes. From this point of view one could perhaps formulate the results by saying that it is not heterozygosity which enhances viability but homozygosity with regard to detrimentals which reduces viability. If the low viability of the homozygotes were due to detrimentals, the much higher viability of the heterozygotes shows that the dominance effect, if any, of these detrimentals must be supposed to be of a small magnitude. At any rate, such homozygotes as our *a1/a1* or *a2/a2* individuals are most certainly, so to say, unnatural creatures, and we think that

our results rather strongly indicate that selection must, in *D. melanogaster*, favour autosomal heterozygotes.

Sex-linked homozygosity and heterozygosity: With regard to our comparisons between X chromosome homozygotes and heterozygotes the results point more or less in the opposite direction when compared to autosomal homozygotes and heterozygotes. The differences are, however, never as conspicuous in the former comparisons as in the latter.

When looking at the diagrams with the aim of comparing X chromosome homozygotes and heterozygotes, one must disregard the w^a effect. One finds then, in the main experiments 1958:1 and 1958:2, that in combination with autosomal heterozygosity *a1/a2*, the wild type homozygous female larvae grew at a higher rate than any of the heterozygotes $+/w^{co}$, $+/w^a$, or $+/w$ (Figures 2 and 4) and that the differences were of a more or less good statistical significance. Also in the case of autosomal homozygosity *a1/a1* the wild type homozygotes were found to grow faster than the heterozygotes $+/w^{co}$ and $+/w$, though without statistical significance in experiment 1958:1 (Figure 1A, C) but with some significance in experiment 1958:2 (Figure 3A, C).

From the point of view of X chromosome homozygosity and heterozygosity the results of the additional experiments were rather erratic, as may be judged directly from Figures 7, 8, 13, 14. As mentioned in the description of the experimental technique of these experiments, they could not be performed with all the precautions taken in the 1958:1 and 1958:2 experiments. Non random environmental influences on larval growth rate which probably never can be wholly avoided may, therefore, be believed to have been more influential in the additional experiments than in the main experiments.

We find it valid to lay more emphasis on the results of the main experiments than on the additional experiments, and it seems, hence, safe to conclude that female larvae which in their X chromosomes are homozygous for a wild type allele and of the same general constitution as our homozygotes, usually, but not always, have a higher viability than those which are X chromosome heterozygotes. As the higher viability of the X chromosome homozygotes in the 1958:1 and 1958:2 experiments was somewhat more marked in combination with autosomal heterozygosity (Figure 2 versus Figure 1 and Figure 4 versus Figure 3) one may suppose that it is easier for the viability promoting nature of X chromosome homozygosity to be expressed if it has the background of the viability enhancing effect of autosomal heterozygosity than if it lacks this background.

When using the results of the present studies in order to try to evaluate the importance of heterozygosity versus homozygosity and to compare the effects of sex-linked genes with autosomal genes, one must remember that the part of the X chromosome which in our experiments was heterozygous was confined to a section of a maximal length of 4.7 map units while the autosomal heterozygosity included the total length of the two long autosomes. If an individual is heterozygous in one single locus and if this individual from some point of view is more viable or more luxuriant or, in general, has to be placed further away on the plus

side of the scale than any of the two homozygotes, one speaks of overdominance. Now, the X chromosomes of our strains could, of course, not be synthesized in such a way as to make the heterozygous part of the heterozygotes be confined to one single locus. But if there really was overdominance for some of the heterozygotes in the *w* locus, then it seems to be evident that also the wild type heterozygotes of the actual constitution as they are in our experiments, should show a higher viability than the wild type homozygotes. As this was not the case we must conclude that our results—as far as they go—do not indicate any kind of overdominance in the *w* locus. As is well-known, several investigations have been made on heterosis in maize. Quite recently JONES (1957) compared plant heights in lines which were either homozygous or heterozygous for two specified loci, but he found no sign of overdominance.

In our experiment 1957:1, Table 1, it was found that the recessive strains w^{co}, w^a, w^t and *w* had a lower viability than the wild type strain. In combination with autosomal heterozygosity a corresponding result was found with regard to w^a (the only recessive tested from this point of view in the 1958 series) in experiments 1958:3 (Figure 10A) and 1958:6 (Figure 12A). MULLER has on several occasions expressed the opinion that most recessives of a low viability show dominance effects, in the sense that their heterozygotes with wild type alleles show a lower viability than wild type homozygotes. From this point of view our results with the *w* alleles fit moderately well with MULLER's opinion. He also pointed out (1956) that "the exceptional cases of the heterozygote being superior are probably represented for the most part . . . by adaptations that have not yet stood the test of geological time". With regard to such special cases as those studied by us it seems also, in accordance with MULLER's views, probable that when such genes as the recessives of the *w* allelic series are found in nature, they are the result of recent mutations.

Concerning the results of the present investigation one may in this connection make the following three points: (1) There is in Drosophila, an important difference in the possibilities for selection to act upon, on the one hand, sex-linked, and, on the other hand, autosomal genes. In wild populations, as well as in mass propagated stock bottles, natural selection must, via the hemizygous males, strongly act in the direction to remove X chromosomes with detrimental genes. Such an action would be counterbalanced only if females heterozygous for the detrimentals had a much higher fecundity than the nondetrimental homozygotes. An action of natural selection against autosomal detrimentals may also be at work but certainly much more indirectly and at a much lower pace. (2) The genes, used in our experiments, besides being visibles in homozygous conditions, were all recessives, and it is not known what the results would have been if our heterozygotes had been heterozygous for different wild type alleles. (3) Our heterozygotes were, in the X chromosomes, heterozygous for very short chromosome sections, but in the autosomes heterozygous for the whole of these chromosomes, i.e. for very long chromosome sections. Now, it does not seem wholly unreasonable to imagine that —even if heterozygotes for one wild type and one recessive gene are less viable

than the wild type homozygotes, when the loci are studied separately—the heterozygosity *per se* would increase the viability of the heterozygotes above that of the wild type homozygotes if one studies several loci simultaneously, i.e. if one studies chromosome sections of a moderate length. It is our intention to try to elucidate these points somewhat more in a new set of experiments.

In this connection the following remark may be made. It is commonplace to emphasize that the different genes of the genome cooperate during development, or to stress that the effects of a certain gene pair depend upon the whole genetic background. A comparison of the curves in Figures 1 and 2, 3 and 4, 5 and 6 give as it seems to us, an unusually strong impression of this fact: the same sex-linked genes have very different effects when associated with the one or the other of the autosomal gene combinations. In genetic class work, when one, for instance, has to demonstrate MENDEL's law of segregation, it is necessary to speak in terms of single genes. Also, when one is studying such difficult problems as mutation frequencies or the mutational process itself, it may be necessary to concentrate the observations on circumstances within single genes or gene pairs. A lot of other examples could easily be given in which it is obviously legitimate to base the discussion on the happenings within single gene pairs. The situation may, however, be different in other cases. In the mathematical treatment of population genetics, one may solve the equations only if he confines and states the problems in terms of single gene pairs. However, we think that it is necessary to be very cautious when discussing or making experiments within the field of experimental population genetics: to confine the discussion to single gene pairs may be a gross simplification of the actual situation; a simplification which easily may lead to quite erroneous conclusions.

There is one more point which we have not mentioned. As may be seen from several of the tables the total number of females in the progeny from crosses between *a1/a1* females and *a2/a2* males was significantly more than 50 percent of the total number of larvae collected. We are trying to investigate this problem somewhat more.

SUMMARY

1. The material for the present study consists of a number of strains which, with regard to the X chromosomes, were made identical except for a short region including the white locus, in which they contained different *w* alleles. These X chromosomes were combined with the one or the other of two different wild type sets of the two long autosomes.

2. In all experiments 200 freshly hatched larvae were put into each of a number of food containing vials. Most of the experiments were performed as larval competition experiments, in which 100 larvae from two different sources competed with each other. Eclosion was checked at several instances before it ceased, and so the relative speed with which the competing types reached eclosion could be followed.

3. The results showed, *inter alia*, that larvae which were heterozygous with regard to the autosomal sets usually grew conspicuously faster than those which

were homozygous with regard to the autosomes. Female larvae which were wild type homozygous with regard to the X chromosomes usually grew faster and had a higher competing ability than those which, in the *w* locus containing segment, were heterozygous for one wild type and one nonwild type *w* allele. Thus, no signs of overdominance were found when a wild type allele was combined in a heterozygote with a recessive *w* allele.

4. In the earlier part of the experiments the competing ability of larvae of the pure strains indicated a seriation following the degree of deviation from normality expressed as deviation in eye color from the wild type red color.

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