# GENETIC ANALYSIS OF SOME INBRED LINES OF *Drosophila melanogaster*

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THESIS
Submitted to the Agra University, Agra
in partial fulfilment of the requirements for the Degree of
MASTER OF VETERINARY SCIENCE
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May 6th, 1968.

# CERTIFICATE

Certified that the research work embodied in this thesis entitled "Genetic analysis of some inbred lines of *Drosophila melanogaster*" is an authentic original work carried out by the candidate Shri P. Rama Krishna Reddy, in this Division, under my supervision and guidance.

Prabhu S.S

( S.S. PRABHU )

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# INTRODUCTION

The animal breeders are mainly concerned in breeding for economic traits like milk, meat, eggs, wool etc. which show continuous variation. Their ultimate aim is to bring about improvement in these characters by selection spread over a short period as possible. In practice, however, due to longer generation interval, large animal breeding is a time consuming and at times a very frustrating vocation. Animal Breeder therefore is on the look out for short cut methods that can bring him to the desired goal in a shorter period and with a greater chance of success than at present.

Modern practices in animal breeding are based on the concepts of population genetics derived from the theoretical investigations of Fisher, Wright, Haldane, and others and their practical application by Lush and his associates. Over the last two decades or so genetical investigations with _Drosophila_ has provided a great deal of factual evidence for theoretical concepts of quantitative inheritance which had a direct bearing on schemes of livestock improvement. The problems posed by a population of _Drosophila_ are essentially the same as those of any other population of biological units. The investigations in _Drosophila_ _melanogaster_ are advantageous because of it's shorter generation interval, low chromosome number, absence of crossing-over in males, availability of marked, multiple inversion stocks for chromosomal manipulations and the existence of thorough information on biology and genetics of this fly which enables conclusions drawn in quantitative studies to be put to rigorous tests both genetically and cytologically. A clear understanding of the properties of genetic variation helps in better interpretation of the effects of selection and problems of stability of adaptive characters, heterosis and inbreeding decline. Drosophila offers facilities to take the challenge of genetic analysis as deep as possible and enable alternative interpretations to be systematically tested with least expenditure of time and money.

The response to selection in which the breeder is mostly interested depends on the nature of selection pressure employed and genetical architecture of the character. These in turn, depend upon the detailed organisation of the system of genes controlling the variation in the expression of the quantitative character. Though our knowledge of the organisation and properties of polygenic systems is limited, chromosomal assay technique developed and extensively used by Muller (1927) and Mather and Harrison (1944) and elaborated by Robertson and Reeve (1953) for genetic analysis of inbred lines of quantitative characters exposed the nature of polygenic organisation on different chromosomes and the presence of inter and intra chromosomal interactions. Mather and Wigan (1949) assayed the different selection lines to study the gene distribution with regard to bristle number and Robertson (1953) for wing size in Drosophila melanogaster but no attempt has been made to study the polygenic organisation of the important characters of fitness such as egg production, hatchability etc. This has been attempted in the present study. The material used was the 4 inbred lines - 2 High and 2 Low developed in the Drosophila Laboratory of the Animal Genetics Division through family selection.

# REVIEW OF LITERATURE

The first work on inbred lines in Drosophila was started by Castle and Coworkers (1906), who inbred Drosophila melanogaster for 59 generations by full-sib mating. They observed slight inbreeding depression in productivity provided selection was carried through by using flies from more productive families. There was no adverse effect on fertility, which was rather increased in crosses between inbred lines. They noticed slight reduction in fly size, and appearance of more sterile flies in early generations than in late ones. These findings were confirmed by Moenkhaus (1911), Wentworth (1913) and Hyde (1914).

Charles and Smith (1939) presented the hypothesis of multiplicative and geometric gene action, instead of simple arithmetic gene effects without dominance and interaction, in the crosses involving quantitative characters.

Wright (1939) discussed the effects of inbreeding and selection and suggested the development of improved strains by successful crosses between strains.

Mather (1942) presented the theory of polygenic concept and balance of polygenic combinations. According to him, recombination was the means by which the hidden genetic variation was released for play of selection. Linkage of polygenes might either increase, or decrease the rate of advance under selection, according to whether the genes were coupled or repulsed. In this way, both recombination frequency and the phase of linkage were adaptive and hence were themselves subject to selective control.

Genetic analysis of certain stocks revealed that

(1) balancing of polygenic combinations occurred in any chromosome.

(2) A large change might occur under the action of selection as a result of unbalancing the polygenes in a small segment of chromosome.

(3) Rearrangement of genes might occur in a chromosome, so that the effects of individual segments were changed but the effect of chromosome as a whole remained nearly constant.

Darlington (1942) showed that the polygenic explanation of Mather's results was not 'a prori', but fitted the required criteria in showing mutation, segregation and linkage and polygenes might occupy the portion of chromosome hitherto regarded as inert.

Discussing the role of polygenic inheritance in evolutionary and adaptive changes under natural selection, Mather (1943) explained that polygenes formed the basis of stored variability and the rate of its release, necessary to give selective changes of the magnitude required for species formation. The breeding system determined the frequency of heterozygosity on which depended the rate of release of potential variability and therefore the breeding system was an adaptive character and as such was subject to selective changes.

Dobzhansky and Spassky (1944) and Ives (1945) investigated the naturally occurring species of Drosophila and showed the selective advantage of heterozygotes over homozygotes. They postulated that recessive autosomal genes mostly concealed in heterozygous state possessed major store of genetic variability.

Gowen (1945) observed that hybrid vigour in Drosophila was chromosomal rather than cytoplasmic and additive gene action accounted for most of hybrid vigour. Dominance and complementary gene action also accounted for a small proportion of genetic variation.

Gowen *et al.* (1946) noticed that the long inbred lines were not frequently homozygous since lethals might be present on chromosome II and III, or both. The superiority of heterozygotes could not be explained as to whether it was due to the tendency of natural selection in favour of heterozygotes or to the existence of a balanced lethal system that maintained additional heterozygosity by linkage.

Dobzhansky and Spassky (1944), Spencer (1944), Ives (1945) and Dubinin (1946) showed the selective advantage of heterozygotes over homozygotes in natural populations of Drosophila. The greatest contribution to the experimental evidence on the selective advantage was provided by the findings of population cage studies of several strains of Drosophila pseudoobscura (Dobzhansky, 1947).

Dobzhansky (1951) reported that heterozygotes for III chromosome inversions had a selective advantage over homozygotes in Drosophila pseudoobscura.

Ives and Hinton (1952) showed the selective advantage of inversion heterozygotes for II chromosome, derived from wild populations of Drosophila melanogaster.

Buzzati-Traverso (1952) reported that obligate heterozygosity for inversions was the rule in Drosophila subobscura.

Robertson (1952) explained the effect of inbreeding on variation due to recessive genes. Variation within lines increased to maximum when coefficient of inbreeding was close to 0.5 and the recessive genes were at low frequency but declined to zero when inbreeding was complete.

Hayman and Mather (1953) had shown that selection in favour of heterozygotes acting within and between inbreeding lines prevented fixation at a locus for which both homozygotes had a selective advantage of as little as 25% for sib-mating and 15% for double first cousin mating.

Bennett (1956) investigated the lethal genes in inbred lines in Drosophila and reported that heterozygotes for lethals were rather less viable than the lethal free homozygotes. Although isolated lethal genes were eliminated by inbreeding, completely linked lethal genes tended to collect in the region of the chromosome, where crossing over could not frequently occur and constituted a balanced lethal system which was perpetuated on further inbreeding.

Spassky *et al*. (1958) analysed the genetic variance released by recombination of the gene content of original chromosomes and concluded that the recombination products of some original chromosomes released more genetic variance than others and that the variability of recombination products was an outcome of epistatic interactions of the genes rather than simple additive products.

Thoday (1959, 1960) concluded on the basis of experiments with Drosophila melanogaster that disruptive selection increased the genetic flexibility and polymorphism.

Review of investigations on specific quantitative traits in Drosophila is given below :

## BODY SIZE

Body size is one of the thoroughly investigated characters in Drosophila. Wing or thorax lengths had long been considered as the representatives of body size measurements. The ease of measurement and convenience of its estimates from lengths of thorax or wing had led many workers to its study.

Zarapkin (1934) observed that the body size of genetically large individuals as compared to genetically smaller ones was due to greater number of cells and not due to difference in cell size. He further showed that artificially induced variation of body size was due to variation in cell size, but cell number was constant.

Stanley (1935) studied the effect of temperature on wing size in Drosophila melanogaster. Experiments were repeated with an inbred unselected strain raised at constant temperature between 14.5$^{o}$-31$^{o}$C involving long winged wild type, vestigial and their offspring. Modifying factors were detected which appeared to be inhibitory, to account for the action of vestigial gene. Temperature effective periods were discussed.

Reeve and Robertson (1952) studied the inheritance of body size in different selected strains and found that the differences of wing and thorax were mainly due to changes in cell size rather than the cell number.

The genetic situation in various lines was analysed to assess the nature and extent of free variation remaining at different stages in selection, to examine the genetic differences between lines of different size and to study the basis for heterosis present in certain crosses.

Robertson and Reeve (1952) discussed the possible effects of continued selection on a quantitative character by conducting a two-way selection experiment for large and small size in lines taken from two wild stocks, namely Nestlebed (Nb) and Edinburgh (E) stocks. Studies were made on size variance, viability and the effects of relaxing and reversing selection in each line.

Four 'Nb' lines were selected in either direction for wing and thorax lengths respectively for 50 generations. Two 'E' lines were selected in either direction for 30 generations.

A cyclic mating system was used to minimise the rate of inbreeding in a small population.

The 'Nb' long wing line after increasing 7% in size entered a long period of unstable equilibrium, characterised by cessation of response to selection, high phenotypic variance and a sharp decline in size. In short. wing line response was noticed until about 37th generation, followed by a lack of response. Its variance became very large after 19th generation and remained higher when response to selection had ceased. Size did not increase when selection was relaxed.

The 'Nb' long thorax line became stable after increasing 11% without changing its variance, but short thorax line showed a decline of 8% with the development of low fertility and high variance.

The 'E' long wing line advanced steadily during 30 generations to 11.5% above control level. After 19th generation, the variance increased and remained consistantly high. Relaxation of selection did not lose the size in contrast to 'Nb' long wing line.

The 'E' short line had declined about 14% but rose to control level on relaxation of selection and fell again when reselected.

Through chromosomal analysis of the lines developed, one II chromosome and two III chromosome lethals were detected. Each of these reduced size slightly when heterozygous but they showed interaction to reduce size greatly when together.

Selection of either of the traits changed both wing and thorax lengths in the same direction but to a different extent. The explanation for a rise in variance of a character after it had been long selected was possibly due to progressive alteration of the genotype in which the alleles previously indistinguishable from each other could be selected, and selected genes which could not be fixed might had their effect on the character magnified by selection of modifying genes.

Reeve and Robertson (1953) observed in a strain of Drosophila melanogaster that long continued selection failed to make it homozygous. Under selection for long wings, the strain remained in unstable genetic equilibrium for more than 50 generations with an increase of 8% in size and about 5% greater phenotypic variance than in the control stock. When selection was relaxed, or reversed, variance declined and the deviations of wing and thorax lengths declined by about 50% and 20% respectively.

Genetic analysis indicated no II chromosome lethals in the unselected stock but the flies were homozygous for a III chromosome gene or block of genes which was lethal in the genetic background of a lethal test.

Progeny tests indicated that 50% of the variance of wing length was due to additive effects compared with 40% after a generation of selection (30% in unselected stock). Selection appeared to increase the additive genetic variance 2½ times leaving the remaining variance unchanged. A genetic asymmetry in the relative changes of wing and thorax lengths during selection for large and small size was discussed by the authors. Wing length declined relatively 2½ times as much as thorax length when selection was relaxed.

This apparent contradiction was explained by the authors as due to a postulated effect of continued selection in modifying the effects of unfixed genes on the selected character. Comparison of genetic variances of the two characters before and after selection led to some support of this hypothesis.

Robertson and Reeve (1953) studied the various effects arising from the substitution of chromosomes from selected strains in different genetic backgrounds using a simple crossing technique. The experiment was conducted to compare three strains selected for large size and one selected for small size with two standard inbred strains. The importance of IV chromosome on size was studied to the extent to which the chromosomes combine additively. The authors summarised their results as follows :

(1) In nearly all the cases substantial non-additive effects on size were noticed.

(2) There was some 'aggregate dominance' i.e. summed dominance effects over a whole chromosome in the direction of large size in crosses of both the large and small lines to the standard strain which varied from complete dominance to a slight deviation from additiveness in different chromosome pairs.

(3) Substantial interactions were demonstrated between genes on non-homologous chromosomes apart from dominance effects. Interaction effects tended to be greatest when chromosomes from unrelated strains were combined.

(4) Selection for large size had generally produced most effect on the III chromosome, while selection for small size in one of the strains analysed produced effects mainly in the X-chromosome.

(5) There was no evidence of any changes in the IV chromosome due to selection for large, or small size.

Robertson (1954) conducted chromosomal analysis of crosses between selected and unselected lines of different body size in <u>Drosophila</u> <u>melanogaster</u> using a simple crossing technique for creating all possible combinations of major chromosomes from pairs of inbred lines. The 27 different genotypes in females and 18 in males, provided the basis for different tests to investigate the genetical control of body size.

When the unselected and small lines were crossed, a highly non-additive effect was noticed. By the analysis of the unselected and small 'E' lines, the size differences could be accounted for by aggregate dominance of the chromosomes of the larger line. In the 'Nb' combination, aggregate dominance and additive combination of non-homologous chromosomes accounted for the size of the majority of the types. There were a number of interactions which increased or decreased the size leading to different dominance relations in different genetic backgrounds. Most of the larger interactions were noticed in genotypes carrying several chromosomes from the small line. The behaviour of X-chromosome of small line was exceptional in being completely recessive in all backgrounds.

When the chromosomes from unrelated and unselected inbred lines were combined, interaction between non-homologous chromosomes were most striking and frequent. Inter-crossing the unrelated inbred lines always demonstrated heterosis in the $F_1$. The heterosis could not be accounted for in terms of the summation of the effects of dominance or overdominance on different chromosomes but was considered in terms of gene interactions.

In a two-way selection experiment for body size in *Drosophila melanogaster* Robertson (1955) observed selection response, and discussed the properties of genetic variations. In 3 of the wild stocks studied, selection produced immediate and sustained response in either direction. There was asymmetry of response, response being greater for smaller size. Response was inversely related to phenotypic variance in large lines, so that most response was shown by least variable lines, but in small lines the reverse was true.

Like lines of different strains were crossed when the response had ceased. $F_1$ of larger strain exhibited increase in size due to heterosis and decline in $F_2$ followed by a response to selection which took the size well beyond parental lines. In small sized strains there was an increase in size and continued selection failed to obtain response.

Tantawy and Reeve (1956) studied the effects of various levels of inbreeding on survival from egg to imago, net fertility and wing length using sib-mating, half-sib mating and cyclic system with 3 pair matings, and found that survival, net fertility and mean size showed little decline with the increase of inbreeding coefficient. Mean size showed about 1% decline upto 80% inbreeding. Phenotypic variance of wing length declined most in the early generations of inbreeding and slightly after about 60% inbreeding. This was attributed to the fact that as the genetic variance decreased, the environmental variance increased particularly during the later stages of inbreeding. On an average heritability of wing length declined much less rapidly than predicted. The differences in heritability between lines inbred at different rates to the same level were not statistically significant, but the most rapidly inbred lines had the lowest heritability and the least rapidly inbred lines the highest heritability of wing length.

It was suggested that

(1) Natural selection against homozygosity at some loci reduced the rate of fixation at these and linked loci.

(2) The genotype became more sensitive to the effects of further selection.

Both these effects probably showed interaction so that selection against fixation became more intense with the increasing levels of homozygosity.

Tantawy (1957) confirmed the earlier views of Clayton, Falconer and Robertson that response to selection was limited. Back selection and relaxed selection in both directions resulted in rapid return to the control in some experiments, but not in others (Tantawy, 1956a).

At higher levels of inbreeding, relaxed selection had no effect on response. Selection combined with intense inbreeding, was effective in the earlier generations followed by a stabilisation due to fixation of alleles favoured by selection.

Based on these results, it was suggested that

(1) Much improvement for a given trait was possible under selection with sib-mating before homozygosity for specific combining genes approached.

(2) Improvements continued until segregating genes became homozygous for those alleles which combined best in the selected lines.

Robertson (1957) studied genetic and environmental correlations between body size and egg production in Drosophila melanogaster and reported that about 50% variance of body size and 60% variance of egg production were due to genetic segregation. Selection for large and small size caused little change in egg production. There was no evidence of genetic correlation between these two traits. Interpreting the results of two-way selection for egg production and body size the author stated that most of the genetic variance for body size behaved as additive, while non-additive predominated in the variability of egg production. Gene environment interaction had been demonstrated for both the traits.

Robertson (1959) reported the findings of his investigation on the effects of different kinds of genetic and environmental variation on wing size of Drosophila melanogaster studied in terms of change in cell size and number in the wings and concluded that :

(1) Higher the temperature during larval growth, the smaller the wing and body size.

(2) Under optimal environmental conditions, the reductions in wing size was accompanied by change in cell number, while cell size remained comparatively constant.

(3) About 70% of the variance of wing cell size and cell number was genetic in origin.

(4) Genetically different individuals of same wing size differed in cell size and number and the genetic variation in size and number of cells were independent of wing size.

Robertson (1960) presented his interesting finding on ecological genetics of growth in Drosophila on varying levels of nutrition. A two-way selection was practiced for large and small size in different environments to investigate the genetic differences and their reactions. The performance of selected lines together with crosses between them had been compared with performance of unselected individuals on different diets and reported a clear gene environment interaction quite early in selection and after 6 generations striking differences were noticed.

Prabhu and Robertson (1960) further studied the gene-environment interaction by comparing the growth of various inbred and non-inbred stocks from pacific cage populations of Drosophila melanogaster at two temperatures on different diets.

Gene-environment interaction was of high magnitude. The phenotypic effects of inbreeding on body size were greatly influenced by temperature. In one set of comparisons, inbred lines averaged 20% smaller at 25°C but only 3% small at 18°C and great differences were found on diets deficient in DNA than on low protein diet.

Sub-optimal diets did not show decline in body size of inbred lines but reduced the size of outbred stock to the extent of 25% or more.

The $F_1$s between various lines showed highest level of homeostasis in relation to body size and development time when reared on sub-optimal diets. The gene environment interaction, among crosses was negligible in comparison to parent lines.

Tantawy (1961) estimated the heritability of body size in a population of Drosophila pseudoobscura and studied the influence of the original temperature condition on such estimates. He showed that temperature and body size effected the rate of egg production and longevity. There was evidence of the presence of considerable amount of additive genetic variance for body size. Changing the original temperature under which the population had been maintained for a long time resulted in decline of the heritability estimates. This was followed by a decrease in the response to selection.

Robertson (1962) estimated the genetic correlation between body size and development time in Drosophila melanogaster which might be zero or close to unity according to the larval diet during selection. On live yeast and various other sub-optimal media, there was little or no evidence of correlation and no change on selection for development time.

Druger (1962) subjected a population of Drosophila pseudoobscura to selection for large and small wings at two different temperatures, 25°C and 16°C. Samples from the original lines selected at 25°C were raised at 25°C, 19°C and 16°C. Selection made in one environment resulted in a qualitatively similar changes in other environments, but the divergence tended to be greater in the environment in which selection was practiced. When the selection was exercised in the same direction as the environment, the carryover of selection effects tended to be incomplete. Selection brought about chromosomal polymorphism in the selected lines.

## BRISTLE NUMBER

Sternite chaetae number may be considered as a metameric quantitative character governed largely by additive genes. Bristles were neutral characters, for they are functionless as far as the fitness of the population was concerned and some bristles had sensory functions.

Karp (1936) studied the effect of 20 different combinations of genes Hw, Br, h and arp and showed that all three types of gene interactions were present i.e. independent action, mutual intensification and mutual suppression, the second type was most frequent, occurring in 45% flies and indicated the presence of dominance relation with reference to the other genes present and the particular substitution.

Karp (1936) further reported that the III chromosome r, th, st, cu, sr, ca reduced the manifestations of the character, sternal bristles by 15-16% as compared with an ebony stock. At least 6 genes were involved. The action was hypothesized to be balanced not only in the chromosome as a whole, but also in its separate regions.

Rokickii (1936) operated selected for high sterno-pleural bristles of 25 generations and observed that the average selection efficiency for one generation was almost twice as high in selection lines as in controls.

Mather (1941) conducted two-way selection experiment for bristle number on IV and V abdominal segments, by two different crosses. In one cross Y x f B'B' the main advance was achieved in the first two selected generations, which was explained as due to the recombination of whole chromosome. In another cross BB with wild type, a similar initial advance was followed by a period of stability. This was followed by a second and larger advance, which was interpreted as due to the action of selection on variation released due to recombination of genes in the same chromosome, as according to Mather (1941) some balanced polygenic combination developed by the action of natural selection. The polygenic combinations would be subjected to an internal balancing process in the homozygotes and a relational balancing process in heterozygotes and heterosis was due to a poor relational balancing and polymorphism in nature to the relative efficiency of internal and relational balances.

Mather (1942a) analysed a stock of Drosophila melanogaster selected for abdominal bristle number and reported that linkage of polygenes either increased or decreased the response under selection according to whether the genes were coupled or repulsed. Both the frequency of recombination and linkage were adaptive and were themselves subjected to selection.

He indicated that balanced polygenic combination provided ample storage for genetic variation, and for the selective changes of the magnitude required for species formation.

Mather (1942b) further stated regarding the association of fertility with bristle number, that 'correlated response to selection would appear to be an inevitable property of polygenic inheritance".

Mather and Wigan (1942) practiced selection and inbreeding in two experiments for 21 and 53 generations respectively for sternopleural and abdominal bristles. In the first experiment the advance was smooth and steady while in the second it occurred with sudden jumps followed by lack of responses. The jumps were explained as due to the recombination of the mutations to which individual polygenes had given rise. These mutations with small individual effects were said to be accumulated until recombinations gave rise to more extreme variants where selection was effective.

Haskel (1943) investigated the polygenic system operating in mutants and non-mutants of Drosophila melanogaster. The gene scute (sc) was introduced by backcrossing, in 4 lines with different chaetae number and found that the abdominal chaetae was approximately halved.

Wigan (1944) studied 'balance and potence' in natural population of Drosophila melanogaster. Haploid sets of the three major chromosomes of Drosophila melanogaster derived from wild males trapped at 5 places in England were kept in the male line and were brought together in various combinations. By means of a factorial experiment, the effects of the chromosome pairs on sterno-pleural bristles, and their interactions were compared with those of marker tester chromosomes, and their wild homologus. It was found in the females that the variability was less between families, where the homologous wild chromosomes were derived from different individuals than those where homologues were identical, which proved that polygenic combinations controlling bristles were relatively balanced. The males showed large effect of interaction. The effects of polygenic combinations when heterozygous were shown not to be exactly intermediate to the effects of two homozygotes and the word 'potence' was introduced to describe measurable relation (analogous to dominance) which existed between polygenic combinations.

Mather and Harrison (1949a, b) carried out extensive two-way selection experiments for bristle number in _Drosophila melanogaster_. Two unrelated inbred lines were crossed and selection practiced from $F_2$. Selection for low bristle number led to an irregular decline for 35 generations and then the line failed due to sterility. Selection was relaxed at 20th generation by mass mating, but no change occurred in spite of repeated attempts to select downwards. Selection for high bristles also failed due to infertility. The lines had thus acquired some sort of balanced infertility system.

Selection for high bristle number responded immediately and continued upto 20 generations followed by infertility. The line continued by mass mating, whereupon bristle number regressed 80% towards the original level in 5 generations.

After a few generations of reselection the line returned to the original high level. This was explained as due to the freeing during the period of relaxed selection of infertility genes linked to the polygenes responsible for high bristle number. The polygenes were presumably tightly linked and behaved as a unit and were therefore quickly selected again.

Analysis of the lines by chromosomal assay it was found that all the three major chromosomes were involved for bristle trait. There was no indication of dominance of bristle gene which was supported by crosses between the lines. The results were interpreted exclusively in terms of 'Mather's theory of polygenes' (1943, 1949). This classical experiment was used to establish nuclear basis of polygenic inheritance.

Wigan (1949a) studied the distribution of polygenic activity on X-chromosome affecting sterno-pleural bristle number in _Drosophila_ _melanogaster_.

Maximum activity was noticed at the left end (0.0-2.8), the region round _ct_ (10-31) and _wy_ (31-49.5), both showed significant activity being in the same direction in any one chromosome. No activity was found near _v_ (26.5-38.7). In the region round _car_ (59.7-centromere) there was significant activity, as shown by significant difference between inbred Oregan chromosome and the tester. Polygenic activity was not directly proportional to the crossing over lengths or to the amount of euchromatin shown on the salivary map, nor was it proportional to the amount of heterochromatin in the metaphase chromosome. No connection between polygenic activity and hetero-chromatin could be established due to the general distribution of intercalary hetero-chromatin along the X-chromosome. Greatest polygenic activity was noticed in a region having a high concentration of visible lethal mutations. Different optimum rates for the release of variability in different characters disfavoured the existence of variability of all characters in all centres of activity. The results obtained on the X-chromosome of Drosophila melanogaster showed relational balance (Wigan, 1944). The polygenic organisation of the X-chromosome which is hemizygous in one sex, showed internal balance, and it was thought that this might not represent the condition in the autosomes, where no such compromise was called for. It was also found that the major genes and polygenes were not antithetical in their distribution.

Rasmuson (1952) used several wild stocks in her selection experiments and noticed that selection was effective, but there was asymmetry of response. The $F_1$s of line crosses were not intermediate, but closer to the parent of smaller number of bristles. She considered the difference in behaviour to be incompatible with the hypothesis of additive polygenes.

Reeve and Robertson (1954) studied the genetic and environmental correlations between the sternites from progeny tests and counts on inbred lines respectively. Under optimal culture conditions, the genetic correlations were virtually unity and environmental correlations virtually zero, so that the elements of the metameric pattern responded identically to genetic variations and independently to non-genetic variations. Overcrowding reduced the size and the sternites whose chaetae were more densely packed and probably smaller.

Durrant and Mather (1954) studied the heritable variation in the second chromosome in a long inbred line of _Drosophila melanogaster_. There was a significant variation in their effects on sterno-pleural and abdominal chaetae. It was found that the differences among the chromosomes were due to recent mutations and not due to inbreeding.

Cocks (1954) investigated the polygenic system controlling the expression of major mutant genes which affected chaetae number in Drosophila melanogaster. He introduced 3 major mutant genes _sp_, _sc_ and _H_ into 10 wild type lines by backcrossing. He reported that polygenic systems of mutants and non-mutants differed for different major genes and might differ for two characters affected by the same major gene. Furthermore the polygenic system controlling abdominal and sterno-pleural chaetae number were distinct, at least, in part. The variation of two characters was found to be similar in mutants and non-mutants.

Breese and Mather (1957) investigated the distribution of genetic differences between the third chromosomes of two selected lines of _Drosophila melanogaster_ in respect of number of abdominal chaetae (for which selection was practiced) and sterno-pleural chaetae. The chromosome was divided into 6 regions by constructing recombinant chromosomes. These were tested for additive variations, for dominance and for genetic interaction and noticed that there was variation of these effects with sexes and with genetic backgrounds. All regions showed genetic activity and most showed dominant effects. Intrachromosomal interactions were of no greater effect than the interchromosomal interactions. Greatest activity was found in the region of centromere but appeared to be more or less evenly distributed all along the chromosome. It is suggested that at least 6 genes might be involved in 3rd chromosomes contribution to the differences between two selected lines. Though some genes might affect abdominal and sterno-pleural chaetae simultaneoulsy, the genetic system governing the two was distinct to a certain extent. Correlated responses were mainly due to linkage relations rather than the pleiotrophy of gene action.

Clayton, Morris and Robertson (1957) studied the short term responses to selection of bristles on 4th and 5th abdominal sternites.

Individual selection at different intensities and family selection of different types i.e. half-sib selection, full-sib selection and family selection with inbreeding were practiced for 7 generations. With certain exceptions there was fair agreement with prediction and it was best in high intensities of selection. The responses to the downward selection were less than expected.

Clayton and Robertson (1957) studied the long term effects of selection for abdominal bristles and found that response had slowed down considerably in many lines after 20 generations, although in some it continued until the 30th generation. In many of the lines the cessation of response was abrupt and lack of response was not due to exhaustion of genetic variability.

In three of the high lines, the high variability was apparently due to continued selection of heterozygotes for a lethal gene both on 2nd and 3rd chromosomes.

In the low lines there was a sudden increase of variation in females followed by a rapid response. This appeared in all lines with different times of onset.

Genetic variation was maintained in all the lines even after the response had ceased. The lethal genes, infertility of extreme females and heterozygosity for inversions played some part in this phenomenon.

Clayton, Morris and Robertson (1957) discussed the correlated response to selection for number of bristles on abdominal sternites of Drosophila melanogaster, and reported that there was no genetic association between bristle count and body size.

Thoday (1958) studied developmental homeostasis of sternopleural chaetae in Drosophila melanogaster. Ten generations of selection for high and low bristle number indicated a deterioration in developmental homeostasis, as evidenced by increased asymmetry. The reason might be that poor homeostasis genes had been selected, or it was postulated that gene complexes, linked to those directly affecting chaetae number, had became unbalanced during selection.

Thoday (1959) studied the effects of disruptive selection on sterno-pleural chaetae number. He used three different systems of selection viz. negative assortative mating, positive assortative mating and stabilising selection. There was increased response under negative assortative mating with slight deterioration of developmental homeostasis.

Positive assortative mating increased the variance, while stabilized selection resulted in decrease of variance from $F_2$ level to approximately $F_1$ level. It was suggested that disruptive selection could maintain coupling linkages of relevant genes against considerable 'recombination pressure' and that stabilising selection could promote repulsion linkage.

Gibson, Parson and Spickett (1961) found that the fly size and chaetae number were generally correlated in Drosophila melanogaster, but correlation might break down in selection for chaetae number.

Thoday and Boam (1961b) described the effects of random mating in a population of Drosophila melanogaster under disruptive selection for sterno-pleural chaetae number. Though selection pressure was low, high variance maintained in the population was so large that it seemed fair to regard that random mating would not prevent disruptive selection from maintaining a wide varieties of genotypes in a population.

Gibson and Thoday (1963) further reported that variance increased and gene flow between two extreme components of population was rapidly reduced to a low level.

McBridge and Robertson (1963) tested the effectiveness of the assortative mating of selected individuals increasing selection response, using abdominal chaetae number in Drosophila melanogaster. In all comparisons assortative mating gave a greater selection response which might be partly due to greater selection differential. It was suggested that assortative mating was a method for increasing selection response in some situations. It became more powerful when heritability was high, whereas, all of the other environmental aids to individual selection were more effective when the heritability was low.

Fraser et al. (1965) practiced selection for scutellar bristles in Drosophila and reported that artificial selection was relatively ineffective when the line attained a new equilibrium value under natural selection.

Nasser (1965) explained the slow and fast responses found in selection experiment for scutellar bristles by analysing the variability of each chromosome. He observed the effects of selection when practiced on one chromosome as compared to whole genome. The results indicated that the 3rd chromosome line gave higher responses than any of the other lines and epistasis and a negative over-dominance model were the possible explanation.

Scowcroft (1966) conducted chromosomal analysis of scuteller bristle selection lines to find the genetic basis of response to selection, and reported that, selection lines which utilised genetic variability on the 1st and/or IIIrd chromosomes had a greater response to selection than those lines which had utilised genetic variability on all the three major chromosomes. He further noticed that interaction between chromosomes were favourable to direction of selection in high lines, but in the lines with lower level response, interactions tended to counter single chromosome effects.

## BODY WEIGHT

Comparatively less work had been done on this quantitative character.

Martin and Bell (1960) estimated population parameters needed for the prediction of response to high-low selection for body weight with inbreeding and correlated response in egg size, fecundity and adult emergence from 12 inbred lines, their crosses and random samples from a population synthesized from the inbred lines. A breeding plan that imposed inbreeding at 3% per generation was used.

The selection differentials were slightly larger than had been predicted, whereas, the realised heritability of body weight was slightly below pre-selection estimates. The genetic correlations of body weight with egg size, fecundity and adult emergence were highly transitory both before, and during selection and were of little value.

The predicted values of inbreeding depression on the assumption that heterosis was due to dominance effect of genes were in close agreement with those calculated independently in each line and generation. They reported that inbreeding depression to be most severe for fecundity, less severe but still larger for adult emergence, definite, but very small for egg size, and of little consequence for body weight. Divergence of body weight was found to be highly repeatable over replications whereas response to selection in a given direction was less repeatable and less predictable.

The results indicated that additive rather than dominance and epistatic gene action influenced the selected trait and agreed with the absence of important inbreeding effects upon body size.

Carson (1961) studied body weight and adult emergence in Drosophila robusta. The flies of central habitat could be improved by the introduction of additional polymorphism but marginal ones could not. This supported the hypothesis of 'chromosomal polymorphism'.

Defries and Touchberry (1961) reported a negative non-genetic path (maternal effect) in the inheritance of body weight in Drosophila and it operated through number of offspring. Through their further investigation on interline and intraline variability in a population of Drosophila affinis selected for body weight in each of two directions they summed the results as follows :

(1) Selection for body weight at two intensities in each of the two directions was accompanied by a definite but variable response when the flies were perpetuated by only two parents which were full-sib mated.

(2) Realised heritability of body weight of Drosophila affinis was approximately 0.06 and this estimate agreed quite closely with that determined from pooled parent offspring regression.

Sheldon (1963) reported response to selection in spite of the apparent absence of additive genetic variation.

Kearsey *et al*. (1967) investigated the genetic architecture of live body weight and egg hatchability by chromosome assay, in four divergent inbred lines of Drosophila. Body weight was governed mainly by additive variations, but hatchability exhibited marked heterosis due to directional dominance and duplicate chromosomal interactions.

## HATCHABILITY, FERTILITY, VIABILITY AND DEVELOPMENT TIME

Zarapkin (1934) investigated the duration of individual development in *Drosophila funebris* and reported that larger flies developed 2.5 days later than the smaller ones, delay being noticed in larval stages. No sex dimorphism was noted.

Maynard-Smith and Maynard-Smith (1954) reported shorter development time in flies heterozygous for chromosomes than those of homozygotes in *Drosophila subobscura*.

Hollingsworth and Maynard-Smith (1955) studied the effects of inbreeding on rate of development and fertility in *Drosophila subobscura*.

In the lines derived by brother-sister mating from wild caught females they noticed a rapid decline in hatchability from 20-50% after 7 generations. The major cause of reduction of hatchability was male infertility and to a little extent female infertility and zygotic inviability. Analysis of male infertility in the '0' line showed that it was not due to the segregation of a single recessive.

In the '0' line, they noticed a marked correlation between slow development and infertility which was explained as due to linkage between polygenes as invoked by Mather and Harrison (1949).

Sang and Clayton (1957) estimated heritability of rate of larval development in Drosophila to be between 0.2-0.25 from the results of two-way selection in (a) an outbred population and (b) $F_2$ of inbred line crosses.

The character showed hybrid-vigour for rapid growth. Examination of $F_2$ and backcross generations suggested that the situation was further complicated by slow growth of one parent being due to interaction between a number of homozygous loci. Ecological interactions between larvae of different genotypes might have played a major role.

Bonnier et al. (1957) conducted studies on the rate of development and viability of mutants in Drosophila melanogaster and concluded that homozygous wild females reached eclosion earlier and had higher competing ability than heterozygous ones.

Marein (1958) exercised selection for developmental rate in 30 lines of Drosophila melanogaster. There was no appreciable change in unselected lines, while significant response to selection was noticed in some of the fast lines and also in slow lines.

Parson (1959) through his studies on inbred lines of Drosophila melanogaster reported that the hatchability of eggs of $F_1$ exhibited heterosis and the variability was less than the inbred lines, thus indicating homeostatic superiority over inbred lines, which was confirmed by larger genotype environmental interaction of the inbreds than the hybrids.

Hiraizumi and Crow (1960) investigated the heterozygous effects on viability, fertility, rate of development and longevity of _Drosophila_ II chromosomes that were lethal, when homozygous. They found that the lethal heterozygotes developed slower and female heterozygous for lethal or semi-lethal produced fewer eggs at an early age. The longevity of males heterozygous for lethals and semi-lethals were slightly reduced, while no significant effect was noticed in females. In general, appreciable deleterious effect on pre-adult viability was noticed in heterozygotes for lethals and semi-lethals from a natural population.

Gilbert (1960-61) concluded that viability, longevity and fertility were affected alike by the substitution of chromosome segments, in _Drosophila_ _melanogaster_ and heterozygosity was always advantageous.

Hiraizumi (1961) studied the relation between rate of development and female fertility for II and III chromosomes of _Drosophila_ _melanogaster_ and reported that the rate of development was negatively correlated with female fertility when the developmental rate was faster than a certain level but positively correlated when it was slower than this level. There was no detectable maternal effect. Both the chromosomes contributed to each component in a simple multiplicative fashion.

Bonnier (1961) reported hybrid superiority in the rate of development, egg hatching and competing ability.

Clark, Smith and Sondhi (1961) found asymmetrical response to selection for the rate of development in Drosophila subobscura. The realised heritability was 0.186 in slow line and 0.063 in fast line. The higher heritability might be due to epistatic interaction between the non-allelic genes.

Bateman (1962) investigated the genetic control of egg hatching in two inbred lines of Drosophila and their hybrids. The following genetic factors were found to increase the proportion of unhatched eggs arranged in order of decreasing importance.

(1) Incompatibility between eggs with '0' cytoplasm and sperm of type 'B' or 'BO' (the $F_1$ hybrid with B as female parent).

(2) Homozygosity of female laying the eggs.

(3) Though 'B' and 'BO' sperm showed overall similarity 'B' sperm gave more unhatched eggs with 'B' cytoplasm but 'BO' sperm gave more unhatched eggs with 'O' cytoplasms.

The following factors had no detectable effect on egg hatching :

(1) Ratio of 'O' genes to 'B' genes in the female and in the unfertilised eggs.

(2) Ratio of 'O' genes to 'B' genes in the fertilised egg.

(3) Heterozygosity of the fertilised egg.

Saxena (1962) reported that there was no correlation between emergence time and egg production, egg size, hatchability and wing size.

Ayala (1965) studied the relative fitness of Drosophila serrata and Drosophila birchii and their inter-specific hybrids, on the basis of the number of flies produced per food unit (Biomass). Both production and population size increased during first few weeks, and reached an equilibrium between 8th and 15th week. Drosophila serrata produced larger number per culture bottle than Drosophila birchii. The hybrid populations of Drosophila serrata performed better than parental lines, while the hybrids of Drosophila birchii were intermediate to their parental lines.

Temin, Rayla and Greenberg (1966) analysed a total of 1083 second chromosomes for their effects on viability and reported that homozygous chromosomes reduced viability by 40.9% in comparison with a group of random heterozygotes. A total load of 14.2% due to complete sterility, partial sterility and infertility based on adult maturity was recorded. Genes leading to partial sterility were less prevalent relative to those causing complete sterility, among males than females and the total sterility load was larger in males. A significant association between complete sterility and low viability was found.

## EGG PRODUCTION AND EGG SIZE

Egg production is a highly variable metric character and a variety of ecological factors determine the phenotypic expression of fecundity. It is closely associated with the fitness of population.

Comparatively less work has been done on egg production and egg size.

Warren (1924) studied the mechanism of inheritance of egg size in *Drosophila melanogaster* and reported that egg size was least affected by environment, age and size of the fly. Neither homozygosity, nor heterozygosity could introduce any correlations between the body size and egg size.

Imai (1934) studied the effect of temperature on egg size and variation in Drosophila melanogaster and reported that under controlled environmental conditions, the egg length and its variability were constant and independent of the age of the flies. The temperature changes at the time of mating affected the egg length during the first days of egg production.

Zarapkin (1934) reported that egg size was inversely proportional to the body size.

Stern (1934) studied the effects of ultraviolet radiation upon fecundity of Drosophila melanogaster. Irradiation of females reduced the length of life and suppressed egg laying. Irradiation for 5 minutes reduced egg laying capacity to about half the normal, while exposure for 8 minutes caused complete sterility. Flies treated within 5 hours after emergence were more susceptible than older flies. The males were more resistent as regards longevity of life and fertility.

Straus and Gowen (1943) studied crosses between two inbred strains of Drosophila melanogaster and found 100% increase in egg production above the average of the parents.

Chromosomal analysis revealed that each of the major chromosome contributed to heterosis. The total heterotic effect was equal to the sum of individual chromosome effects, revealing the additive effects i.e. no interaction. Therefore the relationship between vigour as measured by egg production and chromosomal heterozygous was definitely linear.

Robertson and Sang (1944) enumerated eight ecological factors that influenced fecundity in Drosophila. These were duration of feeding time, quality of food, species of yeast, condition of yeast, larval diet, crowding in cultures, oviposition area and age of females.

Fecundity was influenced by genotype, temperature, humidity, nutrition, oviposition stimuli etc. Dead yeast decreased the rate of egg production and this was correlated with longevity.

Gowen (1945) reported that lifetime egg production varied from 263-1606 eggs in various Drosophila races of different geographical origin. He noticed that the hybrids of 389 x 1000 eggs produced an average of 2034 eggs. The hybrids individually were not better than the best individual of inbred, - simply all the flies were of uniformly high producing. He concluded that heterosis was genetic in origin rather than due to cytoplasmic differences and that the hybrid effect was due to a fairly large number of genes distributed at random over the chromosome pairs.

Burdick and Bell (1954) showed that different pH levels of the medium produced a marked effect on egg production.

Bell, Moore and Warren (1954) evaluated four methods of selection, namely

(1) Selection within a closed population on the basis of family and individual merit.

(2) Recurrent selection in a closed population for specific combining ability with an inbred tester line.

(3) Reciprocal recurrent selection within two closed populations for specific combining ability with each other.

(4) Inbreeding and hybridisation on egg production and egg size in <u>Drosophila melanogaster</u>.

In the first experiment they selected for high egg production and large egg size for 16 generations based on an index giving about equal weight to these two traits. During the early stages of selection individual and family selection proved better than either of recurrent methods in improving a highly heterotic trait in newly formed population. However, in long run reciprocal and recurrent selections were superior.

In the second experiment selection was practiced for 39 generations. Initially egg production increased by practicing individual and family selection within a closed population. The selection response apparently ceased fairly soon and performance was overtaken by the lines selected for specific combining ability, specially that involving reciprocal recurrent selection. The highest yield was noticed in crosses between inbred lines.

Bell, Moore and Warren (1955) studied egg production and egg size in Drosophila melanogaster. They reported that fecundity was a highly heterotic trait with low heritability while egg size showed little or no heterosis in crosses and had relatively high heritability of 30%-60%.

Early testing of combining ability for fecundity was found to have little value in predicting subsequent combining ability for nine inbred lines crossed in all possible combinations. Egg size had more predictive value on early testing. In contrast to fecundity highly significant differences in egg size existed among the initial non-inbred stocks and no genetic-environmental interaction was revealed for egg size. Estimates of general and specific combining ability showed three experiments in Drosophila melanogaster. From two heterogenous stocks four lines were developed and selection was based solely as progeny testing of males. The first experiment was for fecundity, the second for hatchability, and the third for body weight. These experiments were continued for 20, 13 and 6 generations of selection. Summing up the results of all the three experiments, she concluded that RRS method was superior. For egg production the advantage of 6% was clearly significant, whereas for hatchability and body weight, the advantage of less than 2% was not significant. The low advantage compared with theoretical expectation was explained by her as 'loci with over-dominance were scarce with limited number of favourable alleles while the epistatic interactions were striking'.

Through extensive investigations on the genetic variation of ovary size in Drosophila Robertson (1957a) reported that under-feeding of larvae reduced the body size with the corresponding proportional reduction in ovariole number and egg production, but the number of eggs per ovariole was uneffected even by striking changes in body size. No correlation was observed between body size and ovariole number or egg production.

The evidence of genetic variation tending to cause striking increase in ovariole number was provided by comparison of groups of genetically identical individuals created by combining haploid sets of chromosomes from the wild stock with those of an inbred line.

Mass selection in a strain for high and low ovariole number led to an asymmetrical response, since in low line there was 14% reduction, whereas high line increased by more than 50% and the response was continued after 10 generations of selection. The response to selection for high ovariole number was due to increase in frequency and fixation of a recessive gene, which when homozygous increased ovariole number by about 25%.

Maynard-Smith (1958) reported that rate of egg production was correlated with longevity. The egg production cut short longevity.

Mitchell (1958) found positive association of multiple inversion heterozygosity with increased fecundity and male developmental rate.

Vetukhiv and Beardmore (1959) studied the effect of environment upon the manifestation of heterosis and homeostasis of some of the components of Darwinian fitness i.e. larval viability, fecundity, asymmetry of wings in P, $F_1$ and $F_2$ of crosses between geographic population of Drosophila pseudoobscura.

Prabhu (1959-60) conducted extensive studies on the genetic variability for egg production in *Drosophila melanogaster* and reported heritability to be 0.26 ± 0.09 by intrasire regression method. Heritability by Falconer's method of realised heritability was 0.11. The average 10 day egg production of early and late emerging females was not significantly different statistically.

Tantawy and Vetukhiv (1960) reported significant effects of temperature on egg laying capacity in 9 populations of *Drosophila pseudo-obscura*.

Bonnier (1961) studied the hybrid superiority in 3 unrelated wild type stock population of *Drosophila melanogaster* for fecundity and larval survival. Viability experiments were also conducted with pure flies from the stock and with six possible $F_1$ hybrids between them. He reported that hybrids were superior in majority of the cases for all the three characters under study and the hybrid superiority was due to single assumption of over-dominance.

Brown and Bell (1961) discussed the adequacy of a control population in selection experiment for egg number in *Drosophila melanogaster*. Results of an experiment designed to compare alternative methods of selection for increased egg number in plateaued population concluded that the value of control depended more on its genetic constitution than the method of rearing.

Brown and Bell (1961) in continuation of their study (Bell et al, 1955) attempted to identify the genetic factors causing a plateau in response to selection for high fecundity in a closed population of Drosophila melanogaster at generation 7. Using marked inversion technique, 126 genomes were extracted from the population and the frequency of lethal, sterility and subvital factors were determined. The genetic analysis concluded that neither lethal or sterility genes contributed to the lack of response for selection.

The primary cause for the plateau in selection response was caused by exhaustion of the additive genetic variance in fecundity though non-additive genetic variation was present to eliminate the possibility that selection plus the inevitable inbreeding which occurred in a closed population had rendered the population homozygous.

Bhat (1961) studied two-way selection for egg production in Drosophila ananassae and correlated responses for egg length, width and hatchability, following six systems of mating i.e. mass mating, cyclic system with 4 pair of a matings, cyclic system with 3 pair of matings, cyclic system with 2 pair of matings, half-sib and full-sib mating. He reported that egg production of first 10 days of life was correlated with total life time egg production. Fifth day's production gave high significant correlation of 0.4. Hence it was suggested that 4th, 5th and 6th day records of egg production fairly estimated the life time production. There was no overall increase in mean daily egg production in any system after 5 generations of selection. Phenotypic variance decreased in most of the selected lines initially followed by a gradual increase.

Brown (1962) selected two populations of Drosophila melanogaster for high egg production for 4 generations by mass and family selection and noticed a plateau in both the populations. The crosses between them exhibited heterosis indicating that the two populations were genetically distinct. The heritabilities of egg production in two populations were 0.08 ± 0.09 and 0.3 ± 0.12 respectively and in the crosses between plateau lines was 0.19 ± 0.06.

Saxena (1962) studied correlations between egg production, egg size, hatchability and wing size with emergence time in Drosophila melanogaster. He reported no definite correlation between these characters and emergence time.

Prabhu Lal (1962) studied the effect of inbreeding at different rates on egg production and hatchability in *Drosophila melanogaster*. The heritability of egg production was 20% and that of hatchability 30%.

Satya Prakash (1962) studied the effect of various levels of inbreeding on egg size and fertility in *Drosophila melanogaster* and suggested that natural selection favoured heterozygotes and reduced fixation. The egg size tended to decrease at higher levels of inbreeding as inbreeding depression occurred when genetic background was homozygous rather than heterozygous.

Prabhu *et al* (1964a) worked on three sets of two-way selection experiments in *Drosophila melanogaster* for egg production.

In the first experiment 3 stocks were selected in either direction for 24-26 generations using sib-mating. In the second experiment individual selection was practiced avoiding inbreeding, and in the third family selection was practiced for 10-12 generations.

There was a distinct phenotypic response which showed systematic trend in upward direction irrespective of the direction of selection. This was suggested as partly due to segregation of dominant genes for egg production. Family selection was superior in getting response and it was possible to separate high and low lines.

The results of these experiments were interpreted on the basis of diallel analysis of the lines (Singh et al, 1964), as due to the presence of dominant and recessive genes in the proportion of 4:1 affecting egg production in these lines.

Singh et al (1964) studied a 6 x 6 diallel cross for egg production in Drosophila melanogaster and the following conclusions were drawn :

1. There was a considerable amount of gene-environment interaction in egg production.

2. The genes controlling egg production showed both additive genetic effects and dominant deviation. They also showed non-allelic interaction.

3. There was asymmetry in the distribution of positive and negative alleles which was understandable, as 3 lines were selected for high egg production and 3 for low production.

4. The dominant deviation present were largely unidirectional.

5. The ratio of recessives to dominants was of the order of 1:4. Low egg production was due to recessive genes and high egg production to their positive alleles.

Mazumdar (1964) studied the polygenic activity of X-chromosome for egg production, egg size, hatchability and wing size in Drosophila melanogaster and reported that :

1. Bar chromosomes appeared to contain a few genes than normal X-chromosome for egg production.
2. Bar chromosome retarded the hatchability while normal X-chromosome enhanced it.
3. Both the chromosomes were equally effective for egg size and wing size.

Tait (1964) worked on polygenic activity of second chromosome and found that :

1. Marked stock contained less dominant genes for egg production than the normal stock in their second chromosome.
2. Normal stock contained more effective factors for hatchability than marked stock.
3. Marked stock exhibited more dominant genes affecting egg size than normal stock.

Rawat (1966) studied the effect of different methods of selection for egg production on the expression of other quantitative characters such as hatchability, viability, egg length, egg volume and wing length.

The two-way selection experiment was continued upto 13-20 generations and selection was practiced in only one sex (females).

Response to selection was low in all types of selection i.e. mass, full-sib, cyclic two, cyclic three and cyclic four.

An interesting phenomenon of 'ebb and flow' or rise and fall was observed indicating that non-additive gene effects played a major role than additive genes for determining egg production. She further suggested that the severe unidirectional stress imposed by continued artificial selection might not only rearranged the genes on the chromosomes but modified their effect by changing the genetic background, particularly on the selected character.

Chakrabarti (1966) studied relative merits of estimating heritability by two different methods in _Drosophila_.

Jayaramakrishna (1967) studied the nature of genetic response in two-way selection for egg production and correlated responses for hatchability and wing size in _Drosophila melanogaster_. Selection pressure was imposed through individual and sib-selection. The additive component in respect of egg production showed a gradual decline from 1.4% in base population to 0.4 in individual selected high line, but exhibited an increase (15%) in sib-selected high line at the end of 6th generation of selection. Dominant components were all high in all cases except low line of mass selection. The phenotypic variance was doubled after 6 generations of selection in individually selected lines, but in sib-selected lines the coefficient of variability remained at about the same level as in the base population.

Genetic analysis of the lines developed through diallel crossing revealed significant additive genetic effects for egg production, hatchability, and wing length. Large portion of genetic variability was due to over-dominance for egg production and hatchability. No asymmetry for dominant and recessive genes was noticed for egg production but the ratio of dominants to recessives for hatchability was 2:1.

Marinkovic (1967) investigated the genetic loads affecting fecundity in natural populations of Drosophila pseudo-obscura. The correlations between the viability, fecundity and rate of development were low when lethals and semi-lethals were disregarded. Fecundity of the heterozygous females was positively correlated with fecundities of the females homozygous for the chromosomes present in the heterozygotes.

Kidwell and Malick (1967) studied the effect of heterosis, egg production, mating status and weight on longevity in Drosophila melanogaster. Study of reciprocal crosses between two isogenic lines revealed that hybrids lived longer and produced more eggs but not always heavier. Single flies tended to live longer than mated ones. They thought that there was a large phenotypic correlation between longevity, life time production and mean daily egg production, that was largely environmental.

# MATERIALS AND METHODS

## STOCKS USED

The investigations with regard to the 'genetic analysis of inbred lines' were carried out with the following stocks :

1. b 208 (Marker stock)
2. (a) The high line of sib-selection (on half-sib basis) at the end of 20 generations of selection for high egg production ($H_1$).
   (b) The low line of sib-selection (on half-sib basis) at the end of 20 generations of selection for low egg production ($L_1$).
   (c) The high line of sib-selection (on full-sib basis) at the end of 19 generations of selection for high egg production ($H_2$).
   (d) The low line of sib-selection (on full-sib basis) at the end of 19 generations of selection for low egg production ($L_2$).

The marker stock b 208 was obtained from Dr. Oster, Department of Zoology, University of Ohio, U.S.A.

The females of this stock were yellow located at 0.0 and with forked bristles (56.7) on its X-chromosome.

The Xs were attached with one Y chromosome.

The males had in their X-chromosome the following characters.

<u>scute</u> (sc) recessive character located at 0.0 on the genetical map of X-chromosome, characterised by absence of ring bases and the scutellar bristles. Salivary chromosome studies of Demerec and Sutton showed locus of sc to be 1 B3-4. This is one of the half a dozen most useful sex linked characters. Csik and Wolsky reported lower oxygen consumption in pupal period than in wild type.

<u>cross-veinless</u> (cv) recessive character located at 13.7 on the linkage map of X-chromosome, characterised by the absence of crossveins. Salivary chromosome studies by Demerec and Sutton showed the locus to lie between 4 F1-2 and 5 D1-2. Csik and Wolsky (1939) found that cv pupae have lower oxygen consumption than wild type.

<u>vermillion</u> (v) characterised by bright scarlet eye colour, not transluscent and the ocelli colourless. Recessive located at 33.0 on X-chromosome. Recurs frequently by spontaneous mutation. Transplantation studies indicated vermillion flies to be defecit of $v^{+}$ and $cn^{+}$ hormones (Beadle and Ephrussi, 1936). Csik and Wolsky (1939) found lower oxygen consumption in the pupal stage.

_forked_ recessive character located at 56.7 on the genetical map of X-chromosome and is characterised by the bristles being shortened, gnarled and bent with ends split or bent sharply. Demerec and Sutton through salivary chromosome studies indicated that bands 15 F1-5 to be involved. Oxygen consumption lower than wild type in pupal stage (Csik and Wolsky, 1939).

_Bar_ is a dominant character arose as a duplication at 57.0 on X-chromosome. The eye is restricted to narrow verticle bar of 90 ± facets in the male and 70 ± in the homozygous female as contrasted with the normal numbers of 740 ± for males and 780 ± for females (Sturtevant, 1925). Heterozygous female has 360 ± facets and shows reduction on anterior edge with nick and horizontal seam giving kidney shape. Salivary chromosome studies (Bridges, 1936; Muller _et al_., 1936) showed that mutant _Bar_ was a tandem repeat of a section of 6 bands.

The stock was mass cultured for 1-2 generations before used in the present investigation.

## CULTURE MEDIA

In an effort to standardise the live medium for rearing the flies four different standard media (Burdick's, Banana, corn meal and yeast) were tested at two temperature i.e. room and 25°C (Prabhu *et al.*, 1963) and Burdick (1954) medium was found to be the best and was used throughout the present investigation.

The flies were reared in a thermostatic cabinet throughout the experiment whose inside temperature was maintained at 25°C ± 1°C which had given better results earlier (Prabhu *et al.*, *loc. cit.*).

ETHERISATION OF FLIES

Since it was not possible to handle the flies as such the flies were made unconscious before pair mating and also during classification into different genotypes in $F_2$ and $F_3$ generations. Solvant ether in a simple apparatus called "etherizer" was used. Care was taken to see that the flies were not over etherized which might affect the productive capacity of the flies (Prabhu, 1960) and toxic doses prove fatal. The dose of ether required was standardised by trial and error.

## COLLECTION OF VIRGINS

This was the most important aspect of the experiment, since the fundamental genetic consequences mainly depended on this operation.

The generation interval in Drosophila melanogaster was 8-9 days at 25°C. The emergence of the flies was uniform as they were reared under controlled conditions. The newly emerging flies from the individual food vials or bottles in each generation were sexed, and males and females kept separately. As soon as the required number of virgins and males were got pair matings were set as per the design of the experiment.

## EGG LAYING BEHAVIOUR

The fertilised females started laying within 48 hours of emergence but unfertilised ones took much longer time which varies with individual female. In some cases no egg was laid by the latter. Presence of males was found to be essential not only for the initiation but normal continuation of egg production (Prabhu, 1960). Hence care was always taken to replace a male if found dead by chance.

## STUDY OF EGG PRODUCTION, EGG SIZE AND HATCHABILITY

### EGG COLLECTION AND COUNTING

To collect eggs and to facilitate accurate counting the following technique adequated as best by Prabhu (1960) was followed.

Burdick medium was used with the addition of a green edible dye (Permicol of Bush Co.) as it created a proper background for easy counting of eggs and also had soothing effect on the eyes. The earlier investigation (Prabhu, 1960) had proved that Drosophila melanogaster always preferred green colour to colourless medium for laying the eggs.

The green Burdick medium was poured into trays and petridishes upto 1 cm thickness and allowed to cool. The same were stored in refrigerator at 5$^{o}$C. Before use the food was cut into 1 x 1 cm cubes and mounted on card board pieces of 5 cm x 1 cm previously dipped in hot paraffin, in order to prevent absorption of moisture from the food and also to keep the food slab stick to it. Each of the food slab was seeded with a drop of live yeast suspension and allowed to dry up before use. These food chits were introduced into the test tubes of 6" x 3/4" in which the virgin females were pair mated. The food slab acted as oviposition platform.

These food chits were changed every 24 hours and the egg number was recorded from 72-96, 96-120 and 120-144 hours from the time of emergence with a binocular microscope of 6 X and 3 X magnification. After recording the egg production the food chips were transferred to test tube food vials and numbered accordingly to get next generation flies.

## HATCHABILITY

After recording the egg production of the 6th day (120-144 hours) the food chits were kept in sterile test tubes and incubated for 24 hours at 25°C. After 24 hours the number of unhatched eggs was recorded, since all the eggs of *Drosophila* hatch out within 24 hours (Demerec, 1950). By deducting this number from the total eggs produced on the 6th day, hatched eggs were known. Hatchability was expressed in terms of percentage of eggs that hatched from the number of eggs incubated.

## EGG SIZE

The egg size was determined from the eggs of the 7th day. The food chits were transferred to refrigerator to avoid the eggs from hatching. Five unhatched eggs were collected at random from each chit with the help of a fine brush in a drop of normal saline on a clean, sterilised slide.

Measurements of length and width were obtained with an ocular micrometer of 10 X magnification fitted to a monocular microscope with 10 X objective. The length was measured as the linear distance between two ends of the egg (from the base of the operculum to the posterior end of the egg) and the widest part of the egg was taken for measuring the width.

The volume of the egg was calculated by considering the egg as an eliptical body by the following formula :

$$\text{Egg volume} = \frac{II}{6}\, lw^2$$

where,

$II = 22/7$
$l$ = length
$w$ = width

## DESIGN OF EXPERIMENT

The investigation was begun with two stocks

(1) High line of sib selection (on half sib basis) at end of 20 generations selection - denoted as $H_1$

(2) Marker stock b 208.

Fifty pairs of flies were taken from each of these stocks and distributed equally in 5 separate culture bottles. The bottles were incubated at $25^{o}C \pm 1^{o}C$ and the flies were allowed to lay eggs for 24 hours. The imagos that emerged were collected to set up the experiment.

### BASE POPULATION

100 pairs each of $H_1$ and marker were collected and pair mated. The performance of the flies in respect of egg production, hatchability and egg size was recorded and the eggs from individual females were transferred to separate food vials with their identities marked, to raise next generation flies.

Virgin and males from the individual food vials were collected separately at 8 hourly intervals. From among 100 tubes, 37 tubes were selected which gave at least 8-10 each of virgins and males, to have a greater variability in the stock.

## $P_1$ GENERATION

### (1) Controls

#### (a) Half sib high line - 37 x 5 pairs

Five virgins of each vial were mated individually to their vial mates (brothers).

#### (b) Marker stock - 37 x 5 pairs

Five virgins from each vial were mated individually to their vial mates (brothers).

#### (c) Reciprocal cross - 37 x 5 pairs

Five virgins from each vial of half sib high line were individually mated to the males of a particular vial of marker stock. This was to introduce the marked X-chromosome in the genome of $H_1$ inbred line.

The performance of flies in both the controls and reciprocal cross was tested and the eggs incubated separately in separate food vials to raise next generation flies.

The virgins and males from all the tubes of a control line were collected, mixed and 100 pairs were selected at random.

From the reciprocal cross progeny only 100 Bar females were selected.

## $F_1$ GENERATION

### Controls

100 pair matings were set up and performance tested and the procedure to get next generation flies was repeated.

### Bar females x Marker males

100 bar females were individually mated to marker males and performance tested.

The progeny from this cross formed the nucleus of the experiment. The virgins and males from each tube were collected separately and each male and female was individually examined to classify them into various genotypes.

Due to recombination between marked and normal X-chromosomes various combinants were noticed, according to whether there was no crossing over, single or double crossing over. The possible triple crossing over was not noticed though about 3000-4000 flies each of males and females were examined. In all only 12 genotypes could be segregated out of 16 possible genotypes.

Scheme to show the origin of recombinant X-chromosomes from the inbred wild stock and marker b 208 stock.

| Initial types | 1-cross over derivitives | 2-cross over derivitives |
|---|---|---|
| + + + + | + + + + | + cv + fB |
| sc cv v fB | sc cv v fB | sc + v + |
| | sc + + + | + cv v + |
| | + cv v fB | sc + + fB |
| | sc cv + + | |
| | + + v fB | |
| | sc cv v + | |
| | + + + + | |

The same is diagrammatically presented in Fig. 1.

## $F_2$ GENERATION

At least 20 females and males of like phenotype were individually mated and performance tested. Only 8 out of 12 genotypes had sufficient number of pairs. Though the number of pairs in the remaining 4 genotypes was less, they were pair mated to raise next generation flies.

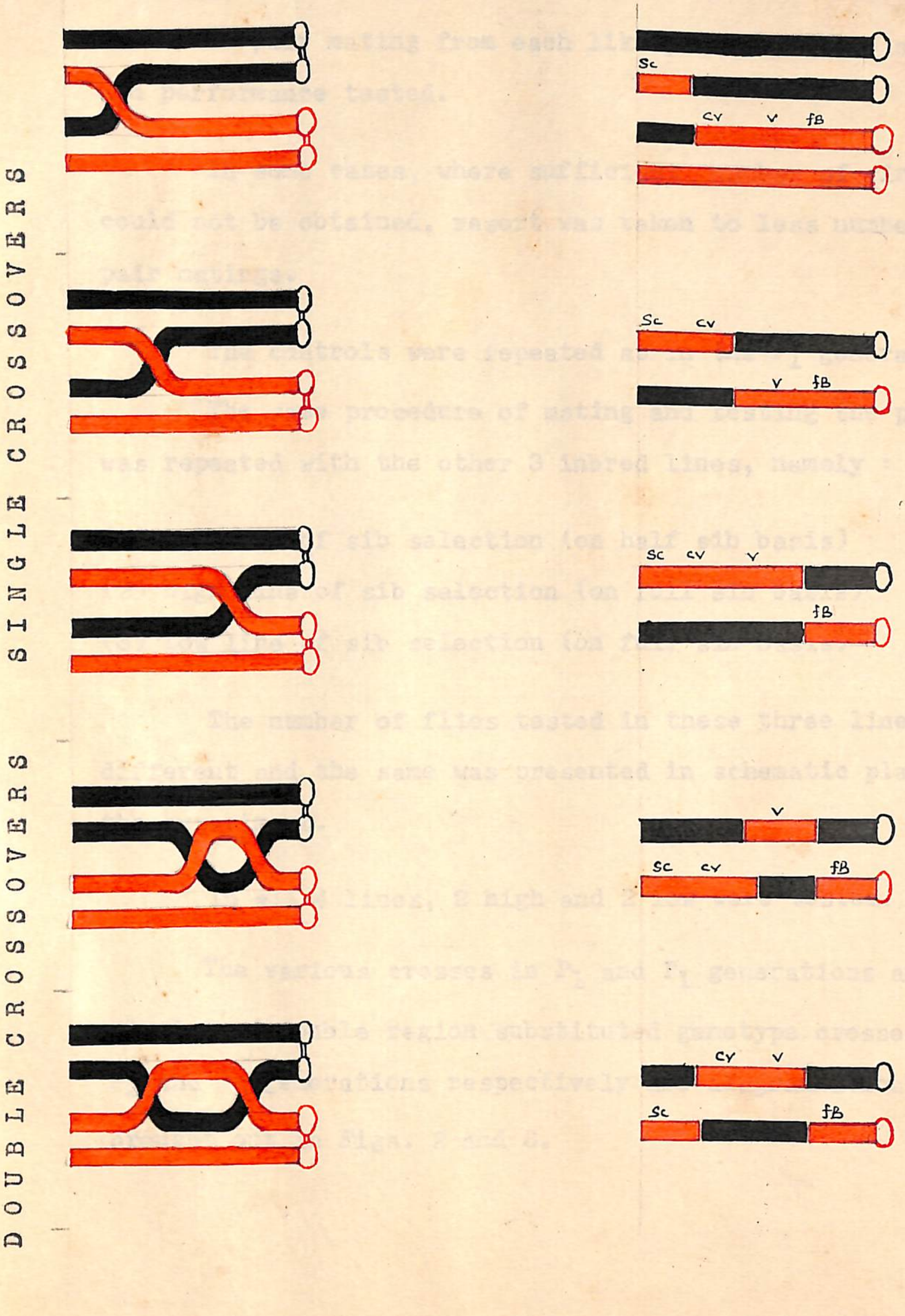
After recording the performance of flies in each genotypes the eggs were transferred to separate food vials taking maximum care to keep their identity perfect.

## $F_3$ GENERATION

The virgins and males from the individual vials of each genotype were collected separately and like phenotypes from

Fig. 1

# SCHEMATIC DIAGRAM SHOWING THE ORIGIN OF VARIOUS RECOMBINANT X CHROMOSOMES FROM THE INBRED WILD STOCK AND MARKER b 208



each batch of tubes were segregated.

20 pair mating from each like phenotype were set up and performance tested.

In some cases, where sufficient number of virgins could not be obtained, resort was taken to less number of pair matings.

The controls were repeated as in the $F_1$ generations.

The same procedure of mating and testing the performance was repeated with the other 3 inbred lines, namely :

(1) Low line of sib selection (on half sib basis)
(2) High line of sib selection (on full sib basis)
(3) Low line of sib selection (on full sib basis)

The number of flies tested in these three lines was different and the same was presented in schematic plan of the experiment.

In all 4 lines, 2 high and 2 low were tested.

The various crosses in $P_1$ and $F_1$ generations and the single and double region substituted genotype crosses in $F_2$ and $F_3$ generations respectively are diagrammatically brought out in Figs. 2 and 3.

## CROSSING SCHEME FOR HALF SIB HIGH LINE

| | $H_1$ x $H_1$ | $H_1$ x M | M x $H_1$ | M x M |
|---|---|---|---|---|
| Base population | 100♀♀ x 100♂♂ | | | 100♀♀ x 100♂♂ |
| $P_1$ | 161♀♀ x 161♂♂ | 155♀♀ x 155♂♂ | 157♀♀ x 157♂♂ | 139♀♀ x 139♂♂ |
| $F_1$ | 100♀♀ x 100♂♂ | 100♀♀ x 100♂♂ | 122♀♀ x 122♂♂ | 100♀♀ x 100♂♂ |
| $F_2$ | 100♀♀ x 100♂♂ | | | 100♀♀ x 100♂♂ |
| $F_3$ | 100♀♀ x 100♂♂ | | | 100♀♀ x 100♂♂ |

| | $F_2$ genotypes<br>24 pairs each<br>♀♀ | | ♂♂ | $F_3$ genotypes<br>22 pairs each<br>♂♂ | | ♀♀ |
|---|---|---|---|---|---|---|
| 1 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | x | $\frac{+\ +\ +\ +\ +}{\ }$ | $\frac{+\ +\ +\ +\ +}{\ }$ | x | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ |
| 2 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | x | $\frac{sc\ cv\ v\ f\ B}{\ }$ | $\frac{sc\ cv\ v\ f\ B}{\ }$ | x | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ |
| 3 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | x | $\frac{sc\ +\ +\ +\ +}{\ }$ | $\frac{sc\ +\ +\ +\ +}{\ }$ | x | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ |
| 4 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | x | $\frac{+\ cv\ v\ f\ B}{\ }$ | $\frac{+\ cv\ v\ f\ B}{\ }$ | x | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ |
| 5 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | x | $\frac{sc\ cv\ +\ +\ +}{\ }$ | $\frac{sc\ cv\ +\ +\ +}{\ }$ | x | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ |
| 6 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | x | $\frac{+\ +\ v\ f\ B}{\ }$ | $\frac{+\ +\ v\ f\ B}{\ }$ | x | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ |
| 7 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | x | $\frac{sc\ cv\ v\ +\ +}{\ }$ | $\frac{sc\ cv\ v\ +\ +}{\ }$ | x | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ |
| 8 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | x | $\frac{+\ +\ +\ f\ B}{\ }$ | $\frac{+\ +\ +\ f\ B}{\ }$ | x | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ |
| 9 | | | | $\frac{+\ +\ v\ +\ +}{\ }$ | x | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ |
| 10 | | | | $\frac{sc\ cv\ +\ f\ B}{\ }$ | x | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ |
| 11 | | | | $\frac{+\ cv\ v\ +\ +}{\ }$ | x | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ |
| 12 | | | | $\frac{sc\ +\ +\ f\ B}{\ }$ | x | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ |

## CROSSING SCHEME FOR HALF SIB LOW LINE

| | $L_1$ x $L_1$ (CONTROL) | $L_1$ x M | | $F_2$ Genotypes 20 pairs each | $F_3$ Genotypes 20 pairs each | M x M (CONTROL) |
|---|---|---|---|---|---|---|
| | 60 ♀♀ x 60 ♂♂ | | | | | 60 ♀♀ x 60 ♂♂ |
| $P_1$ | 100♀♀ x 100 ♂♂ | 85 ♀♀ x 85 ♂♂ (CROSS) | | | | 99 ♀♀ x 99 ♂♂ |
| $F_1$ | 50♀♀ x 50 ♂♂ | 75 ♀♀ x 75 ♂♂ | | | | 50 ♀♀ x 50 ♂♂ |
| $F_2$ | 50♀♀ x 50 ♂♂ | | | | | 50 ♀♀ x 50 ♂♂ |
| | | | 1 | $\frac{\text{+ + + + +}}{\text{sc cv v f B}}$ x $\underline{\text{+ + + + +}}$ | $\underline{\text{+ + + + +}}$ x $\frac{\text{+ + + + +}}{\text{+ + + + +}}$ | |
| | | | 2 | $\frac{\text{sc cv v f B}}{\text{sc cv v f B}}$ x $\underline{\text{sc cv v f B}}$ | $\underline{\text{sc cv v f B}}$ x $\frac{\text{sc cv v f B}}{\text{sc cv v f B}}$ | |
| | | | 3 | $\frac{\text{sc + + + +}}{\text{sc cv v f B}}$ x $\underline{\text{sc + + + +}}$ | $\underline{\text{sc + + + +}}$ x $\frac{\text{sc + + + +}}{\text{sc + + + +}}$ | |
| $F_3$ | 50♀♀ x 50 ♂♂ | | 4 | $\frac{\text{+ cv v f B}}{\text{sc cv v f B}}$ x $\underline{\text{+ cv v f B}}$ | $\underline{\text{+ cv v f B}}$ x $\frac{\text{+ cv v f B}}{\text{+ cv v f B}}$ | 46 ♀♀ x 46 ♂♂ |
| | | | 5 | $\frac{\text{sc cv + + +}}{\text{sc cv v f B}}$ x $\underline{\text{sc cv + + +}}$ | $\underline{\text{sc cv + + +}}$ x $\frac{\text{sc cv + + +}}{\text{sc cv + + +}}$ | |
| | | | 6 | $\frac{\text{+ + v f B}}{\text{sc cv v f B}}$ x $\underline{\text{+ + v f B}}$ | $\underline{\text{+ + v f B}}$ x $\frac{\text{+ + v f B}}{\text{+ + v f B}}$ | |
| | | | 7 | $\frac{\text{sc cv v + +}}{\text{sc cv v f B}}$ x $\underline{\text{sc cv v + +}}$ | $\underline{\text{sc cv v + +}}$ x $\frac{\text{sc cv v + +}}{\text{sc cv v + +}}$ | |
| | | | 8 | $\frac{\text{+ + + f B}}{\text{sc cv v f B}}$ x $\underline{\text{+ + + f B}}$ | $\underline{\text{+ + + f B}}$ x $\frac{\text{+ + + f B}}{\text{+ + + f B}}$ | |
| | | | 9 | | $\underline{\text{+ + v + +}}$ x $\frac{\text{+ + v + +}}{\text{+ + v + +}}$ | |
| | | | 10 | | $\underline{\text{sc cv + f B}}$ x $\frac{\text{sc cv + f B}}{\text{sc cv + f B}}$ | |
| | | | 11 | | $\underline{\text{+ cv v + +}}$ x $\frac{\text{+ cv v + +}}{\text{+ cv v + +}}$ | |
| | | | 12 | | $\underline{\text{sc + + f B}}$ x $\frac{\text{sc + + f B}}{\text{sc + + f B}}$ | |

# CROSSING SCHEME FOR FULL SIB HIGH LINE

|  | $H_2$ x $H_2$ | $H_2$x M | M x M |
|---|---|---|---|
|  | 60♀♀ x 60♂♂ |  | 60♀♀ x 60♂♂ |
| $P_1$ | 97♀♀ x 97♂♂ | 95♀♀ x 95♂♂ | 78♀♀ x 78♂♂ |
| $F_1$ | 50♀♀ x 50♂♂ | 50♀♀ x 50♂♂ | 46♀♀ x 46♂♂ |
| $F_2$ | 50♀♀ x 50♂♂ |  | 50♀♀ x 50♂♂ |
| $F_3$ | 50♀♀ x 50♂♂ |  | 50♀♀ x 50♂♂ |

|  | $F_2$ Genotypes<br>20 pairs each<br>♀♀ |  | ♂♂ | $F_3$ Genotypes<br>20 pairs each<br>♂♂ |  | ♀♀ |
|---|---|---|---|---|---|---|
| 1 | $\dfrac{\text{+ + + + +}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{+ + + + +}}}$ | $\underline{\underline{\text{+ + + + +}}}$ | x | $\dfrac{\text{++ + + +}}{\text{++ + + +}}$ |
| 2 | $\dfrac{\text{sc cv v f B}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{sc cv v f B}}}$ | $\underline{\underline{\text{sc cv v f B}}}$ | x | $\dfrac{\text{sc cv v f B}}{\text{sc cv v f B}}$ |
| 3 | $\dfrac{\text{sc + + + +}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{sc + + + +}}}$ | $\underline{\underline{\text{sc + + + +}}}$ | x | $\dfrac{\text{sc + + + +}}{\text{sc + + + +}}$ |
| 4 | $\dfrac{\text{+ cv v f B}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{+ cv v f B}}}$ | $\underline{\underline{\text{+ cv v f B}}}$ | x | $\dfrac{\text{+ cv v f B}}{\text{+ cv v f B}}$ |
| 5 | $\dfrac{\text{sc cv + + +}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{sc cv + + +}}}$ | $\underline{\underline{\text{sc cv + + +}}}$ | x | $\dfrac{\text{sc cv + + +}}{\text{sc cv + + +}}$ |
| 6 | $\dfrac{\text{+ + v f B}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{+ + v f B}}}$ | $\underline{\underline{\text{+ + v f B}}}$ | x | $\dfrac{\text{+ + v f B}}{\text{+ + v f B}}$ |
| 7 | $\dfrac{\text{sc cv v + +}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{sc cv v + +}}}$ | $\underline{\underline{\text{sc cv v + +}}}$ | x | $\dfrac{\text{sc cv v + +}}{\text{sc cv v + +}}$ |
| 8 | $\dfrac{\text{+ + + f B}}{\text{sc cv v f B}}$ | x | $\underline{\underline{\text{+ + + f B}}}$ | $\underline{\underline{\text{+ + + f B}}}$ | x | $\dfrac{\text{+ + + f B}}{\text{+ + + f B}}$ |
| 9 |  |  |  | $\underline{\underline{\text{+ + v + +}}}$ | x | $\dfrac{\text{+ + v + +}}{\text{+ + v + +}}$ |
| 10 |  |  |  | $\underline{\underline{\text{sc cv + f B}}}$ | x | $\dfrac{\text{sc cv + f B}}{\text{sc cv + f B}}$ |
| 11 |  |  |  | $\underline{\underline{\text{+ cv v + +}}}$ | x | $\dfrac{\text{+ cv v + +}}{\text{+ cv v + +}}$ |
| 12 |  |  |  | $\underline{\underline{\text{sc + + f B}}}$ | x | $\dfrac{\text{sc + + f B}}{\text{sc + + f B}}$ |

## CROSSING SCHEME FOR FULL SIB LOW LINE

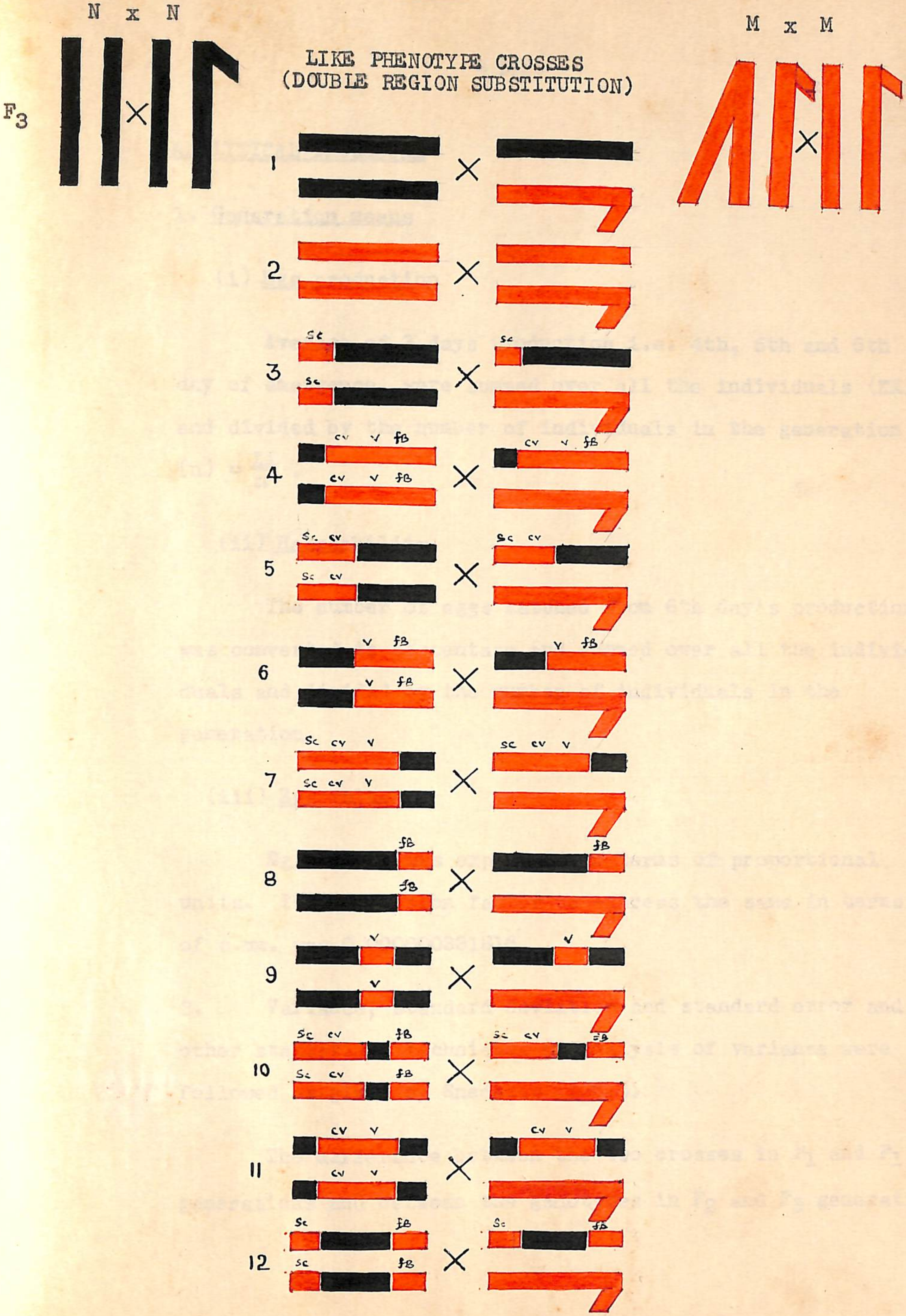
| | $L_2$ x $L_2$ (Control) | $L_2$ x M | M x M (Control) |
|---|---|---|---|
| | 50♀♀ x 50♂♂ | | 60♀♀ x 60♂♂ |
| $P_1$ | 100♀♀ x 100♂♂ | 100♀♀ x 100♂♂ | 99♀♀ x 99♂♂ |
| $F_1$ | 50♀♀ x 50♂♂ | 60♀♀ x 60♂♂ | 50♀♀ x 50♂♂ |
| $F_2$ | 50♀♀ x 50♂♂ | | 50♀♀ x 50♂♂ |
| $F_3$ | 40♀♀ x 40♂♂ | | 46♀♀ x 46♂♂ |

| | $F_2$ Genotypes<br>20 pairs each<br>♀♀ | | ♂♂ | $F_3$ Genotypes<br>22 pairs each<br>♂♂ | | ♀♀ |
|---|---|---|---|---|---|---|
| 1 | $\dfrac{+\ +\ +\ +\ +}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{+\ +\ +\ +\ +}{}$ | $\dfrac{+\ +\ +\ +\ +}{}$ | x | $\dfrac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ |
| 2 | $\dfrac{\mathrm{sc\ cv\ v\ f\ B}}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{\mathrm{sc\ cv\ v\ f\ B}}{}$ | $\dfrac{\mathrm{sc\ cv\ v\ f\ B}}{}$ | x | $\dfrac{\mathrm{sc\ cv\ v\ f\ B}}{\mathrm{sc\ cv\ v\ f\ B}}$ |
| 3 | $\dfrac{\mathrm{sc}\ +\ +\ +\ +}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{\mathrm{sc}\ +\ +\ +\ +}{}$ | $\dfrac{\mathrm{sc}\ +\ +\ +\ +}{}$ | x | $\dfrac{\mathrm{sc}\ +\ +\ +\ +}{\mathrm{sc}\ +\ +\ +\ +}$ |
| 4 | $\dfrac{+\ \mathrm{cv\ v\ f\ B}}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{+\ \mathrm{cv\ v\ f\ B}}{}$ | $\dfrac{+\ \mathrm{cv\ v\ f\ B}}{}$ | x | $\dfrac{+\ \mathrm{cv\ v\ f\ B}}{+\ \mathrm{cv\ v\ f\ B}}$ |
| 5 | $\dfrac{\mathrm{sc\ cv}\ +\ +\ +}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{\mathrm{sc\ cv}\ +\ +\ +}{}$ | $\dfrac{\mathrm{sc\ cv}\ +\ +\ +}{}$ | x | $\dfrac{\mathrm{sc\ cv}\ +\ +\ +}{\mathrm{sc\ cv}\ +\ +\ +}$ |
| 6 | $\dfrac{+\ +\ \mathrm{v\ f\ B}}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{+\ +\ \mathrm{v\ f\ B}}{}$ | $\dfrac{+\ +\ \mathrm{v\ f\ B}}{}$ | x | $\dfrac{+\ +\ \mathrm{v\ f\ B}}{+\ +\ \mathrm{v\ f\ B}}$ |
| 7 | $\dfrac{\mathrm{sc\ cv\ v}\ +\ +}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{\mathrm{sc\ cv\ v}\ +\ +}{}$ | $\dfrac{\mathrm{sc\ cv\ v}\ +\ +}{}$ | x | $\dfrac{\mathrm{sc\ cv\ v}\ +\ +}{\mathrm{sc\ cv\ v}\ +\ +}$ |
| 8 | $\dfrac{+\ +\ +\ \mathrm{f\ B}}{\mathrm{sc\ cv\ v\ f\ B}}$ | x | $\dfrac{+\ +\ +\ \mathrm{f\ B}}{}$ | $\dfrac{+\ +\ +\ \mathrm{f\ B}}{}$ | x | $\dfrac{+\ +\ +\ \mathrm{f\ B}}{+\ +\ +\ \mathrm{f\ B}}$ |
| 9 | | | | $\dfrac{+\ +\ \mathrm{v}\ +\ +}{}$ | x | $\dfrac{+\ +\ \mathrm{v}\ +\ +}{+\ +\ \mathrm{v}\ +\ +}$ |
| 10 | | | | $\dfrac{\mathrm{sc\ cv}\ +\ \mathrm{f\ B}}{}$ | x | $\dfrac{\mathrm{sc\ cv}\ +\ \mathrm{f\ B}}{\mathrm{sc\ cv}\ +\ \mathrm{f\ B}}$ |
| 11 | | | | $\dfrac{+\ \mathrm{cv\ v}\ +\ +}{}$ | x | $\dfrac{+\ \mathrm{cv\ v}\ +\ +}{+\ \mathrm{cv\ v}\ +\ +}$ |
| 12 | | | | $\dfrac{\mathrm{sc}\ +\ +\ \mathrm{f\ B}}{}$ | x | $\dfrac{\mathrm{sc}\ +\ +\ \mathrm{f\ B}}{\mathrm{sc}\ +\ +\ \mathrm{f\ B}}$ |

Fig. 2

DIAGRAMATIC REPRESENTATION OF VARIOUS CROSSES IN DIFFERENT GENERATIONS

Fig. 3



LIKE PHENOTYPE CROSSES
(DOUBLE REGION SUBSTITUTION)

## ANALYTICAL PROCEDURE

### 1. Generation means

### (i) Egg production

Average of 3 days production i.e. 4th, 5th and 6th day of emergence, were summed over all the individuals ($\Sigma X$) and divided by the number of individuals in the generation (n) $= \frac{\Sigma X}{n}$.

### (ii) Hatchability

The number of eggs hatched from 6th day's production was converted to percentage and summed over all the individuals and divided by the number of individuals in the generation.

### (iii) Egg volume

Egg volume was expressed in terms of proportional units. The conversion factor to express the same in terms of c.mm. was 0.000000331816.

2. Variance, standard deviation and standard error and other statistical techniques of analysis of variance were followed as given by Snedecor (1961).

The difference between the two crosses in $P_1$ and $F_1$ generations and between the genotypes in $F_2$ and $F_3$ generations was found by critical difference test as per the following formula :

$$C.D. = t_{05} \sqrt{\left(\frac{1}{K_1} + \frac{1}{K_2}\right) \sigma^2_e}$$

where $t_{05}$ = tabulated value of 't' at 0.05 level for error degrees of freedom

$K_1$ & $K_2$ = number of observations in two groups

$\sigma^2_e$ = error mean square

3. Main Effects

For calculating the main effects of various segments of the chromosome linear contrast method as in the analysis of factorial design was followed.

Taking the four segments of X-chromosome as four factors A, B, C and D at two levels of presence or absence of normal segments as against the marker segments, the main effects of the segments were calculated as follows :

$$\text{Main effects of } A = \frac{1}{8}\left[(a-1)(b+1)(c+1)(d+1)\right]$$

$$= \frac{1}{8}\left[abcd+acd+abd+abc+ac+ab+ad+a-b-c-d-bc-cd-bd-bcd-1\right]$$

$$B = \frac{1}{8}\left[(a+1)(b-1)(c+1)(d+1)\right]$$

$$= \frac{1}{8}\left[abcd+abc+abd+ab+bcd+bc+bd+b-acd-ac-ad-a-cd-c-d-1\right]$$

$$C = \frac{1}{8}\left[(a+1)(b+1)(c-1)(d+1)\right]$$

$$= \frac{1}{8}\left[abcd+abc+acd+ac+bcd+bc+cd+c-abd-ab-ad-a-bd-b-d-1\right]$$

$$D = \frac{1}{8}\left[(a+1)(b+1)(c+1)(d-1)\right]$$

$$= \frac{1}{8}\left[abcd+abd+acd+ad+bcd+bd+cd+d-abc-ab-ac-a-bc-b-c-1\right]$$

As all the possible combinations of various segments could not be got, main effects were calculated with available contrasts.

Representing in terms of linear contrasts of the genotypes, in $F_3$ the main effects of various segments could be had as follows :

$$A = \frac{1}{4}\left[abcd-bcd+abc-bc+ad-d+a-1\right]$$

$$= \frac{1}{4}\left[\left(\frac{\text{++++}}{\text{++++}} - \frac{\text{sc +++}}{\text{sc +++}}\right) + \left(\frac{\text{+++ fB}}{\text{+++ fB}} - \frac{\text{sc ++ fB}}{\text{sc ++ fB}}\right) + \left(\frac{\text{+ cv v +}}{\text{+ cv v +}} - \frac{\text{sc cv v +}}{\text{sc cv v +}}\right) + \left(\frac{\text{+ cv v fB}}{\text{+ cv v fB}} - \frac{\text{sc cv v fB}}{\text{sc cv v fB}}\right)\right]$$

$$B = \frac{1}{4}\left[\frac{abd-ad}{1} + \frac{ab-a}{2} + \frac{bcd-cd}{3} + \frac{bc-c}{4}\right]$$

$$= \frac{1}{4}\left[\left(\frac{\text{++ v +}}{\text{++ v +}} - \frac{\text{+ cv v +}}{\text{+ cv v +}}\right) + \left(\frac{\text{++ v fB}}{\text{++ v fB}} - \frac{\text{+ cv v fB}}{\text{+ cv v fB}}\right) + \left(\frac{\text{sc +++}}{\text{sc +++}} - \frac{\text{sc cv ++}}{\text{sc cv ++}}\right) + \left(\frac{\text{sc ++ fB}}{\text{sc ++ fB}} - \frac{\text{sc cv + fB}}{\text{sc cv + fB}}\right)\right]$$

$$C = \frac{1}{4}\left[ abcd - abd + abc - ab + cd - d + c - 1 \right]$$

$$\begin{aligned}
&= \frac{1}{4}\Big[ \Big(\frac{\text{++++}}{\text{++++}} - \frac{\text{++ v +}}{\text{++ v +}}\Big) + \Big(\frac{\text{+++ fB}}{\text{+++ fB}} - \frac{\text{++ v fB}}{\text{++ v fB}}\Big) + \\
&\qquad \Big(\frac{\text{sc cv ++}}{\text{sc cv ++}} - \frac{\text{sc cv v +}}{\text{sc cv v +}}\Big) + \Big(\frac{\text{sc cv + fB}}{\text{sc cv + fB}} - \frac{\text{sc cv v fB}}{\text{sc cv v fB}}\Big) \Big]
\end{aligned}$$

$$D = \frac{1}{6}\left[ abcd - abc + ad - a + bcd - bc + cd - c + d - 1 + abd - ab \right]$$

$$\begin{aligned}
&= \frac{1}{6}\Big[ \Big(\frac{\text{++++}}{\text{++++}} - \frac{\text{+++ fB}}{\text{+++ fB}}\Big) + \Big(\frac{\text{sc +++}}{\text{sc +++}} - \frac{\text{sc ++ fB}}{\text{sc ++ fB}}\Big) + \\
&\qquad \Big(\frac{\text{+ cv v +}}{\text{+ cv v +}} - \frac{\text{+ cv v fB}}{\text{+ cv v fB}}\Big) + \Big(\frac{\text{sc cv ++}}{\text{sc cv ++}} - \frac{\text{sc cv + fB}}{\text{sc cv + fB}}\Big) + \\
&\qquad \Big(\frac{\text{sc cv v +}}{\text{sc cv v +}} - \frac{\text{sc cv v fB}}{\text{sc cv v fB}}\Big) + \Big(\frac{\text{++ v +}}{\text{++ v +}} - \frac{\text{++ v fB}}{\text{++ v fB}}\Big) \Big]
\end{aligned}$$

The various interactions as in the factorial analysis could not be calculated because 4 out of 16 possible genotypes due to recombination could not be segregated.

# RESULTS

## EGG PRODUCTION

In Table 1 are presented the mean daily egg production data of half sib high line ($H_1$) and the marker stock (M) and their reciprocal crosses.

$H_1$ produced higher number of eggs than M. Though the actual number of eggs in a given generation showed variation, this relationship was borne throughout the duration of the experiment which lasted for about 5 generations. Thus in the base population $H_1$ produced 50 eggs which were 5 more than produced by M. In $F_3$, $H_1$ produced about 63 eggs, while M produced 52 eggs, which were 11 more in favour of $H_1$. In $F_1$ generation, for example, $H_1$ produced only 40 eggs. M produced 30 which was 10 lower than $H_1$.

$H_1$ ♀♀ fertilised by M ♂♂ gave on an average 40 eggs per day. On the other hand M ♀♀ fertilised by $H_1$ males gave an average of 44 eggs daily. Theoretically, the production of $H_1$ and M females should have been the same as the 2 controls. Stimulation by males for producing eggs could not be ruled out as Prabhu (1960) had shown that the presence of males to be essential for the normal reaction of egg producing behaviour in females. Apparently, the $H_1$ male was capable of inducing M female to produce more eggs than $H_1$ female when mated by M males.

## Table 1

Mean daily egg production in $H_1$, M and crosses

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $H_1$ ♂ x $H_1$ ♀ (a) | 50.0 | 51.9±1.12 | 40.2±1.83 | 62.4±1.48 | 62.9±1.51 |
| M ♂ x M ♀ (b) | 45.4 | 46.2±1.33 | 30.2±2.22 | 51.3±1.73 | 52.0±1.92 |
| $H_1$ ♀ x M ♂ (c) | - | 40.4±1.20 | 55.4±2.41 | | |
| M ♀ x $H_1$♂ (d) | - | 44.1±1.10 | 58.3±2.00 | | |
| **Differences** | | | | | |
| (a-b) | 4.6* | 5.7* | 10.0* | 11.1* | 10.0* |
| (c-d) | | -3.7 NS | -2.9 NS | | |
| (a-c) | | 11.5* | -15.1* | | |
| (a-d) | | 7.8* | -18.1* | | |
| (b-c) | | 5.8* | -25.2* | | |
| (b-d) | | 2.1 NS | -28.1* | | |

## Performance of $F_2$ females

The $F_2$ genotypes were produced through backcrossing of $F_1$ females arising from the $H_1$ ♀♀ x M ♂♂ cross to M ♂♂. Due to crossing over in the $F_1$ female between $H_1$ and M - X chromosomes, actually 8 types of genotypes containing various proportion of $H_1$ and M X chromosome in one of the X homologue were got. The other homologue had the full M stock X chromosome that contained the genes sc, cv, v, f and B. The mean daily egg production found in the different types of $F_2$ females are given in Table 2.

### Table 2

Mean daily egg production of $F_2$ females of
$H_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production Mean | S.E. |
|---|---|---|---|---|
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 24 | 18.5 | 4.11 |
| 2 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 20.1 | 3.39 |
| 3 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 24 | 34.1 | 4.30 |
| 4 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 24 | 37.8 | 4.82 |
| 5 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 24 | 40.6 | 4.32 |

Table 2 (contd)

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 6 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 24 | 48.5 | 3.36 |
| 7 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 23 | 56.8 | 2.97 |
| 8 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 24 | 58.9 | 2.80 |

An analysis of variance carried out on the basic performance data of the 8 genotypes showed highly significant differences in performance among the genotypes. Critical difference test further showed that genotypes 1 and 2; 3, 4, 5 and 6 and 7 and 8 did not differ significantly among themselves, but each group differed significantly from the other. The results are shown below using Bar notation.

```
1  2  3  4  5  6  7  8
----
   ----
      ----------
               --------
```

As the performance in the 8 genotypes had been arranged in ascending order, close examination of the genetic construction of the flies showed that those that contained both the X chromosomes of M line gave the least production (18.5 eggs) and those that contained one X of M and the other of $H_1$ gave the highest (58.9 eggs) number of eggs. The difference due to the substitution of one $H_1$ X chromosome in $M_1$ stock was the increase of about 40 eggs per day. No doubt part of the increase could be due to interaction of the two chromosomes, yet the inescapable fact remained that the $H_1$ X chromosome had *dominant* genes affecting production so that they could show their effect even when present in a single dose.

Coming to the contribution of part of a given X chromosome, if we deduct the performance of the females of the genotypes ($\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$) from genotype 2 females, we get the probable contribution of the region from 0 to 13 crossover units in the chromosome map (cv is at 13 units). This comes to 20.1 - 18.5 = 1.6 eggs. Another estimate can be obtained by deducting the performance of females having genotype 7 i.e. $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ from that of genotype 8 i.e. $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ . This comes to 2.1. This meant that the region left of *crossveinless* had no major dominant genes affecting egg production.

Next the effect of the portion represented by the region of the chromosome round about *cv* was considered. This was obtained by deducting performance of genotype 2 ($\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$) from genotype 3 ($\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$). This gave 34.1 - 20.1 = 14 eggs. The effect of *cv* region of X chromosome can also be obtained by deducting mean daily egg production of genotype 6 ($\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$) from that of genotype 7 i.e. $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$. This came to 56.8 - 48.5 = 8.3 eggs.

Now the effect of the region on X chromosome was considered round about the gene <u>vermilion</u> (v). The effect was studied by deducting the performance of females having genotype 3 i.e. $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ from that of genotype 4 i.e. $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$. This came to 37.8 - 34.1 = 3.7 eggs. We can also get an idea of the effect of <u>vermilion</u> region by deducting the performance of females having genotype 6, i.e. $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ from those of genotype 5 i.e. $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$. This came to 48.5 - 40.6 = 7.9 eggs. Even if the higher estimate (7.9 eggs) was taken the figure was very much less than for the region <u>crossveinless</u>.

Because of close proximity of <u>forked</u> and <u>Bar</u>, crossovers between the two were rare and not found in the cultures raised in this experiment. Hence the region of the chromosome represented by these 2 genes could not be considered separately. They were therefore taken together and described as <u>forked-Bar</u> region. The effect of <u>forked-Bar</u> region on egg production could be estimated by deducting the performance of females having genotype 4 i.e. $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ from those of genotype 8 i.e. $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ or by deducting the performance of females having genotype 1 i.e. $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ from those of genotype 5 i.e. $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$. The two estimates obtained worked out to 21.1 and 22.1 respectively which were practically equal.

The relative effects of various regions of X chromosome on egg production could be summarised as under in Table 3.

Table 3

Effect of portions of one X chromosome of $H_1$ on egg production

| Sl. No. | Region of X chromosome | No. of eggs | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | *scute* (sc) | 1.6<br>2.1 | 1.9 |
| 2 | *crossveinless* (cv) | 14.0<br>8.3 | 11.2 |
| 3 | *vermilion* (v) | 7.9<br>3.7 | 5.8 |
| 4 | *forked-Bar* (fB) | 21.1<br>22.1 | 21.6 |
| 5 | Entire X chromosome | 40.4 | |

The discripancies in the 2 estimates at serial Nos. 2 and 3, probably was due to inclusion or non-inclusion of region containing the dominant genes affecting egg production.

All the same, conclusions could be drawn without hesitation that the *forked-Bar* region of X chromosome contained major dominant genes affecting egg production. Some of these dominants affecting egg production were also located in the region *right* of *crossveinless*. In other regions of X chromosome, there appeared to be fewer dominant genes affecting egg production.

An $F_3$ was raised by crossing like $F_2$ genotypes. This was done to ensure that $F_2$ results were not masked by heterotic effects. The results of the $F_3$ cross are presented in Table 4.

## Table 4

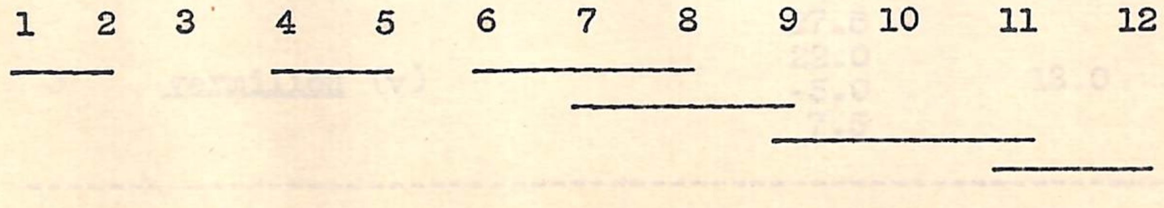
Mean daily egg production of $F_3$ females of
$H_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 8.7 | 2.70 |
| 2 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 20 | 11.4 | 2.16 |
| 3 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 22 | 25.1 | 4.76 |
| 4 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 22 | 34.1 | 4.21 |

Table 4 (contd)

| Sl. No. | Genotype | No. of females tested | Mean daily egg production Mean | Mean daily egg production S.E. |
|---|---|---|---|---|
| 5 | $\frac{\text{sc cv + f B}}{\text{sc cv + f B}}$ | 22 | 36.2 | 4.23 |
| 6 | $\frac{\text{+ + + f B}}{\text{+ + + f B}}$ | 21 | 47.1 | 4.86 |
| 7 | $\frac{\text{+ cv v + +}}{\text{+ cv v + +}}$ | 22 | 49.3 | 3.24 |
| 8 | $\frac{\text{sc cv + + +}}{\text{sc cv + + +}}$ | 22 | 51.8 | 3.06 |
| 9 | $\frac{\text{sc cv v + +}}{\text{sc cv v + +}}$ | 22 | 54.8 | 2.80 |
| 10 | $\frac{\text{sc + + + +}}{\text{sc + + + +}}$ | 20 | 62.5 | 1.35 |
| 11 | $\frac{\text{+ + v + +}}{\text{+ + v + +}}$ | 20 | 65.0 | 3.82 |
| 12 | $\frac{\text{+ + + + +}}{\text{+ + + + +}}$ | 22 | 72.5 | 2.48 |

Analysis of variance of the above results showed that the differences among genotypes were statistically significant. Using critical difference test and Bar notation, the significance of differences in mean daily egg production of the 12 genotypes are brought out graphically below :



The difference in number of eggs between genotypes 1 and 12 gave the effect of the homozygous X on egg production. Thus instead of the 2 X-chromosomes of M stock, if we have 2 of $H_1$ stock, then there would be an increase of about 64 eggs in daily production. The effect of various regions had been worked out and the results are brought out below (Table 5). In the present instance the effect was due to duplicate regions and not due to single regions as considered earlier. There were 4 estimates for all regions except fB region for which there were 6 estimates. They were averaged to get a firm estimate.

Table 5

Effect of portions of X chromosome of $H_1$ on egg production (duplicate effects)

| Sl. No. | Region of X chromosome | No. of eggs Estimates | No. of eggs Mean |
|---|---|---|---|
| 1 | scute (sc) | 10.0<br>2.7<br>-7.5<br>13.0 | 4.6 |
| 2 | crossveinless (cv) | 10.7<br>13.7<br>15.7<br>-2.1 | 9.5 |
| 3 | vermilion (v) | 27.5<br>22.0<br>-5.0<br>7.5 | 13.0 |

Table 5 (contd)

| Sl. No. | Region of X chromosome | No. of eggs<br>Estimates | <br>Mean |
|---|---|---|---|
| 4 | forked-Bar (fB) | 25.0<br>48.1<br>28.4<br>37.9<br>15.6<br>39.9 | 32.6 |

The variation which one observed among estimates within a region might be due to sampling or due to the compared genotypes containing not exactly the same complement of genes in the regions taken as same or identical. With the markers used, it was not possible to probe further into this aspect of the problem.

In spite of the rather crude analysis employed, one thing came to clear again that the forked-Bar region of X-chromosome contained a highly potence region affecting egg production. Since the earlier result had shown that the effect was seen even when in one dose, it was equally patent that the genes concerned were dominant ones. Next in order came vermilion, region followed next by crossveinless and scute regions. The higher contribution of vermilion region could have been due to inclusion of potent regions of crossveinless region in the genotypes considered for testing the effect of vermilion region. It might be remembered that earlier study had shown that next to forked-Bar was the crossveinless region.

## Crosses with half sib low line ($L_1$)

In Table 6 are summarised the mean daily egg production in half sib low line ($L_1$), the marker stock M and their cross.

Table 6

Mean daily egg production in $L_1$, M and their cross

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $L_1$ ♂ x $L_1$ ♀ (a) | 33.8 ±1.43 | 43.2 ±1.65 | 40.7 ±2.05 | 47.5 ±1.92 | 47.5 ±2.29 |
| M ♂ x M ♀ (b) | 46.1 ±1.99 | 60.3 ±1.55 | 32.5 ±3.59 | 62.8 ±4.41 | 60.6 ±4.07 |
| $L_1$ ♀ x M ♂ (c) | - | 39.6 ±1.44 | 49.3 ±3.19 | - | - |
| Differences | | | | | |
| (a-b) | -12.3* | -17.1* | 8.0* | -15.3* | -13.1* |
| (a-c) | - | 3.6 NS | -8.6* | - | - |
| (b-c) | - | 20.7* | -16.8* | - | - |

The average daily egg production in M line was higher than in $L_1$ line by about 12 eggs. This difference was maintained in subsequent generations except in generation $F_1$ where the $L_1$ line produced about 8 eggs more than the M line. This was probably due to chance. In $L_1$ females fertilised by M males, the production did not show a significant departure from the production of $L_1$ line. The $F_1$ females arising from the cross however, as expected yielded higher than either of the two parents. The actual production was 49 eggs as opposed to 33 of M and 41 of $L_1$ lines. The differences were significant.

## Performance of $F_2$ females from $L_1$ x M cross

In Table 7 are presented the mean daily egg production of different females of $F_2$.

Table 7

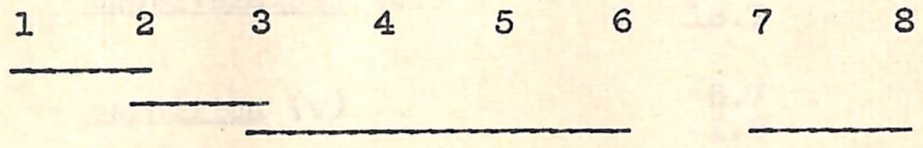
Mean daily egg production of $F_2$ females from $L_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 17 | 15.2 | 3.57 |
| 2 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 18.3 | 5.15 |
| 3 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 30.1 | 5.11 |

Table 7 (contd)

| Sl. No. | Genotype | No. of females tested | Mean daily egg production<br>Mean | <br>S.E. |
|---|---|---|---|---|
| 4 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 31.9 | 5.51 |
| 5 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 35.9 | 4.73 |
| 6 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 42.6 | 5.61 |
| 7 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 61.3 | 4.21 |
| 8 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 67.7 | 2.85 |

An analysis of variance carried out on the above data revealed significant differences in the performance of different genotypes. Using critical difference and Bar notation, the results are represented graphically below :



There was no significant variation in genotypes 1 and 2, 3 to 6 and 7 to 8. In addition 2 did not differ significantly from 3. In other cases, each group differed significantly from the other groups. The situation which was found here was exactly as in $F_2$ of $H_1$ x M with minor difference and that was that the last 3 genotypes in the former did not differ from each other, whereas only the last 2 did not differ from each other in the present instance.

The difference between the performance of flies of genotypes 8 and 2 will give an idea of the contribution of one homologous $L_1$ chromosome for egg production. It worked out to 49 eggs. The contributions of the different regions of X chromosome had been worked out and are given in Table 8.

Table 8

Effect of portions of one X chromosome of $L_1$ on egg production

| Sl. No. | Region of X chromosome | No. of eggs | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | *scute* (sc) | -3.1<br>6.4 | 1.7 |
| 2 | *crossveinless* (cv) | 16.7<br>18.7 | 17.7 |
| 3 | *vermilion* (v) | 6.7<br>-1.8 | 2.5 |
| 4 | *forked-Bar* (fB) | 17.6<br>37.6 | 27.6 |
| 5 | Whole X chromosome | 49.4 | |

As in $H_1$, it was observed that the *forked-Bar* region had the most potent effect on egg production in $L_1$ line as well. It was higher than that in $H_1$ in fact by about 6 eggs. Next in order of importance came the *crossveinless* region, *vermilion* region and the *scute* region respectively. The total of all the regions came upto the same value as the total for the whole of X chromosome.

Results of $F_3$ are given in Table 9.

### Table 9

Mean daily egg production in $F_3$ females of $L_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 20 | 16.5 | 3.08 |
| 2 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 20 | 20.2 | 5.39 |
| 3 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 20 | 21.9 | 5.15 |
| 4 | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ | 20 | 22.9 | 4.77 |
| 5 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 23.8 | 3.92 |
| 6 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | 20 | 31.1 | 4.33 |

Table 9 (contd)

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 7 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | 20 | 50.7 | 4.78 |
| 8 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | 20 | 51.7 | 3.86 |
| 9 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 20 | 53.2 | 4.75 |
| 10 | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ | 20 | 61.0 | 3.65 |
| 11 | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ | 20 | 61.2 | 2.30 |
| 12 | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ | 11 | 62.4 | 2.67 |

The difference in egg production between genotypes 11 and 5 gave the effect of homozygous X chromosomes on egg production. Here it worked out to be 37.9 eggs. In case of $H_1$ it came to 63.7 eggs nearly one and a half times that of $L_1$ line.

The difference between the genotypes was significant. Genotypes not differing were grouped together.

1 2 3 4 5 6 7 8 9 10 11 12

The effect of various regions in homozygous conditions have been worked out and shown in Table 10.

Table 10

Effect of portions of X chromosome of $L_1$ on egg production (duplicate effects)

| Sl. No. | Region of X chromosome | No. of eggs Estimates | Mean |
|---|---|---|---|
| 1 | scute (sc) | 6.4<br>0.2<br>-3.6<br>-1.5 | 0.3 |
| 2 | crossveinless (cv) | 10.3<br>1.7<br>10.7<br>-14.6 | 2.0 |
| 3 | vermilion (v) | 7.3<br>1.0<br>-2.5<br>-1.2 | 1.2 |
| 4 | forked-Bar (fB) | 38.3<br>29.4<br>44.5<br>31.5<br>19.6<br>40.5 | 34.0 |

As in $H_1$ line, here too it was found that the forked-Bar (fB) region gave the maximum effect on egg production. Curiously enough, the effect in terms of eggs was of the same order in both the $H_1$ and $L_1$ lines. On the other hand, there was a general effect of reduction in the contribution of other regions of X chromosome. Thus instead of 13 eggs effect in *vermilion* region in $H_1$ we got only 1.2 eggs effect in $L_1$; instead of 9.5 eggs effect in *crossveinless* region of $H_1$, we got only 2.0 eggs effect in $L_1$; instead of 4.6 eggs effect in *scute* region of $H_1$ we got in $L_1$ only 2.7 eggs effect. It would seem that the reduction in egg production had been effected in the $L_1$ line through elimination of dominants in regions *scute* to *vermilion*, only the *forked-Bar* region offered greater resistance to be so eliminated. As it happens *forked-Bar* region in the chromosome is situated close to the centromere.

## Crosses with full sib high line ($H_2$)

In Table 11 are presented the mean daily egg production in full sib high line ($H_2$), the marker stock M and their cross.

Table 11

Mean daily egg production in $H_2$, M and their cross

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $H_2$ ♂ x $H_2$ ♀ (a) | 49.6<br>±1.82 | 72.0<br>±2.12 | 58.6<br>±2.52 | 65.4<br>±2.08 | 67.9<br>±1.86 |
| M ♂ x M ♀ (b) | 45.2<br>±2.23 | 63.5<br>±1.84 | 51.2<br>±3.05 | 64.2<br>±2.52 | 72.5<br>±2.33 |

Table 11 (contd)

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $H_2$ ♀ x M ♂ (c) | - | 56.9<br>±1.81 | 62.2<br>±3.68 | - | - |
| Differences | | | | | |
| (a-b) | 4.4 | 8.5 | 7.4 | 1.2 | -4.6 |
| (a-c) | - | 15.1 | -3.1 | - | - |
| (b-c) | - | 8.6 | -11.0 | - | - |

$H_2$ control line produced significantly more eggs than M control line in $P_1$ generation but M stock produced more than $H_2$ stock in $F_3$ generation and in $F_1$ and $F_2$ they did not vary significantly.

There was significant variation between groups in $P_1$ and $F_1$ generations. In $P_1$ generation $H_2$ x $H_2$ cross had an average daily egg production of 72.0 ± 2.12 and that of M x M cross was 63.55 ± 1.84 eggs. The difference was significant indicating the presence of more effective factors in $H_2$ as compared to M for expressing the trait egg production.

In $F_1$ generation there was significant difference between Bar females x Marker males cross and M x M cross. The egg production of Bar females was apparently more but not significantly different from $H_2$ control. If all the gene affecting egg production were recessive and additive in nature the production was expected to be mid way i.e. 54.9 eggs, but the actual performance noted in $F_1$ was 62.2 ± 3.68 eggs i.e. 7.3 eggs more. The difference was significant rejecting the hypothesis of additivity and recessive nature of polygenes affecting egg production. There was significant interaction between normal and marker chromosomes in expressing egg production in $F_1$ females.

## Performance of $F_2$ females from $H_2$ x M cross

Table 12 gives the mean daily egg output of different $F_2$ females of $H_2$ x M cross.

Table 12

Mean daily egg production of $F_2$ females from $H_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 24.9 | 4.57 |
| 2 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 13 | 26.1 | 4.61 |
| 3 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 27.3 | 3.91 |

Table 12 (contd)

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 4 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 33.1 | 4.38 |
| 5 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 53.8 | 4.62 |
| 6 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 53.8 | 6.02 |
| 7 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 56.6 | 3.14 |
| 8 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 56.8 | 4.71 |

An analysis of variance carried out on the above data revealed that there was no significant variation in performance among females with genotypes 1-4 and among females with genotypes 5-8, whereas the former group females differed significantly from the latter group females. The results are depicted graphically below using Bar notation :

$$\underline{1\quad 2\quad 3\quad 4}\qquad \underline{5\quad 6\quad 7\quad 8}$$

The difference between the performance of flies in group 1 and 8 will give an idea of the overall effect of one complete $H_2$ X chromosome when substituted for the M X chromosome.

The actual difference worked out to 32 eggs. As opposed to this, the effect of one complete $H_1$ and $L_1$ X chromosomes were 40 and 49 respectively. The contribution of the different regions of X chromosome of $H_2$ line had been worked out and are shown in Table 13.

Table 13

Effect of portions of one X chromosome of $H_2$ on egg production

| Sl. No. | Region of X chromosome | No. of eggs | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | scute (sc) | 3.0<br>1.2 | 2.1 |
| 2 | crossveinless (cv) | 0<br>1.2 | 0.6 |
| 3 | vermilion (v) | -2.8<br>5.8 | 1.5 |
| 4 | forked-Bar (fB) | 23.7<br>31.7 | 27.7 |
| 5 | Whole X chromosome | 31.9 | |

The forked-Bar region had the most potent effect on egg production. Unlike the $H_1$ and $L_1$ lines, in $H_2$ line, none of the other regions showed significant contribution. In fact in the present case, the total contribution of the first 3 regions came to only about 4 eggs as opposed to about 28 eggs of <u>forked-Bar</u> region.

Results of $F_3$ of $H_2$ x M cross are given in Table 14.

Table 14

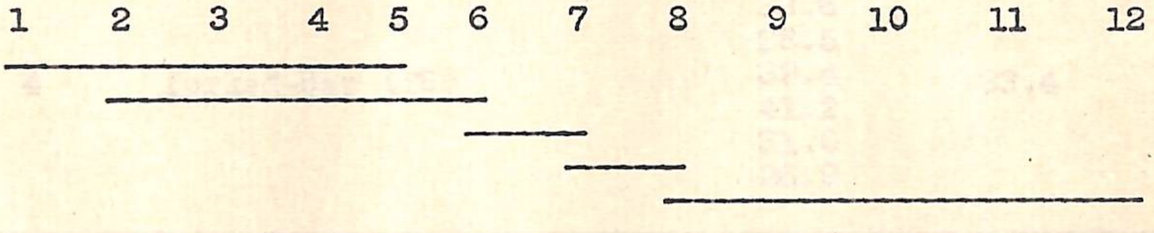
Mean daily egg production in $F_3$ females
from $H_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 13.7 | 5.23 |
| 2 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | 16 | 21.9 | 4.38 |
| 3 | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ | 20 | 23.5 | 4.24 |
| 4 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 20 | 23.5 | 5.77 |
| 5 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 20 | 25.9 | 4.40 |
| 6 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 20 | 31.0 | 6.29 |
| 7 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 20 | 42.2 | 6.29 |
| 8 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | 20 | 52.9 | 6.08 |
| 9 | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ | 20 | 57.1 | 4.23 |

Table 14 (contd)

| Sl. No. | Genotype | No. of females tested | Mean daily egg production<br>Mean | <br>S.E. |
|---|---|---|---|---|
| 10 | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ | 20 | 57.9 | 5.83 |
| 11 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | 20 | 64.7 | 2.75 |
| 12 | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ | 20 | 65.3 | 5.85 |

The above was analysed using the technique of analysis of variance. Using critical difference test and bar notation, the results are shown graphically below :



The effect of 2 $H_2$ X chromosomes was about 43 eggs. The effect of duplicate portions of $H_2$ X chromosome as worked out is shown in Table 15.

## Table 15

Effect of portions of X chromosome of $H_2$ on egg production (duplicate effects)

| Sl. No. | Region of X chromosome | No. of eggs | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | *scute* (sc) | -8.2<br>9.8<br>-22.5<br>-2.5 | 5.4 |
| 2 | *crossveinless* (cv) | 12.4<br>7.5<br>-6.8<br>4.0 | 4.3 |
| 3 | *vermilion* (v) | 8.2<br>-7.5<br>10.7<br>-0.8 | 2.7 |
| 4 | *forked-Bar* (fB) | 33.6<br>28.5<br>39.4<br>41.2<br>31.0<br>26.9 | 33.4 |

*forked-Bar* (fB) gave the highest effect. As compared to this the effect produced by other regions was small and negligible.

The value for *forked-Bar* region found was of the same order as found in the $H_1$ and $L_1$ lines.

## Crosses with full sib low line ($L_2$)

In Table 16 are presented the mean daily egg production of full sib low line ($L_2$), marker stock (M) and their cross flies.

Table 16

Mean daily egg production in $L_2$, M and their cross

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $L_2$ ♂ x $L_2$ ♀ (a) | 30.1<br>±2.68 | - | 31.3<br>±1.67 | 37.8<br>±1.87 | 32.1<br>±1.86 |
| M ♂ x M ♀ (b) | 46.1<br>±1.99 | - | 32.5<br>±3.59 | 62.8<br>±4.41 | 60.6<br>±4.07 |
| $L_2$ ♀ x M ♂ (c) | - | - | 56.2<br>±3.22 | - | - |
| Differences | | | | | |
| (a-b) | -16.0* | - | -1.2 | -25.0* | -28.5* |
| (a-c) | - | - | -24.9* | - | - |
| (b-c) | - | - | -23.7* | - | - |

The $L_2$ produced lower number of eggs than M, in all generations though the actual number produced showed variation from generation to generation.

## Performance of $F_2$ females from $L_2$ x M cross

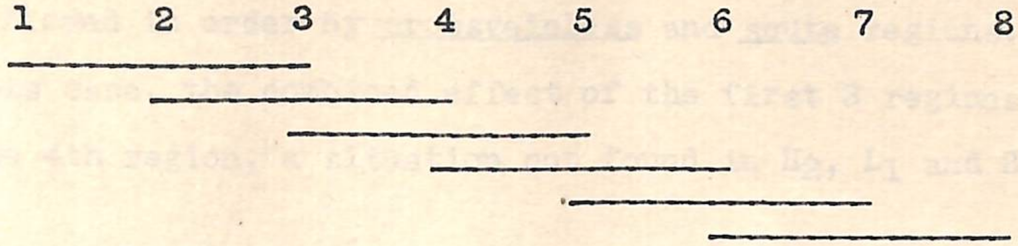
In Table 17 are given the mean daily output of different $F_2$ females from $L_2$ x M cross.

Table 17

Mean daily egg production of $F_2$ females from $L_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 33.7 | 4.63 |
| 2 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 37.5 | 3.13 |
| 3 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 43.8 | 4.51 |
| 4 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 45.2 | 4.25 |
| 5 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 51.8 | 4.22 |
| 6 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 56.5 | 4.04 |
| 7 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 61.2 | 3.57 |
| 8 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 63.3 | 4.24 |

Results of analysis of variance carried out on the above data, after using critical difference test and bar notation are shown below :



The effect of the entire X chromosome of $L_2$ line and of its various parts are given in Table 18.

Table 18

Effect of portions of one X chromosome of $L_2$ on egg production

| Sl. No. | Region of X chromosome | No. of eggs<br>Estimates | Mean |
|---|---|---|---|
| 1 | scute (sc) | 2.1<br>3.8 | 3.0 |
| 2 | crossveinless (cv) | 4.7<br>6.3 | 5.5 |
| 3 | vermilion (v) | 11.3<br>8.0 | 9.7 |
| 4 | forked-Bar (fB) | 11.5<br>11.5 | 11.5 |

The *forked-Bar* region once again had the maximum effect on egg production, but surprisingly, it was not as high as seen in $H_1$ $L_1$ and $H_2$ lines. *vermilion* region came next, followed in order by *crossveinless* and *scute* regions. In this case, the combined effect of the first 3 regions exceeded the 4th region, a situation not found in $H_2$, $L_1$ and $H_1$.

Performances of $F_3$ females of $L_2$ x M cross are given in Table 19.

Table 19

Mean daily egg production in $F_3$ females from $L_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean daily egg production Mean | S.E. |
|---|---|---|---|---|
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 22 | 11.2 | 2.60 |
| 2 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | 22 | 18.1 | 2.89 |
| 3 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 22 | 26.8 | 2.62 |
| 4 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 22 | 27.7 | 0.82 |
| 5 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 22 | 28.6 | 4.77 |
| 6 | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ | 22 | 31.3 | 2.83 |

Table 19 (contd)

| Sl. No. | Genotype | No. of females tested | Mean daily egg production<br>Mean | <br>S.E. |
|---|---|---|---|---|
| 7 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | 22 | 40.6 | 4.08 |
| 8 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | 22 | 41.0 | 2.56 |
| 9 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 22 | 46.3 | 4.12 |
| 10 | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ | 22 | 48.4 | 3.54 |
| 11 | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ | 22 | 48.8 | 2.72 |
| 12 | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ | 22 | 52.6 | 1.77 |

The above was analysed using the technique of analysis of variance. Using critical difference test, the means of different genotypes were compared and the results using bar notation are shown below :

$$\begin{array}{cccccccccccc} 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 & 11 & 12 \\ \cline{1-2} \cline{3-6} \cline{7-11} & & & & & & & & & & & \\ \cline{9-12} \end{array}$$

The mean overall effect of 2 $L_2$ X chromosomes on egg production was about 41 eggs. This was about the same as in $H_2$ and $L_1$. In case of $H_1$ however, the value was about $1\frac{1}{2}$ times this figure.

The effect of duplicate portions of $L_2$ X chromosome was worked out. Results are given in Table 20.

Table 20

Effect of duplicate portions of X chromosome of $L_2$ on egg production

| Sl. No. | Region of chromosome | No. of eggs | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | *scute* (sc) | 3.8<br>17.4<br>-5.4<br>3.6 | 4.9 |
| 2 | *crossveinless* (cv) | 8.2<br>-1.8<br>7.5<br>9.6 | 5.9 |
| 3 | *vermilion* (v) | 6.9<br>4.5<br>-5.7<br>4.2 | 2.5 |
| 4 | *forked-Bar* (fB) | 21.6<br>21.3<br>35.1<br>21.1<br>12.3<br>22.5 | 22.3 |

*forked-Bar* region had the highest effect followed in order by crossveinless, scute and vermilion. Compared to $H_2$ the effects of the like regions on egg production was practically the same, except in case of forked-Bar region, where a marked difference was observed, the $H_2$ having about 11 eggs more effect than $L_2$.

Comparison of the 4 inbred lines in respect of a single entire X chromosome or parts thereof or their duplicates, both entire and parts, on egg production. For ease of ready comparison the data summarised in Table 21, and graphically brought out as histogram in Figs. 4 and 5.

Table 21

Effect of various segments of X chromosomes singly or doubly on fecundity

| Regions of X chromosome | Substitution | Lines | | | |
|---|---|---|---|---|---|
| | | $H_1$ | $L_1$ | $H_2$ | $L_2$ |
| scute (sc) | Single | 1.9 | 1.7 | 2.1 | 3.0 |
| | Double | 4.6 | 0.3 | 5.4 | 4.9 |
| crossveinless (cv) | Single | 11.2 | 17.7 | 0.6 | 5.5 |
| | Double | 9.5 | 2.0 | 4.3 | 5.9 |
| vermilion (v) | Single | 5.8 | 2.4 | 1.5 | 9.7 |
| | Double | 13.0 | 1.2 | 2.7 | 2.5 |
| forked-Bar (fB) | Single | 21.6 | 27.7 | 27.7 | 11.5 |
| | Double | 32.6 | 34.0 | 33.4 | 22.3 |
| Entire X chromosome | Single | 40.4 | 49.4 | 31.9 | 29.6 |
| | Double | 63.8 | 37.4 | 43.4 | 41.4 |

From Table 21, the following salient facts emerge :

(1) The single X chromosome substitution did not produce the same effect on egg production. Though the actual values differed, the $H_2$ and $L_2$ were close to each other and $H_1$ and $L_1$ - though not so close, differed by about 9 eggs.

(2) Normally one would have expected doubling effect on egg production when instead single, there was two chromosome substitution. This was <u>not the case</u> in all the 4 lines tested.

(3) Considering portions of single chromosome, in all the four lines, the potency of <u>forked-Bar</u> region was the highest. It was about the same in 3 out of the 4 lines and half as much in the fourth.

(4) In case of duplicated portions <u>forked-Bar</u> region again gave the highest contribution. As in single chromosome portions the value was about the same in 3 out of the 4 cases. In the fourth case ($L_2$), it was very much less and the value was double that found for single region substitution.

(5) Next in importance in single region substitution, <u>crossveinless</u> region showed presence of dominants affecting egg production in 2 ($H_1$ and $L_1$) and of the 4 cases. In the other regions, in all cases, the contribution detected was small and negligible.

(6) The double region substitution figures showed some effect only in vermilion region of $H_1$. This was about double of what was observed when this region was substituted singly.

(7) With a few exceptions, in the majority of cases involving regions other than forked-Bar, the duplicated substitution did not produce expected double effects. In fact in most cases they were lower than single region substitution effects.

## 2. HATCHABILITY

### Crosses with half sib high line ($H_1$)

In Table 22 are given the relevant data of mean egg hatchability (expressed in percentages) with their standard errors in various crosses in different generations.

Mean hatchability percentage did not vary significantly from generation to generation in both control stocks i.e. $H_1$ and M stocks, except in $F_1$ generation, when it was lower in both the cases. Mean hatchability was maximum in H1 x H1 cross and minimum in M x M cross in all the generations.

In $P_1$ generation there was significant difference in the mean hatchability of $H_1$ and M stocks. $H_1$ had mean

Table 22

Mean egg hatchability percentages with standard errors in $H_1$, M and their cross in different generations

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $H_1$ ♂ x $H_1$ ♀ (a) | 88.4±1.89 | 88.5±1.76 | 79.2±3.00 | 92.4±1.78 | 91.5±1.98 |
| M ♂ x M ♀ (b) | 56.0±1.77 | 56.5±1.74 | 35.4±2.66 | 56.4±1.95 | 57.6±1.66 |
| $H_1$ ♀ x M ♂ (c) | - | 88.5±1.72 | 71.3±3.88 | - | - |
| M ♀ x $H_1$♂ (d) | - | 65.8±1.28 | 49.0±2.14 | - | - |
| **Differences** | | | | | |
| (a-b) | 32.4* | 32.0* | 43.8* | 36.0* | 33.9* |
| (a-c) | | 0 NS | 7.9 NS | | |
| (b-c) | | -32.0* | -35.9* | | |
| (a-d) | | 12.7* | 30.2* | | |
| (b-d) | | -9.3* | -13.6* | | |
| (c-d) | | 22.7* | 22.3* | | |

## Table 23

Mean egg hatchability percentages of $F_2$
females of $H_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability Percentage | S.E. |
|---|---|---|---|---|
| 1 | $\frac{\text{sc cv v f B}}{\text{sc cv v f B}}$ | 15 | 60.4 | 5.80 |
| 2 | $\frac{\text{+ cv v f B}}{\text{sc cv v f B}}$ | 10 | 63.7 | 9.60 |
| 3 | $\frac{\text{+ + + f B}}{\text{sc cv v f B}}$ | 19 | 74.4 | 7.32 |
| 4 | $\frac{\text{sc cv v + +}}{\text{sc cv v f B}}$ | 20 | 75.7 | 6.74 |
| 5 | $\frac{\text{+ + v f B}}{\text{sc cv v f B}}$ | 20 | 77.1 | 2.64 |
| 6 | $\frac{\text{sc cv + + +}}{\text{sc cv v f B}}$ | 22 | 82.2 | 6.17 |
| 7 | $\frac{\text{sc + + + +}}{\text{sc cv v f B}}$ | 23 | 87.6 | 4.34 |
| 8 | $\frac{\text{+ + + + +}}{\text{sc cv v f B}}$ | 23 | 88.1 | 4.77 |

Analysis of variance on the performance data of 8 genotypes exhibited significant differences in the mean hatchability of different genotypes. Critical difference test further indicated that the genotypes 1 to 5, 2 to 6 and 3 to 8 did not differ significantly among themselves but each group differed significantly from the other. The results are presented below with bar notation :

$$\begin{array}{cccccccc} 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 \\ \cline{1-5} \\ \cline{2-6} \\ \cline{3-8} \end{array}$$

As the performance of 8 genotypes had been arranged in ascending order, it is clear by seeing the different genotypes that the flies that contained both Xs from the M stock had least hatchability (60.4%) while those that contained one X of M and the other of $H_1$ had highest hatchability (88.1%). The effect of substituting one X chromosome of $H_1$ was thus 27.7% which could be partly due to interaction between the $H_1$ and M chromosomes but mainly due to the fact that $H_1$ X chromosome contained more <u>dominant</u> genes affecting egg hatchability and showed their effect even when present in single dose.

The main effects of various regions of X chromosome on egg hatchability as derived by linear contrast of various combinations of genotypes, given in analytical procedure, are summarised below in Table 24.

## Table 24

Effects of various regions of one X chromosome on egg hatchability

| Sl. No. | Region of X chromosome | Egg hatchability percentage Estimates | Mean |
|---|---|---|---|
| 1 | *scute* (sc) | 0.5<br>3.3 | 1.9 |
| 2 | *crossveinless* (cv) | 5.4<br>13.3 | 9.3 |
| 3 | *vermilion* (v) | 6.6<br>-2.6 | 2.0 |
| 4 | *forked-Bar* (fB) | 13.7<br>15.2 | 14.4 |
| 5 | Whole X chromosome | 27.7 | |

The discripancies in the two estimates in the first three regions were probably due to inclusion or non-inclusion of the region containing *dominant* genes affecting hatchability. It is clear from the contributions of various regions that *forked-Bar* region of X chromosome contained maximum dominant genes affecting egg hatchability. Some dominant genes also seemed to be located right of *crossveinless*. The regions of *scute* and *vermilion* had equal effect and there appeared to be least number of *dominant* genes in those regions. It is interesting to note that the regions of forked-Bar and crossveinless exhibited more polygenic activity affecting both egg production and hatchability in $H_1$ stock.

The mean hatchability percentage of different genotypes in $F_3$ generation are presented in Table 25.

Table 25

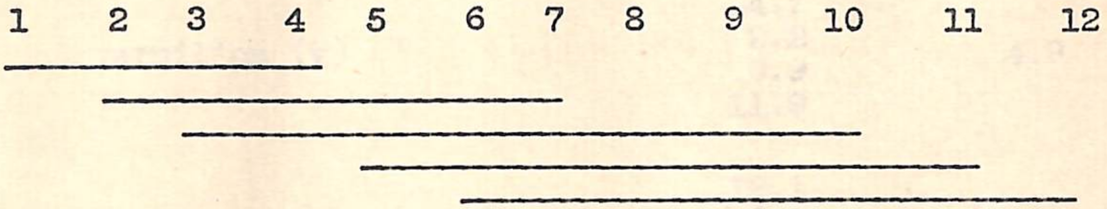
Mean egg hatchability of $F_3$ females of $H_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability Percentage | S.E. |
|---|---|---|---|---|
| 1 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 13 | 65.2 | 6.24 |
| 2 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 9 | 69.0 | 11.69 |
| 3 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | 18 | 73.7 | 3.87 |
| 4 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 15 | 77.4 | 4.27 |
| 5 | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ | 20 | 79.6 | 4.79 |
| 6 | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ | 20 | 79.9 | 3.68 |
| 7 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 17 | 81.0 | 4.27 |
| 8 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 20 | 85.2 | 4.11 |

Table 25 (contd)

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability<br>Percentage | <br>S.E. |
|---|---|---|---|---|
| 9 | $\frac{sc\ cv + + +}{sc\ cv + + +}$ | 20 | 86.1 | 5.91 |
| 10 | $\frac{sc + + + +}{sc + + + +}$ | 20 | 87.3 | 3.43 |
| 11 | $\frac{+\ cv\ v + +}{+\ cv\ v + +}$ | 20 | 90.3 | 4.10 |
| 12 | $\frac{+ + + + +}{+ + + + +}$ | 20 | 91.7 | 1.97 |

The differences among the genotypes are significant as revealed by analysis of variance. On the basis of critical difference test the genotypes not differing significantly in their mean hatchabilities are grouped together by bar notation as under :



The difference in egg hatchability of the genotype 2 and 12 gave the effect of homozygous X on hatchability. By substituting two X chromosomes of $H_1$ stock for two X chromosomes of M there will be an increase of 22.7% in egg hatchability.

The effects of various segments of X chromosome had been worked out, on the same basis as in egg production and the results are brought out in Table 26. Here the effect will be due to duplicate regions instead of single regions as in $F_2$.

Table 26

Effect of portion of X chromosome of $H_1$ on hatchability (duplicate effects)

| Sl. No. | Region of X chromosome | Egg hatchability percentage | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | scute (sc) | 4.4<br>-3.8<br>5.1<br>-1.4 | 1.1 |
| 2 | crossveinless (cv) | 1.2<br>12.2<br>-10.5<br>7.3 | 2.6 |
| 3 | vermilion (v) | 4.7<br>2.2<br>0.9<br>11.9 | 4.9 |
| 4 | forked-Bar (fB) | 12.1<br>16.2<br>6.3<br>25.1<br>12.4<br>2.4 | 12.4 |
| 5 | Whole X chromosome | 22.7 | |

The large variation observed among the estimates for a given region might be due to sampling, or due to the genotypes not identical in the complement of genes because of the inclusion or non-inclusion of the regions containing *dominant* genes, affecting egg hatchability.

It was quite clear that the *forked-Bar* region had maximum polygenic activity affecting egg hatchability. Next in order came *vermilion* region followed by *crossveinless* and *scute* regions. The results of the activity of various regions on egg hatchability were exactly in accordance with those of egg production.

## Crosses with half sib low line ($L_1$)

In Table 27 are presented the mean egg hatchability percentages with standard errors of $L_1$, M and their cross in various generations.

Table 27

Mean egg hatchability percentages with standard errors in $L_1$, M and their cross in various generations

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $L_1$ ♂ x $L_1$ ♀<br>(a) | 72.9<br>±4.95 | 64.6<br>±4.35 | 61.1<br>±5.63 | 56.7<br>±6.04 | 51.3<br>±5.73 |
| M ♂ x M ♀<br>(b) | 49.1<br>±2.89 | 54.6<br>±1.44 | 47.1<br>±2.70 | 53.2<br>±2.82 | 56.3<br>±2.95 |

Table 27 (contd)

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $L_1$ ♀ x M ♂<br>(c) | | 82.5<br>±3.12 | 76.6<br>±4.56 | | |
| Differences | | | | | |
| (a-b) | 23.8* | 10.0* | 14.0* | 3.5 NS | -5.0 NS |
| (a-c) | | -17.9* | -15.5* | | |
| (b-c) | | -27.9* | -29.5* | | |

The mean hatchability percentage in $L_1$ stock showed a gradual decrease from 72.9% ± 4.95 in the base population to 51,3% ± 5.73 in $F_3$ generation while M stock exhibited a gradual increase from 49.1% ± 2.89 in the base population to 56.3%± 2.95 in $F_3$ generation. In $F_1$ generation it was 47.1% ± 2.70 which was less than in the base population by 2.0%.

Mean hatchability of $L_1$ females fertilised by M males was 82.5% ± 3.12 which is significantly higher than both the parents. This indicated significant interaction between the $L_1$ and M chromosomes. The eggs of $F_1$ females of the cross, mated to M males exhibited higher percentage of hatchability than either parents, revealing positive interaction of $L_1$ and

M chromosomes.

The difference between mean egg hatchability of $L_1$ and M stocks was not significant in $F_2$ and $F_3$ generations.

Performance of $F_2$ females

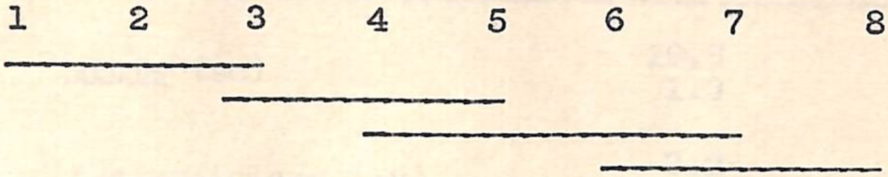
Mean egg hatchability percentages with their standard errors of the females of different genotypes in $F_2$ are presented in Table 28.

Table 28

Mean egg hatchability percentage with standard errors of $F_2$ females of $L_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability | |
|---|---|---|---|---|
| | | | Percentage | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 15 | 51.5 | 10.12 |
| 2 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 13 | 52.4 | 9.69 |
| 3 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 16 | 61.4 | 5.82 |
| 4 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 74.8 | 7.62 |
| 5 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 16 | 75.2 | 5.83 |
| 6 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 83.0 | 5.37 |
| 7 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 18 | 86.1 | 5.67 |
| 8 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 93.8 | 2.40 |

Analysis of variance of the above data showed that the differences among the genotypes were statistically significant. On the basis of critical difference test the genotypes not significantly differing in mean hatchability were grouped by bar notation, as follows :



The difference between the hatchabilities of the two genotypes 1 and 8 gave the effect of the substitution of one X chromosome of $L_1$ on mean hatchability, which was 42.3%. This substitution effect was much greater than that of $H_1$ (27.7%) indicating significantly larger interaction effect between $L_1$ and M chromosomes than $H_1$ and M chromosomes.

The relative effects of various regions of X chromosome on egg hatchability could be summarised as under in Table 29.

## Table 29

Effects of various regions of one X chromosome on hatchability

| Sl. No. | Region of X chromosome | Egg hatchability percentage<br>Estimates | <br>Mean |
|---|---|---|---|
| 1 | scute (sc) | 10.9<br>1.3 | 6.1 |
| 2 | crossveinless (cv) | -3.2<br>9.0 | 2.9 |
| 3 | vermilion (v) | 11.3<br>13.8 | 12.5 |
| 4 | forked-Bar (fB) | 18.6<br>23.7 | 21.2 |
| 5 | Whole X chromosome | 42.3 | |

From the derived effects of various regions on hatchability it could be concluded that forked-Bar region of X chromosome contained major dominant genes affecting hatchability. Some of the dominant genes also seemed to be located in the vermilion region and most probably on the left of vermilion. The crossveinless region showed least effect while scute region had the same effect on egg hatchability.

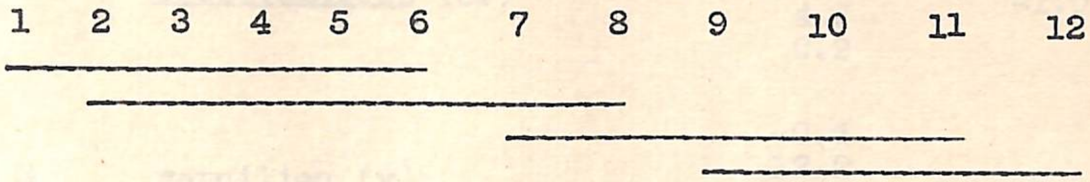
Mean hatchability percentage of different genotypes in $F_3$ generation are tabulated in Table 30.

## Table 30

Mean hatchability percentages with standard errors of different $F_3$ genotypes

| Sl. No. | Genotype | No. of females tested | Egg hatchability percentage Mean | S.E. |
|---|---|---|---|---|
| 1 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | | 49.5 | 8.18 |
| 2 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | | 61.6 | 8.42 |
| 3 | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ | | 61.6 | 9.71 |
| 4 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | | 63.4 | 2.94 |
| 5 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | | 63.7 | 5.13 |
| 6 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | | 63.8 | 7.26 |
| 7 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | | 72.4 | 4.40 |
| 8 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | | 75.8 | 6.32 |
| 9 | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ | | 80.5 | 3.35 |
| 10 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | | 81.4 | 5.54 |
| 11 | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ | | 84.8 | 3.44 |
| 12 | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ | | 92.8 | 2.33 |

Analysis of variance of the basic data showed significant differences in mean hatchability among the different genotypes. On the basis of critical difference test the significance of differences in mean hatchability of the 12 genotypes is brought out graphically below :



The difference between the hatchabilities of the genotypes 6 and 12 gave the effect of homozygous X chromosome, on hatchability. By the substitution of two X chromosomes of $H_1$ stock there was an increase of 29% in mean hatchability. It was curious to note that the double dose substitution effect was much less than the single dose substitution effect (42.3%).

The effects of various segments of X chromosome as calculated by linear contrast of various sets of genotypes, are provided in Table 31.

Table 31

Effects of portions of X chromosome of $L_1$ on hatchability (duplicate effects)

| Sl. No. | Region of X chromosome | Egg hatchability percentage<br>Estimates | Means |
|---|---|---|---|
| 1 | scute (sc) | 8.0<br>-2.2<br>3.4<br>-2.0 | 1.8 |

Table 31 (contd)

| Sl. No. | Region of X chromosome | Egg hatchability percentage<br>Estimates | <br>Mean |
|---|---|---|---|
| 2 | crossveinless (cv) | 3.5<br>-12.2<br>4.7<br>0.2 | -1.0 |
| 3 | vermilion (v) | -0.4<br>12.2<br>8.9<br>12.3 | 8.3 |
| 4 | forked-Bar (fB) | 31.2<br>8.6<br>21.2<br>14.2<br>17.9<br>31.3 | 20.7 |
| 5 | Whole X chromosome | 29.0 | |

From the mean values of various estimates of the effects of different regions on hatchability, it was clear that forked-Bar region contained large number of dominant genes. The vermilion region also seemed to contain some dominant genes whereas crossveinless region looked to contain recessive genes depressing hatchability.

Crosses with full sib high line

Table 32 provided the mean hatchability percentages with standard errors of $H_2$, M and their cross in various generations.

## Table 32

Mean hatchability with their standard errors of $H_2$, M and their cross in various generations

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $H_2$ ♂ x $H_2$ ♀ (a) | 58.3<br>±6.18 | 66.4<br>±3.60 | 79.3<br>±3.75 | 75.2<br>±4.45 | 89.0<br>±3.23 |
| M ♂ x M ♀ (b) | 42.5<br>±2.91 | 51.9<br>±1.90 | 39.2<br>±3.20 | 54.7<br>±2.06 | 53.3<br>±2.45 |
| $H_2$ ♀ x M ♂ (c) | | 83.3<br>±3.00 | 80.4<br>±4.61 | | |
| <u>Differences</u> | | | | | |
| (a-b) | 15.8* | 14.5* | 40.1* | 20.5* | 35.7* |
| (a-c) | | -16.9* | -1.1 NS | | |
| (b-c) | | -31.4* | -41.2* | | |

The mean hatchability percentage of $H_2$ exhibited a gradual increase from 58.3% ± 6.18 in base population to 89.0% ± 3.23 in $F_3$ generation while M stock also showed a gradual increase in mean hatchability from base population to $F_3$ generation. It had 39.2% ± 3.20 in $F_1$ generation which was less than in the base population by 3.3%.

The $H_2$ females fertilised by M males had mean hatchability of 83.3% ± 3.00 which was significantly higher than the both parents indicating positive interaction between the $H_2$ and M chromosomes.

The females of this cross mated to M males had mean hatchability of 80.4% ± 4.61 which was not significantly different from the $H_2$ stock.

There was significant difference between mean hatchability of $H_2$ and M stocks in both $F_2$ and $F_3$ generations.

## Performance of $F_2$ females

Mean egg hatchability percentage with their standard errors of the females of different genotypes in $F_2$ generation are presented in Table 33.

Table 33

Mean hatchability of $F_2$ females of $H_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Egg hatchability percentage Mean | S.E. |
|---|---|---|---|---|
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 17 | 58.7 | 7.82 |
| 2 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 8 | 59.6 | 2.17 |
| 3 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 67.6 | 6.74 |

Table 33 (contd)

| Sl. No. | Genotype | No. of females tested | Egg hatchability percentage<br>Mean | <br>S.E. |
|---|---|---|---|---|
| 4 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 16 | 77.5 | 3.14 |
| 5 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 19 | 79.1 | 6.90 |
| 6 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 19 | 80.5 | 6.14 |
| 7 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 11 | 88.9 | 3.46 |
| 8 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 92.9 | 1.81 |

An analysis of variance carried out on the above data indicated significant differences in the performance of different genotypes. On the basis of critical difference test the genotypes not differing significantly in the mean hatchability are grouped together by using bar notation as under :

```
1   2   3   4   5   6   7   8
-----------
    ------------
        ----------------
            ----------------
```

The difference between the performance of the flies of genotypes 1 and 8 gave an idea of the contribution of one homologous $H_2$ chromosome towards hatchability. The effects of the 4 regions of X chromosome have been worked out and are given in Table 34.

Table 34

Effect of portions of one X chromosome of $H_2$ on egg production

| Sl. No. | Region of X chromosome | Egg hatchability percentage Estimates | Egg hatchability percentage Mean |
|---|---|---|---|
| 1 | scute (sc) | 4.0<br>0.9 | 2.5 |
| 2 | crossveinless (cv) | 9.8<br>17.9 | 13.8 |
| 3 | vermilion (v) | -1.4<br>-9.9 | -5.6 |
| 4 | forked-Bar (fB) | 25.3<br>21.8 | 23.5 |
| 5 | Whole X chromosome | 34.2 | |

As in $H_1$ and $L_1$, maximum activity was noticed in forked-Bar region. Next came crossveinless region with significant effect. The scute region seemed to have some activity but vermilion region seemed to have more of recessive genes depressing hatchability. It was interesting to note in both the high lines $H_1$ and $H_2$, only forked-Bar and crossveinless regions seemed to have major activity while the other two regions had negligible activity affecting hatchability.

Performance of $F_3$ females of various genotypes are presented in Table 35.

Table 35

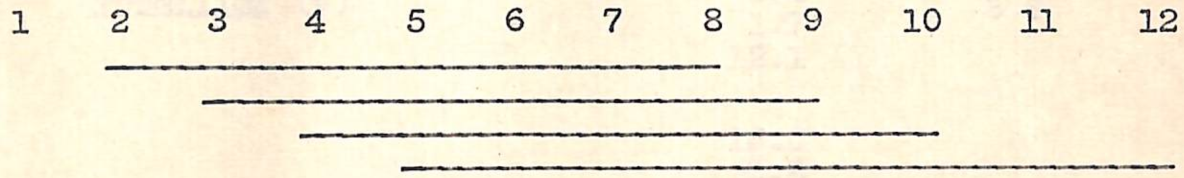
Mean egg hatchability in $F_3$ females of $H_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability Percentage | S.E. |
|---|---|---|---|---|
| 1 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | 13 | 57.7 | 8.32 |
| 2 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 10 | 61.7 | 7.49 |
| 3 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 20 | 64.8 | 3.53 |
| 4 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 15 | 69.2 | 8.41 |
| 5 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 13 | 72.0 | 7.99 |
| 6 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 20 | 72.5 | 7.73 |
| 7 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | 20 | 74.2 | 8.01 |
| 8 | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ | 16 | 74.6 | 7.01 |
| 9 | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ | 20 | 77.6 | 5.95 |

Table 35 (contd)

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability | |
|---|---|---|---|---|
| | | | Percentage | S.E. |
| 10 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | 20 | 85.5 | 6.29 |
| 11 | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ | 20 | 88.5 | 5.48 |
| 12 | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ | 20 | 89.6 | 4.45 |

Analysis of variance revealed significant differences among the mean hatchability percentage of different genotypes. Significant differences in mean hatchability of 12 genotypes based on critical difference test is brought out graphically using bar notation.



The difference in hatchability between genotypes 12 and 2 gave the effect of homozygous X chromosomes on egg production. Here it worked out to 27.9%. It was curious to note that double substitution had comparatively smaller effect than single dose substitution (34.2%). The effects of various regions in homozygous conditions have been worked out and presented in Table 36.

Table 36

Effects of different portions of X chromosome of $H_2$ on egg hatchability (duplicate effects)

| Sl. No. | Region of X chromosome | Egg hatchability percentage | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | scute (sc) | 1.1<br>10.3<br>12.9<br>9.8 | 8.5 |
| 2 | crossveinless (cv) | 14.3<br>-2.8<br>7.9<br>7.2 | 2.7 |
| 3 | vermilion (v) | -4.1<br>5.4<br>1.7<br>12.1 | 3.8 |
| 4 | forked-Bar (fB) | 15.0<br>10.8<br>23.7<br>13.4<br>16.6<br>8.3 | 14.6 |
| 5 | Whole X chromosome | 27.9 | |

Mean effects of various segments of X chromosome of $H_2$

revealed that major activity was stationed in forked-Bar region. The scute region also indicated more activity affecting hatchability than cv and y regions. In this case, the polygenic activity affecting egg hatchability more or less confined to the ends of the chromosomes than the middle portion.

Crosses with full sib low line ($L_2$)

The relevant data of mean egg hatchability with standard errors was brought out in Table 37 with regard to $L_2$, M and their cross in various generations.

Table 37

Mean hatchability with standard errors of $L_2$, M and their cross in different generations

| Cross | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $L_2$ ♂ x $L_2$ ♀<br>(a) | 81.9<br>±2.56 | - | 84.4<br>±2.66 | 82.4<br>±3.40 | 84.5<br>±3.15 |
| M ♂ x M ♀<br>(b) | 49.1<br>±2.89 | - | 47.1<br>±2.70 | 53.2<br>±2.82 | 56.3<br>±2.95 |
| $L_2$ ♂ x M ♂<br>(c) | | | 88.3<br>±3.63 | | |
| Differences | | | | | |
| (a-b) | 32.8* | - | 37.3* | 29.2* | 28.2* |
| (a-c) | | | -3.9NS | | |
| (b-c) | | | -41.2* | | |

The $L_2$ females fertilised by M males had mean hatchability of 88.3% ± 3.63 which was not significantly different from the $L_2$ stock indicating that $L_2$ had more dominant factors affecting hatchability than M stock.

Performance of $F_2$ females

Mean egg hatchability of the females of different genotypes in $F_2$ generations are presented in Table 38.

Table 38

Mean hatchability of $F_2$ females of $L_2$ and M cross

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability | |
|---|---|---|---|---|
| | | | Percentage | S.E. |
| 1 | $\frac{\text{sc cv v f B}}{\text{sc cv v f B}}$ | 18 | 64.8 | 4.31 |
| 2 | $\frac{\text{+ cv v f B}}{\text{sc cv v f B}}$ | 11 | 68.9 | 10.30 |
| 3 | $\frac{\text{sc cv v + +}}{\text{sc cv v f B}}$ | 17 | 80.7 | 6.18 |
| 4 | $\frac{\text{+ + v f B}}{\text{sc cv v f B}}$ | 18 | 82.0 | 3.30 |
| 5 | $\frac{\text{+ + + f B}}{\text{sc cv v f B}}$ | 20 | 84.1 | 4.74 |
| 6 | $\frac{\text{sc + + + +}}{\text{sc cv v f B}}$ | 10 | 90.6 | 4.03 |
| 7 | $\frac{\text{+ + + + +}}{\text{sc cv v f B}}$ | 20 | 91.1 | 3.18 |
| 8 | $\frac{\text{sc cv + + +}}{\text{sc cv v f B}}$ | 19 | 94.7 | 1.64 |

Significant differences among the different genotypes were brought out by an analysis of variance on the above data. Using the critical difference test, the genotypes not differing significantly are grouped by using bar notation as under :

```
1    2    3    4    5    6    7    8
_____
     __________
          ______________________
                    ________________
```

The effect of one homologous X chromosome could be derived by taking the difference between the hatchabilities of the genotypes 1 and 7 which came to 26.3%. The effects of 4 regions of X chromosome were calculated and presented in Table 39.

Table 39

Effects of various portions of one X chromosome of $L_2$ on egg hatchability

| Sl. No. | Region of X chromosome | Egg hatchability percentage<br>Estimates | Mean |
|---|---|---|---|
| 1 | scute (sc) | 0.5<br>4.1 | 2.3 |
| 2 | crossveinless (cv) | -4.1<br>13.1 | 4.5 |
| 3 | vermilion (v) | 14.0<br>2.1 | 8.0 |
| 4 | forked-Bar (fB) | 7.0<br>15.9 | 11.4 |
| 5 | Whole X chromosome | 26.3 | |

The effects of various segments on egg hatchability indicated that as in the other lines, in this line also forked-Bar region proved to be potent in affecting egg hatchability. Next came vermilion region followed by cv and sc regions.

The relevant data of mean egg hatchability of $F_3$ females of various genotypes is brought out in Table 40.

Table 40

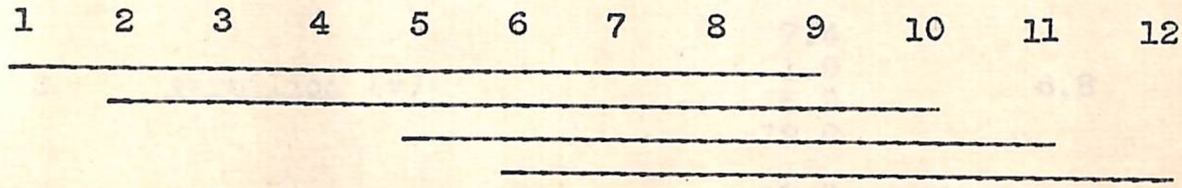
Mean egg hatchability percentage with standard errors in $F_3$ females of $L_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability | |
|---|---|---|---|---|
| | | | Percentage | S.E. |
| 1 | $\frac{\text{sc cv v f B}}{\text{sc cv v f B}}$ | 13 | 66.3 | 8.08 |
| 2 | $\frac{\text{sc + + f B}}{\text{sc + + f B}}$ | 14 | 72.6 | 6.25 |
| 3 | $\frac{\text{sc cv + f B}}{\text{sc cv + f B}}$ | 14 | 73.7 | 6.89 |
| 4 | $\frac{\text{+ cv v f B}}{\text{+ cv v f B}}$ | 16 | 74.6 | 4.40 |
| 5 | $\frac{\text{+ + v f B}}{\text{+ + v f B}}$ | 18 | 75.9 | 5.85 |
| 6 | $\frac{\text{+ + + f B}}{\text{+ + + f B}}$ | 20 | 77.8 | 3.50 |
| 7 | $\frac{\text{+ + v + +}}{\text{+ + v + +}}$ | 20 | 79.7 | 6.33 |

Table 40 (contd)

| Sl. No. | Genotype | No. of females tested | Mean egg hatchability Percentage | S.E. |
|---|---|---|---|---|
| 8 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | 20 | 80.0 | 5.98 |
| 9 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 20 | 80.4 | 5.50 |
| 10 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | 20 | 86.3 | 4.87 |
| 11 | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ | 20 | 89.6 | 4.59 |
| 12 | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ | 20 | 91.7 | 2.27 |

Analysis of variance conducted on basic data revealed significant differences among mean hatchabilities of different genotypes. Significance of mean differences in 12 genotypes based on critical difference test is brought out graphically below :



The difference between the hatchabilities of genotypes 1 and 12 gave the effect of homozygous X chromosomes of $L_2$ on egg hatchability. The effect was 25.4%. There was no significant difference between single (26.3%) and double substitution effects. One might expect double substitution effect to be twice the single effect if the effect of chromosome was additive in nature.

The effects of different regions in homozygous condition, derived, are presented in Table 41.

Table 41

Effects of different portions of X chromosome of $L_2$ on egg hatchability (duplicate effects)

| Sl. No. | Region of X chromosome | Egg hatchability percentage<br>Estimates | Mean |
|---|---|---|---|
| 1 | *scute* (sc) | 2.1<br>8.3<br>-0.4<br>5.2 | 3.8 |
| 2 | *crossveinless* (cv) | 3.3<br>1.3<br>-0.3<br>-1.1 | 0.8 |
| 3 | *vermilion* (v) | 7.4<br>1.9<br>5.9<br>12.0 | 6.8 |
| 4 | *forked-Bar* (fB) | 13.9<br>14.1<br>17.0<br>5.4<br>12.6<br>3.8 | 11.1 |
| 5 | Whole X chromosome | 25.4 | |

The effects of various segments of X chromosome indicated that fB region was more potent with significant polygenic activity in that region of the chromosome. The vermilion region also had some activity but cv region had least activity.

It was interesting to note that in both of the low lines the distribution of polygenic activity was identical in having more activity in fB and v region and least activity in cv and sc regions.

Comparison of 4 inbred lines in respect of single entire X chromosome or parts thereof or their duplicates both entire and parts on egg hatchability.

For ready comparison the main effects of various segments of X chromosome are summarised in Table 42.

Table 42

Effect of various segments of X chromosome singly or in duplicate on egg hatchability

| Regions of X chromosome | Substitution | Lines $H_1$ | $L_1$ | $H_2$ | $L_2$ |
|---|---|---|---|---|---|
| scute (sc) | Single | 1.9 | 6.1 | 2.4 | 2.3 |
| | Double | 1.1 | 1.8 | 8.5 | 3.8 |
| crossveinless (cv) | Single | 9.3 | 2.9 | 13.8 | 4.5 |
| | Double | 2.6 | -1.0 | 2.7 | 0.8 |

Table 42 (contd)

| Regions of X chromosome | Substitution | Lines | | | |
|---|---|---|---|---|---|
| | | $H_1$ | $L_1$ | $H_2$ | $L_2$ |
| vermilion (v) | Single | 2.0 | 12.5 | -5.6 | 8.0 |
| | Double | 4.9 | 8.3 | 3.8 | 6.8 |
| forked-Bar (fB) | Single | 14.4 | 21.2 | 23.5 | 11.4 |
| | Double | 12.4 | 12.4 | 14.6 | 11.1 |
| Entire X chromosome | Single | 27.7 | 42.3 | 34.2 | 26.3 |
| | Double | 22.7 | 29.0 | 27.9 | 25.4 |

The above data is brought out as histogram in Figs. 4 & 5.

Close examination of the above table brought the following facts to light.

(1) Single X chromosome substitution did not produce the same effect on hatchability.

(2) Double substitution had rarely doubling effect. But in most of the cases double substitution had lower effect than single substitution.

(3) When the effects of various regions of single chromosome were considered, the potency of fB region was highest of all the regions.

(4) In case of duplicated portions also forked-Bar (fB) region showed highest effect. As in single chromosome portions the value was about the same in two out of 4 lines,

but in the other two lines double substitution had marked depressing effect on hatchability.

(5) In the two high lines, the region of cv seemed to have significant activity, but in the two low lines the vermilion region showed the presence of dominants affecting hatchability.

(6) The polygenic activity affecting hatchability was least in sc portion except in $L_1$ when single region was substituted in $H_2$ when double region was substituted.

## 3. EGG SIZE

### Crosses with half sib high line ($H_1$)

Table 43 provided the mean egg size of $H_1$, M and their reciprocal crosses in various generations.

$H_1$ produced larger eggs than M. The extent of variation between $H_1$ and M stocks in each generation was maintained in all the generations. The difference in mean egg size of $H_1$ and M stocks was significant in all the generations.

$H_1$ females fertilised by M males produced eggs of 32993 ± 238 proportional units, and the M females fertilised by $H_1$ males produced eggs of 26507 ± 206 which were not different from the respective controls. Hence the relative

## Table 43

Mean egg size (proportional units) with standard errors of $H_1$, M and their cross in different generations

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $H_1$ ♂ x $H_1$ ♀ (a) | 33578±189 | 32480±209 | 34836±266 | 33509±206 | 31856±199 |
| M ♂ x M ♀ (b) | 25868±210 | 26527±315 | 29029±332 | 27210±297 | 25408±201 |
| $H_1$ ♀ x M ♂ (c) | | 32993±238 | 32595±298 | | |
| M ♀ x $H_1$♂ (d) | | 26507±206 | 30992±252 | | |
| <u>Differences</u> | | | | | |
| (a-b) | 7710* | 5953* | 5807* | 6299* | 6448* |
| (a-c) | | -513 NS | 2241* | | |
| (a-d) | | 5973* | 3844* | | |
| (b-c) | | -6466* | -3566* | | |
| (b-d) | | 27 NS | -1963* | | |
| (c-d) | | 6486* | 1603* | | |

stimulation of males might not have any effect on egg size. In $F_1$ however the difference between the egg size of $H_1$ and that of Bar female was significant. There was significant difference between the egg sizes of M and yellow females.

## Performance of $F_2$ females

The mean egg size of 8 different genotypes is tabulated in Table 44.

Table 44

Mean egg size (proportional units) of $F_2$ females of $H_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{+\ +\ +\ +\ +}{\text{sc cv v f B}}$ | 20 | 27713 | 288 |
| 2 | $\frac{\text{sc cv v f B}}{\text{sc cv v f B}}$ | 14 | 26701 | 566 |
| 3 | $\frac{\text{sc}\ +\ +\ +\ +}{\text{sc cv v f B}}$ | 20 | 27496 | 273 |
| 4 | $\frac{+\ \text{cv v f B}}{\text{sc cv v f B}}$ | 9 | 26988 | 342 |
| 5 | $\frac{\text{sc cv}\ +\ +\ +}{\text{sc cv v f B}}$ | 18 | 27256 | 336 |
| 6 | $\frac{+\ +\ \text{v f B}}{\text{sc cv v f B}}$ | 18 | 27356 | 257 |
| 7 | $\frac{\text{sc cv v}\ +\ +}{\text{sc cv v f B}}$ | 16 | 26871 | 465 |
| 8 | $\frac{+\ +\ +\ \text{f B}}{\text{sc cv v f B}}$ | 20 | 27509 | 332 |

Analysis of variance indicated no significant difference between the egg size of different genotypes.

A close examination revealed that the flies that contained one X of M and the other from $H_1$ had larger eggs and the flies that contained both the X chromosomes from M line gave smallest eggs. The difference due to the substitution of one X chromosome in M stock was an increase of 1012 proportional units in the mean egg size. This might be due to the fact that $H_1$ X chromosome had more dominant genes compared to M X chromosome.

The effects of various segments of X chromosome of $H_1$ on egg size are summarised in Table 45.

Table 45

Effects of various regions of one X chromosome on egg size

| Sl. No. | Region of X chromosome | Egg size (proportional units) Estimates | Mean |
|---|---|---|---|
| 1 | scute (sc) | 217<br>287 | 252 |
| 2 | crossveinless (cv) | 240<br>368 | 304 |
| 3 | vermilion (v) | 385<br>153 | 269 |
| 4 | forked-Bar (fB) | 204<br>170 | 187 |
| 5 | Whole X chromosome | 1012 | |

The effects of various segments indicated that the region of *crossveinless* (*cv*) was more active affecting egg size than other regions. The next in order were *y* and *sc* regions. *fB* region showed least activity.

The results of $F_3$ females is summarised in Table 46.

### Table 46

Mean egg size (proportional units) with standard errors of $F_3$ females of $H_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 11 | 26412 | 623 |
| 2 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 20 | 26733 | 371 |
| 3 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | 19 | 26908 | 383 |
| 4 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 12 | 26972 | 609 |
| 5 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 13 | 27318 | 503 |
| 6 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | 20 | 27404 | 364 |
| 7 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | 20 | 27647 | 240 |
| 8 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 17 | 27827 | 233 |

Table 46 (contd)

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) Mean | S.E. |
|---|---|---|---|---|
| 9 | $\frac{+ + + f B}{+ + + f B}$ | 18 | 27993 | 266 |
| 10 | $\frac{+ + v + +}{+ + v + +}$ | 20 | 28238 | 713 |
| 11 | $\frac{sc + + + +}{sc + + + +}$ | 20 | 28303 | 360 |
| 12 | $\frac{+ + + + +}{+ + + + +}$ | 20 | 28808 | 119 |

Analysis of variance of above results showed that the differences in mean egg size among genotypes were statistically significant. Using critical difference test and bar notation the significance of differences in mean egg size of the 12 genotypes are brought out as under :

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| ─ | ─ | ─ | ─ | ─ | ─ | ─ |  |  |  |  |  |
|  |  | ─ | ─ | ─ | ─ | ─ | ─ | ─ |  |  |  |
|  |  |  |  | ─ | ─ | ─ | ─ | ─ | ─ | ─ |  |
|  |  |  |  |  |  |  | ─ | ─ | ─ | ─ | ─ |

The effects of various regions in homozygous condition and also of whole chromosome are summarised in Table 47.

## Table 47

Effects of portions of X chromosome of $H_1$ on egg size (duplicate effects)

| Sl. No. | Region of X chromosome | Egg size (proportional units) Estimates | Mean |
|---|---|---|---|
| 1 | scute (sc) | 505<br>560<br>914<br>166 | 536 |
| 2 | crossveinless (cv) | 899<br>346<br>591<br>919 | 689 |
| 3 | vermilion (v) | 496<br>675<br>671<br>570 | 603 |
| 4 | forked-Bar (fB) | 815<br>321<br>476<br>675<br>496<br>920 | 615 |
| 5 | Whole X chromosome | 2396 | |

The results of the effects of various segments again indicated that cv region was more active affecting egg size but more or less the polygenic activity affecting this trait was evenly distributed along X chromosome.

## Crosses with half sib low line ($L_1$)

The mean egg size with standard errors of $L_1$, M and their cross in various generations are presented in Table 48.

Table 48

Mean egg size (proportional units) with standard errors of $L_1$, M and their cross in various generations

| Crosses | Bar population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $L_1$ ♂ x $L_1$ ♀ (a) | 34517<br>±580 | 35563<br>±304 | 34069<br>±442 | 34627<br>±278 | 33669<br>±325 |
| M ♂ x M ♀ (b) | 24222<br>±449 | 27118<br>±256 | 27283<br>±255 | 25965<br>±286 | 26697<br>±230 |
| $L_1$ ♀ x M ♂ (c) | | 32452<br>±290 | 32126<br>±282 | | |
| Differences | | | | | |
| (a-b) | 10295* | 8445* | 6786* | 8662* | 6972* |
| (a-c) | | 3111* | 1943* | | |
| (b-c) | | -5334* | -4843* | | |

The difference between mean egg size of $L_1$ and M was significant in all the generations. $L_1$ had significantly larger eggs than M. The extent of variation in $P_1$, $F_2$ and $F_1$, $F_3$ was uniform. The difference in mean egg size in base population was largest.

The $L_1$ females mated to M males had significantly smaller eggs than the $L_1$ stock. The Bar females in $F_1$ produced significantly smaller eggs than $L_1$ but were larger in comparison to M stock indicating that $L_1$ had more dominant factors affecting egg size.

Performance of $F_2$ females

The mean egg size of 8 different $F_2$ genotypes is presented in Table 49.

Table 49

Mean egg size (proportional units) with standard errors of $F_2$ females of $L_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27808 | 214 |
| 2 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 10 | 26902 | 517 |
| 3 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27598 | 230 |
| 4 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 12 | 27022 | 307 |
| 5 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 17 | 27329 | 368 |
| 6 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 13 | 27412 | 346 |
| 7 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 18 | 26932 | 222 |
| 8 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 10 | 27611 | 232 |

Analysis of variance on the above data indicate no significant differences in mean egg size of different genotypes.

The effects of various segments of X chromosome of $L_1$ on egg size are given in Table 50.

Table 50

Effects of various regions of one X chromosome on egg size

| Sl. No. | Region of X chromosome | Egg size (proportional units) | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | scute (sc) | 210<br>120 | 165 |
| 2 | crossveinless (cv) | 269<br>390 | 329 |
| 3 | vermilion (v) | 397<br>199 | 298 |
| 4 | forked-Bar (fB) | 197<br>30 | 113 |
| 5 | Whole X chromosome | 906 | |

The contributions of various segments revealed that crossveinless region had comparatively more affect on egg size than other regions. Next in order were v, sc and fB respectively. It was interesting to note that fB region was more active in affecting egg production and hatchability but least active for egg size.

The mean egg size of $F_3$ females was tabulated in Table 51.

Table 51

Mean egg size (proportional units) with standard errors of $F_3$ females of $L_1$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 15 | 26759 | 734 |
| 2 | $\frac{+\ cv\ v\ f\ B}{+\ cv\ v\ f\ B}$ | 13 | 26976 | 439 |
| 3 | $\frac{sc\ cv\ +\ f\ B}{sc\ cv\ +\ f\ B}$ | 20 | 27079 | 422 |
| 4 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ +\ +}$ | 20 | 27110 | 445 |
| 5 | $\frac{+\ cv\ v\ +\ +}{+\ cv\ v\ +\ +}$ | 20 | 27647 | 330 |
| 6 | $\frac{+\ +\ v\ f\ B}{+\ +\ v\ f\ B}$ | 12 | 27694 | 285 |
| 7 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ +\ +\ +}$ | 20 | 27782 | 260 |
| 8 | $\frac{sc\ +\ +\ f\ B}{sc\ +\ +\ f\ B}$ | 7 | 27915 | 209 |
| 9 | $\frac{+\ +\ +\ f\ B}{+\ +\ +\ f\ B}$ | 12 | 28266 | 779 |

Table 51 (contd)

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 10 | $\frac{sc\ +\ +\ +\ +}{sc\ +\ +\ +\ +}$ | 20 | 28402 | 518 |
| 11 | $\frac{+\ +\ v\ +\ +}{+\ +\ v\ +\ +}$ | 11 | 28493 | 414 |
| 12 | $\frac{+\ +\ +\ +\ +}{+\ +\ +\ +\ +}$ | 20 | 28945 | 238 |

There was significant difference in mean egg size of different genotypes. Genotypes not differing significantly are grouped as under :

```
1    2    3    4    5    6    7    8    9    10   11   12
_____________________________________
     _____________________________________
                    ________________________________
                         _________________________________
```

The effects of various regions in homozygous condition and also of whole X chromosome are given in Table 52.

## Table 52

Effects of portions of X chromosome of $L_1$ on egg size (duplicate effects)

| Sl. No. | Region of X chromosome | Egg size (proportional units) | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | *scute* (sc) | 543<br>217<br>537<br>351 | 412 |
| 2 | *crossveinless* (cv) | 620<br>718<br>846<br>836 | 755 |
| 3 | *vermilion* (v) | 320<br>572<br>672<br>452 | 504 |
| 4 | *forked-Bar* (fB) | 679<br>351<br>487<br>671<br>703<br>799 | 615 |
| 5 | Whole X chromosome | 2186 | |

The results of the main effects indicated more activity in *crossveinless* region. Next in order were *fB*, *v* and *sc* regions.

## Crosses with full sib high line ($H_2$)

Table 53 provided the relevant data of mean egg size of $H_2$, M and their cross in various generations.

### Table 53

Mean egg size (proportional units) with standard errors of $H_2$, M and their cross in various generations

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $H_2$ ♂ x $H_2$ ♀<br>(a) | 30732<br>±383 | 30680<br>±250 | 30622<br>±321 | 30489<br>±345 | 30476<br>±297 |
| M ♂ x M ♀<br>(b) | 28318 | 27943<br>±264 | 27123<br>±389 | 26185<br>±345 | 26697<br>±230 |
| $H_2$ ♀ x M ♂<br>(c) | | 30884<br>±267 | 32117<br>±347 | | |
| <u>Differences</u> | | | | | |
| (a-b) | 2414* | 2737* | 3599* | 4304* | 3779* |
| (a-c) | | -204 NS | -1495* | | |
| (b-c) | | -2941* | -4994* | | |

$H_2$ produced significantly larger eggs than M in all the generations.

$H_2$ females mated to M males produced eggs of almost the same size as $H_2$, making it clear that stimulation of male had no effect on egg size.

The Bar females produced larger eggs than $H_1$ which was not expected. Some environmental factor might have played the role.

Performance of $F_2$ females

Table 54 provided mean egg size of 8 different genotypes.

Table 54

Mean egg size (proportional units) with standard errors of $F_2$ females of $H_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27632 | 259 |
| 2 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 17 | 26549 | 394 |
| 3 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27383 | 215 |
| 4 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 11 | 26789 | 352 |
| 5 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 19 | 27172 | 343 |
| 6 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 15 | 27229 | 350 |

Table 54 (contd)

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 7 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 26802 | 310 |
| 8 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 15 | 27481 | 342 |

Analysis of variance on the above data indicated no significant differences between the egg size of different genotypes.

A close examination of the mean egg size of different genotypes revealed that flies that contained two X chromosomes from marker had smallest egg while the flies with one X from marker and the other from $H_2$ had largest eggs. The effect of the substitution of one X chromosome was an increase of 1083 proportional units. This indicated that $H_2$ chromosomes had more dominant genes than M stock.

The effects of various regions of X chromosome of $H_2$ on egg size are summarised in Table 55.

### Table 55

Effects of various regions of one X chromosome of $H_2$ on egg size

| Sl. No. | Region of X chromosome | Egg size (proportional units) | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | scute (sc) | 279<br>240 | 254 |
| 2 | crossveinless (cv) | 211<br>440 | 325 |
| 3 | vermilion (v) | 370<br>252 | 311 |
| 4 | forked-Bar (fB) | 151<br>253 | 202 |
| 5 | Whole X chromosome | 1083 | |

The effects of various segments revealed relatively more activity in cv region but was not significantly different from other regions. The polygenic activity affecting egg size was more or less evenly distributed on X chromosome.

The mean egg size of $F_3$ females is summarised in Table 56.

## Table 56

Mean egg size (proportional units) with standard errors of $F_3$ females of $H_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | + + + + + / + + + + + | 20 | 27810 | 250 |
| 2 | sc cv v f B / sc cv v f B | 10 | 25919 | 249 |
| 3 | sc + + + + / sc + + + + | 20 | 27366 | 375 |
| 4 | + cv v f B / + cv v f B | 11 | 26564 | 481 |
| 5 | sc cv + + + / sc cv + + + | 20 | 26726 | 405 |
| 6 | + + v f B / + + v f B | 12 | 26889 | 309 |
| 7 | sc cv v + + / sc cv v + + | 20 | 26392 | 172 |
| 8 | + + + f B / + + + f B | 20 | 27261 | 207 |
| 9 | + + v + + / + + v + + | 20 | 27459 | 342 |
| 10 | sc cv + f B / sc cv + f B | 16 | 26494 | 471 |
| 11 | + cv v + + / + cv v + + | 20 | 26684 | 254 |
| 12 | sc + + f B / sc + + f B | 20 | 26835 | 289 |

Analysis of variance on the above data revealed no significant differences in mean egg size of different genotypes.

The effects of various regions of X chromosome of $H_2$ have been derived and brought out in Table 57.

Table 57

Effect of portions of X chromosome of $H_2$ on egg size (duplicate effects)

| Sl. No. | Region of X chromosome | Egg size (proportional units) Estimates | Egg size (proportional units) Mean |
|---|---|---|---|
| 1 | scute (sc) | 444<br>645<br>295<br>426 | 452 |
| 2 | crossveinless (cv) | 640<br>325<br>775<br>341 | 520 |
| 3 | vermilion (v) | 575<br>372<br>334<br>351 | 408 |
| 4 | forked-Bar (fB) | 549<br>473<br>531<br>120<br>232<br>570 | 412 |
| 5 | Whole X chromosome | 1891 | |

The results again indicated that cv region was relatively more active but the polygenic activity looked to have been distributed evenly along the length of X chromosome.

## Crosses with full sib low line ($L_2$)

The data of mean egg size (proportional units) with standard errors of $L_2$, M and their cross was summarised in Table 58.

Table 58

Mean egg size (proportional units) with standard errors of $L_2$, M and their cross in different generations

| Crosses | Base population | $P_1$ | $F_1$ | $F_2$ | $F_3$ |
|---|---|---|---|---|---|
| $L_2$ ♂ x $L_2$ ♀ (a) | 34082<br>±351 | 34312<br>±322 | 34854<br>±237 | 34289<br>±369 | 34255<br>±298 |
| M ♂ x M ♀ (b) | 24222<br>±449 | 27118<br>±256 | 27283<br>±255 | 25965<br>±286 | 26697<br>±230 |
| $L_2$ ♀ x M ♂ (c) | | 34563<br>±329 | 31115<br>±202 | | |
| **Differences** | | | | | |
| (a-b) | 9860* | 7194* | 7571* | 8324* | 7558* |
| (a-c) | | -251 NS | 3739* | | |
| (b-c) | | -7445* | -3832* | | |

$L_2$ produced uniform eggs in all the generations and were significantly larger than those of M, in all the generations.

The egg size of L2 females mated to M males did not differ significantly from that of $L_2$. In $F_1$ Bar females had significantly smaller eggs than $L_2$ but larger than M, indicating the location of more dominant genes affecting egg size in $L_2$.

Performance of $F_2$ females

Mean egg size (proportional units) with standard errors of 8 different genotypes is presented in Table 59.

Table 59

Mean egg size (proportional units) with standard errors of $F_2$ females of $L_2$ x M cross

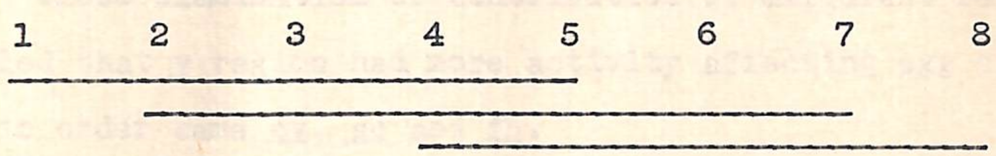
| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{sc\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 16 | 26898 | 386 |
| 2 | $\frac{sc\ cv\ v\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27032 | 267 |
| 3 | $\frac{+\ cv\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 27100 | 363 |
| 4 | $\frac{+\ +\ v\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 27358 | 238 |

Table 59 (contd)

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 5 | $\frac{sc\ cv\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27409 | 203 |
| 6 | $\frac{+\ +\ +\ f\ B}{sc\ cv\ v\ f\ B}$ | 20 | 27709 | 239 |
| 7 | $\frac{sc\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27709 | 204 |
| 8 | $\frac{+\ +\ +\ +\ +}{sc\ cv\ v\ f\ B}$ | 20 | 27916 | 213 |

Analysis of variance on the above data revealed significant differences in mean egg size values of different genotypes.

The genotypes not differing significantly in their mean egg size are group as under :



The effects of various segments of X chromosome of $L_2$ on egg size are summarised in Table 60.

## Table 60

Effects of various regions of one X chromosome of $L_2$ on egg size

| Sl. No. | Region of X chromosome | Egg size (proportional units) | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | scute (sc) | 207<br>202 | 204 |
| 2 | crossveinless (cv) | 300<br>258 | 279 |
| 3 | vermilion (v) | 377<br>351 | 364 |
| 4 | forked-Bar (fB) | 207<br>134 | 170 |
| 5 | Whole X chromosome | 1018 | |

Close examination of contribution of different regions revealed that v region had more activity affecting egg size. Next in order came cv, sc and fB.

The mean egg size of $F_3$ females is summarised in Table 61.

## Table 61

Mean egg size (proportional units) with standard errors of $F_3$ females of $L_2$ x M cross

| Sl. No. | Genotype | No. of females tested | Mean egg size (proportional units) | |
|---|---|---|---|---|
| | | | Mean | S.E. |
| 1 | $\frac{\text{sc cv v f B}}{\text{sc cv v f B}}$ | 20 | 27452 | 487 |
| 2 | $\frac{\text{+ cv v + +}}{\text{+ cv v + +}}$ | 20 | 27649 | 337 |
| 3 | $\frac{\text{+ cv v f B}}{\text{+ cv v f B}}$ | 18 | 27671 | 369 |
| 4 | $\frac{\text{sc + + f B}}{\text{sc + + f B}}$ | 20 | 27680 | 278 |
| 5 | $\frac{\text{sc cv + f B}}{\text{sc cv + f B}}$ | 16 | 27852 | 183 |
| 6 | $\frac{\text{+ + v f B}}{\text{+ + v f B}}$ | 18 | 27942 | 289 |
| 7 | $\frac{\text{sc cv v + +}}{\text{sc cv v + +}}$ | 20 | 27980 | 286 |
| 8 | $\frac{\text{sc cv + + +}}{\text{sc cv + + +}}$ | 20 | 28050 | 333 |
| 9 | $\frac{\text{sc + + + +}}{\text{sc + + + +}}$ | 20 | 28469 | 483 |
| 10 | $\frac{\text{+ + + f B}}{\text{+ + + f B}}$ | 20 | 28663 | 365 |
| 11 | $\frac{\text{+ + v + +}}{\text{+ + v + +}}$ | 20 | 28719 | 253 |
| 12 | $\frac{\text{+ + + + +}}{\text{+ + + + +}}$ | 20 | 29034 | 279 |

Analysis of variance on the above data revealed significant variation in mean egg size of different genotypes. The genotypes not significantly differing were grouped together based on critical difference tests.

```
1   2   3   4   5   6   7   8   9   10  11  12
_____________________________
    __________________________________
                ___________________________
                                ______________
```

The effects of various regions in homozygous condition and also of whole chromosome are presented in Table 62.

Table 62

Effects of portions of X chromosome of $L_2$ on egg size (duplicate effects)

| Sl. No. | Region of X chromosome | Egg size (proportional units) | |
|---|---|---|---|
| | | Estimates | Mean |
| 1 | *scute* (sc) | 565<br>219<br>-331<br>983 | 359 |
| 2 | *crossveinless* (cv) | 419<br>271<br>1070<br>-172 | 397 |
| 3 | *vermilion* (v) | 400<br>721<br>70<br>315 | 376 |

Table 62 (contd)

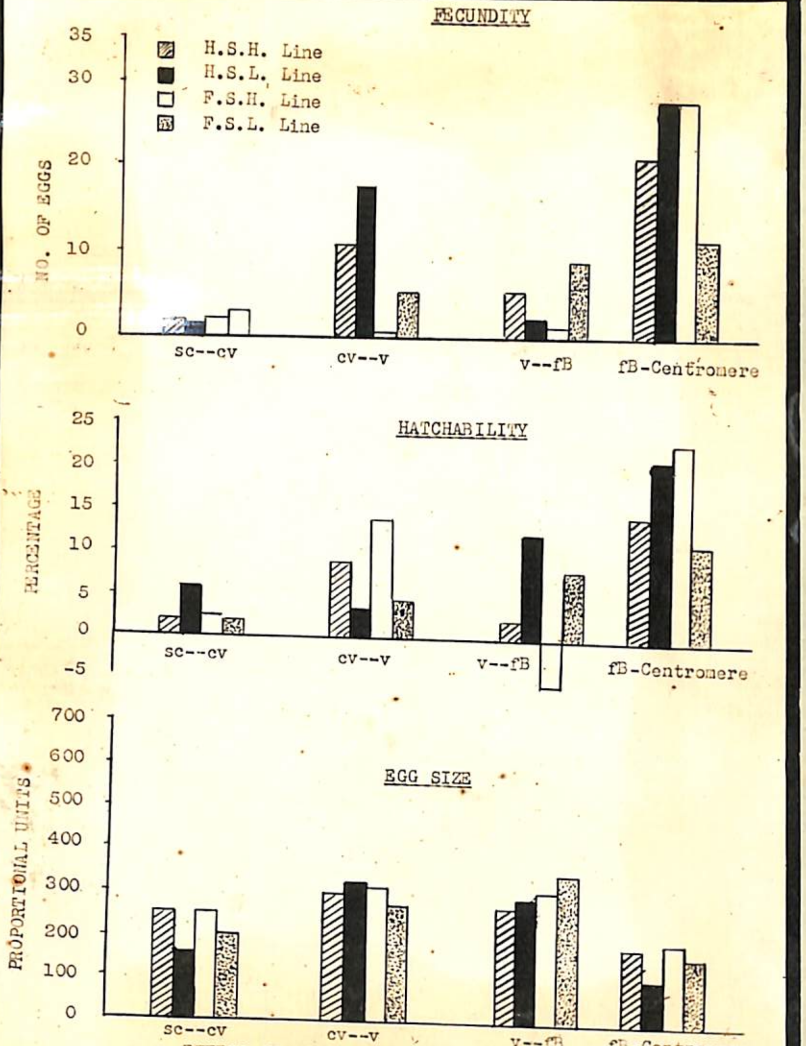
| Sl. No. | Region of X chromosome | Egg size (proportional units) | |
|---|---|---|---|
| | | Estimates | Mean |
| 4 | forked-Bar (fB) | 371<br>528<br>789<br>-22<br>198<br>777 | 440 |
| 5 | Whole X chromosome | 1582 | |

The effects of various regions indicated more or less even distribution of polygenic activity affecting egg size, on X chromosome of this line.

## Comparison of four inbred lines

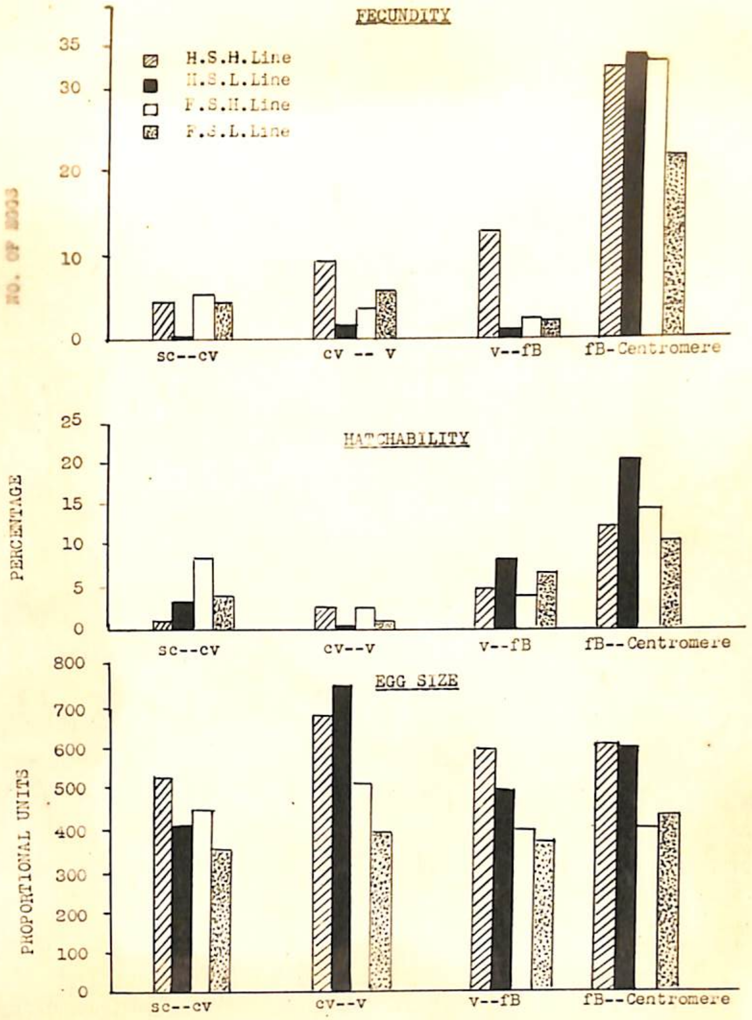
For ready comparison the main effects of various segments of X chromosome in single and double dose, on egg size are presented in Table 63, and the same is graphically brought out as histogram in Figs. 4 and 5.

Fig. 4.



EFFECT OF SINGLE SUBSTITUTION OF VARIOUS SEGMENTS OF X CHROMOSOME IN FOUR INBRED LINES

Fig 5



EFFECT OF VARIOUS SEGMENTS OF X-CHROMOSOME IN FOUR INBRED LINES ($F_3$ data)

## Table 63

Effect of various segments of X chromosome singly or in duplicate on egg size

| Region of X chromosome | Substitution | Lines | | | |
|---|---|---|---|---|---|
| | | $H_1$ | $L_1$ | $H_2$ | $L_2$ |
| *scute* (sc) | Single | 252 | 165 | 254 | 204 |
| | Double | 536 | 412 | 452 | 359 |
| crossveinless (cv) | Single | 304 | 329 | 325 | 279 |
| | Double | 689 | 755 | 520 | 397 |
| *vermilion* (v) | Single | 269 | 298 | 311 | 364 |
| | Double | 603 | 504 | 408 | 376 |
| *forked-Bar* (fB) | Single | 187 | 113 | 202 | 170 |
| | Double | 615 | 615 | 412 | 440 |
| Entire X chromosome | Single | 1012 | 906 | 1083 | 1018 |
| | Double | 2396 | 2186 | 1891 | 1582 |

From Table 63 the following conclusions could be drawn :

(1) Double substitution had always greater effect than when single and the effect was almost double.

(2) Comparing the effects of various regions *crossveinless* region seemed to have more activity in 3 of 4 lines, both in single and double substitution. In $L_2$ variation region showed more activity.

(3) In general, the polygenic activity affecting egg size

seemed to be evenly distributed along the X chromosome.

(4) Double substitution in fB region exhibited more than double effect, and in half sib lines it was 3-4 times that of single effect.

(5) The results indicated the additive nature of this trait.

## DISCUSSION

Knowledge about the organisation of polygenic activity of a quantitative character on chromosomes can be worked out in some detail in biological material where synthetic stocks are available.

Thus in Drosophila melanogaster, Wigan (1949a) investigated the polygenic organisation controlling sternopleural bristles on X chromosome and Breese and Mather (1957) studied the situation on III chromosome in case of abdominal bristles. Robertson and Reeve (1953) studied the like question in case of body size of Drosophila melanogaster. In case of egg production Gowen and Strauss (1942) found that 11% of the total variance for egg production in Drosophila could be attributed to the X chromosome, 44% to the II chromosome and 22% to the III chromosome. Interactions between the chromosomes were not significant. According to the findings of Robertson and Reeve (1955) the relative activity of III, II and I chromosomes was roughly in the proportion of 100:60:20 respectively. Singh et al. (1964) using a 6 x 6 diallel cross showed that low egg production was due to recessive genes and the high production due to their positive alleles and the ratio of recessives to dominants was 1:4 in the lines studied by them. Mazumdar and Prabhu (1967) who studied the fecundity in Drosophila melanogaster with an

X chromosome held unchanged found that the contribution of autosomes was more than the X chromosome. Finding of Win Moi Tait and Prabhu (1967) appeared to suggest that the II chromosome contained genes for fecundity which were more than in all the other chromosomes put together.

The present work carries the work on the organisation of polygenic activity along the length of X chromosome of *Drosophila melanogaster*, for egg production a step further. The technique employed made possible the study of polygenic activity for egg production, hatchability and egg size, in four sib selected lines for egg production. Two of the lines - one selected for high and another for low - came from half sib mated lines and the other two - one high and one low from full sib mated lines. In both the cases family selection was used.

The results made the study interesting. When the single region substitution was considered i.e. only a portion of the X chromosome in marker homozygous stock was replaced by the inbred line X chromosome, different results for different regions in the four inbred lines, were observed. Thus for *sc* region, the effect was the same in all the four inbred lines. As regard the *cv* region, the half sib high and low lines gave different results from full sib high and low lines. In the former two significantly higher activity for egg production was still retained, whereas it had almost lost in the latter two lines. In the _v_ region, half sib low and full sib high line had negligible activity (2.5 and 1.5 eggs respectively) while there was fairly high activity in half sib high and full sib low lines (5.8 and 9.7 eggs effect respectively). In the _fB_ region however with the exception of full sib low line, in the remaining 3 lines highest activity was observed. Since only a single chromosome segment substitution was involved in these trials, one had to conclude that the higher activity observed was due to the presence of dominants and less or absence of activity was due to the lack of dominants in the region concerned. On this basis, which was supported by the findings of Singh _et al_. (1964) that high production was due to dominant genes and low egg production due to recessives, one could conclude that the major dominant genes affecting egg production were largely concentrated around _fB_ region of X chromosome. This region occupies about 25 crossover units on X chromosome covering a region from 45 to 70 crossover units (from mid way between _vermilion_ and _forked-Bar_ to centromere). Prabhu (1939) had observed that the _garnet-forked_ region which covers the region from 44 to 56.7 units on the X chromosome had the highest concentration of sterility genes which meant that the actual effective region controlling fecundity in the *forked-Bar* region was on the left of *forked*. The total single region substitution worked out to 40 eggs in the case of full sib high line, and 49 eggs for half sib low line and 32 and 30 eggs respectively for the full sib high and low lines respectively. These results pointed out clearly that for selection of high and low lines with family system of mating half sib mating should be preferred to full sib mating. In this method the chances of perpetuating selection of *dominants* affecting egg production were greater in not only in the *forked-Bar* region but also in the region left of the same. With full sib low line selection, elimination of dominants affecting higher egg production was the highest.

The reason for continued retention of higher activity in the *forked-Bar* region might in all the probability be due to the greater resistence to crossing over offered by this region as it is close to the centromere. In the regions away from *forked-Bar* the chances of crossing over are greater and accordingly the elimination of *dominants* bringing about higher egg production. Similar finding had been recorded by Breese and Mather (1957) for bristle trait in *Drosophila melanogaster*.

Coming to the experiments involving substitution of duplicate portion of X chromosome once again it was found that different regions gave different results, though the most effective region was found to be once again the *forked-Bar* region. The sc region gave about the same effect in all the lines except half sib low line, whereas the contribution was practically nil as opposed to about 5 eggs in the other three lines.

In the cv region too the half sib low line had the least contribution being only 2 eggs. The full sib high and low lines had about the same potency, but highest effect (about 10 eggs) was found in half sib high line, in this region.

In the v region, only the half sib high line gave fairly high value being 13 eggs. The rest of the lines had negligible contribution in this region.

In the fB region the contribution recorded was about the same high level (33-34 eggs) except in full sib low line, which gave 22 eggs effect.

Considering the total of all the parts as a whole, we find that the maximum eggs were found in half sib high line and the rest of the lines had very much less number of total eggs than this line. It would therefore seem that to get high line producers one should have recourse to family selection with half sib mating. For getting low lines it is immaterial whether half or full sib matings were employed in family selection.

Comparison of single and double substitutions of parts of X chromosome tell interesting stories. Thus if the higher egg production was due to dominants, then one would expect either the same effect in both the 2 cases or higher in double than single substitution, on the assumption that the 2 segments of chromosome though alike carried different dominant genes affecting egg production. If on the other hand recessives determined low production then there should be lower production in duplicated than in single substitutions.

Examination of the data showed that both kinds of phenomenon were at work. Thus in sc region, in 3 out of 4 cases, the effect seen in duplicated cases was about two times that in single dose. In one case it was less than what was seen in single dose. This might be due to the segregation of recessives in that region bringing down production.

In cv region similar affects were noticed. In addition, in case of full sib low line single or double substitution gave the same results as expected. Segregation of recessives determining low production apparently had nearly exhausted, the higher affects seen in single dose in the double dose flies with half sib low line. Similar results were noted in v region also.

Only in the fB region no reduction in effect was noticed in double substitution as compared to single substitution. The effects were either 1½ times or 2 times in duplicated cases as that found in single substitution of parts of chromosomes. This leads one to conclude that possibly in this region recessives producing low production were not found.

HATCHABILITY

Study of the nature of polygenic organisation on X chromosome affecting hatchability had also yielded interesting conclusions. When the single region substitution was considered the results were different for different regions in the 4 lines.

In the scute region the effect was almost the same in all the lines except in half sib low line in which the effect was about three times to that of other lines.

Coming to cv region the effects in half sib and full sib high lines were fairly high (9.3% and 13.8% respectively) while the activity in half sib and full sib low lines was significantly less (2.9% and 4.5% respectively). In the two high lines this region was more active.

In v region half sib and full sib high lines had negligible activity (2.0% and -5.6%) while the two low lines had considerable activity (12.5% and 8% respectively). In the fB region however higher activity was noted in half sib low line and full sib high line while the other two lines exhibited lower activity. The higher activity in this region was due to the presence of dominants and lower or absence of activity was attributed to lack of dominants in these regions. Basing on the relative effects of various segments on hatchability it could be concluded that major dominant genes were located in fB region in all the four lines. Significant activity was also noticed in cv region of high lines and y region of low lines. The higher activity of fB region might be due to the fact that the genes for hatchability were tightly linked with the genes affecting egg production in this region of the chromosome. Pleiotropy of gene action could not be ruled out. The higher activity of cv region in half sib high line and of y region of full sib low line were similar to like activity for egg production. Retention of higher activity was mainly due to the restriction of crossing over in the fB region.

The total single region substitution worked out to be 27.6% in case of half sib high line, 42.7% for half sib low line, 34.1% for full sib high line, and 26.2% in case of full sib low line. Half sib low line and full sib high line had higher effect on hatchability.

When the substitution of duplicate portions were considered, the results differed with different regions though the most effective region once again was found to be fB region.

The sc region gave same effects in half sib lines but in full sib lines higher activity was noticed, specially in full sib high line, in which the activity was increased by about 3½ times.

The cv region had the same effects in both the high lines (2.6 and 2.7% respectively) while in the low lines the effect was negligible.

In the v region, high lines had lesser activity (4.92 and 3.8% respectively) while the low lines had higher activity in this region (8.3 and 6.8%).

In the fB region the contribution of the three lines ($H_1$, $H_2$ and $L_2$) was almost the same (about 11-14%) while higher activity was noticed in half sib low line (20.7%).

Considering the effect of the substitution of whole chromosome, maximum activity was noted in half sib low line and full sib high line and it looked that either selection for low production by half sib mating or for high egg production by full sib mating had similar effect on hatchability.

Comparison of single and double substitution gave important conclusions. If higher hatchability was due to dominant genes, then the effect of single and double substitution would be the same but if the double substitution resulted in higher hatchability it could be assumed that the two segments of the chromosome though similar, carried different dominant genes. If the low hatchability was due to recessive genes double substitution would markedly depress egg hatchability.

Examination of the effects of various segments due to single and double substitution brought out that both these phenomenon were operating.

Thus in sc region double substitution markedly increased hatchability in full sib high line and to a certain extent in full sib low line, but there was marked depression in hatchability due to segregation of recessive genes, in half sib low lines while no effect was noticed in half sib high line.

In cv region, the hatchability due to double substitution was lowered in all the lines indicating segregation of more and more recessive genes, affecting hatchability, in this region.

In v region the high lines exhibited marked improvement in hatchability while in low lines the decrease was slight, on double substitution.

In _fB_ region double substitution had no effect in 3 out of 4 lines, but in full sib high line there was reduction from 23.5% due to single substitution to 14.6% on double substitution. This leads one to conclude that recessive genes affecting hatchability were rare in _fB_ region in 3 lines ($H_1$, $L_1$, $L_2$) but were sufficient in full sib high line.

## EGG SIZE

The nature of polygenic distribution on X chromosome affecting egg size was different from those of egg production and hatchability in all the four lines.

Considering the single substitution effects, _sc_ region had similar effect in both the high lines. In the low lines the effect was less.

In the _cv_ region the effects were found to be the same in all the lines except in full sib low line which exhibited lesser activity. In _v_ region similar activity was found in all the lines except in full sib low line which showed more activity in this region. This might be due to the inclusion of _cv_ region in genotypes considered for _vermilion_.

The contribution of fB region was similar in all the lines except half sib low line which had lesser activity.

On the assumption that larger egg size was due to dominant genes it could be concluded that more dominant factors affecting egg size were located in cv region in all the lines. But as the difference in the activity of various segments in 4 lines was not significantly different it could be assumed that the polygenes were more or less distributed evenly along the X chromosome.

Examining the total chromosome substitution effects it was clear that the activity was similar in all the lines except in half sib low line.

Double substitution of each of the regions had almost similar effects in all cases. With few exceptions, the maximum activity was noted again in cv region.

sc region had similar effect in all the lines except in full sib low line which had lesser activity.

In cv region the half sib high and low lines had more activity (689 and 755 proportional units respectively). The full sib low line had least effect (397 proportional units).

The half sib high and low lines had more activity in v region (603 and 504 proportional units) than the full sib high and low lines (408 and 376 proportional units respectively).

In fB region also half sib high and low lines had more activity (615 and 615 proportional units) as compared to 412 and 440 proportional units of full sib high line and low line respectively.

Taking the effects of double substitution of whole chromosome, it was concluded that the half sib lines were more active than the full sib lines.

Comparison of the single and double substitution of parts of X chromosome gave some interesting conclusions.

In sc region double substitution had doubling effect in all the cases. The effect was 3 fold in half sib low line. The dominant genes affecting egg size were probably different in two similar segments.

Considering the cv region the expected doubling effect was noticed in all the lines except in full sib low line in which the effect was more than the single effect. Similar was the case in v region, but in fB region double substitution in half sib high and low lines had 3-4 times the effect of single substitution indicating that the dominant genes greatly differ in the two homologues in this region. Further the greater activity due to double substitution led one to conclude that the genes affecting egg size were mainly additive in nature.

# SUMMARY

1. The investigation on "Genetic analysis of some inbred lines of *Drosophila melanogaster*" was taken up to find the genetic architecture of X chromosome in four sib selected lines in either direction i.e.

   (a) Half sib high and low lines at the end of 20 generations of selection.

   (b) Full sib high and low lines at the end of 19 generations of selection.

2. Marker X chromosome from the males of b-208 stock having 5 important marker genes i.e. *sc*, *cv*, *v*, *f* and *B* was introduced in the genome of each of the four inbred lines, to enable particular segment of X chromosome to be identified and followed. There were also controls of both inbred and marker lines.

3. The X chromosome was divided into 4 regions i.e. *sc* (6.8 units), *cv* (16.4 units), *v* (21.6 units) and *fB* (25.0 units), disregarding crossing over between *forked* and *Bar* (0.3 units).

4. The experiment with each line, lasted upto $F_3$ generation, when the different genotypes could be segregated and performance tested. $F_2$ provided single region substituted genotypes.

5. Genetic architecture of the X chromosome of the inbred lines with regard to fecundity, hatchability and egg size were studied.

6. Polygenic organisation along the X chromosome for the trait egg production followed a definite pattern in both the high and low lines. The region around forked-Bar was polygenically active in expressing egg production. crossveinless region was also active with single region substitution in half sib lines.

   Double substitution had marked depressing effect in many cases. The fB region in half sib lines was more or less resistent to downward selection.

7. Polygenic activity affecting egg hatchability had also shown a definite pattern, specially in low lines. The fB region was active in all the lines. Single substitution of cv region had marked effect in half sib low line. Linkage of polygenes affecting fecundity and hatchability in the 4 lines was found. Double substitution of different regions had marked deleterious effect on egg hatchability.

8. Polygenes affecting egg size were found to be almost uniformly distributed along the length of X chromosome

in all the lines. Comparatively cy region was more active in 3 lines ($H_1$, $L_1$ and $H_2$) and y region in $L_2$. Double substitution of various regions had doubling effect in many cases but in fB region the effect was 3-4 times. Polygenes affecting egg size were hypothesized to have acted additively in all the four lines. At least 4 genes might have been involved in expressing egg size as the genes were more or less evenly distributed along the chromosome.

# BIBLIOGRAPHY

Ayala, F.T. (1965). Relative fitness of *Drosophila serrata* and *Drosophila birchii*.

Genetics, *51*:527-544.

Bateman, A.J. (1962). The genetics of egg hatching in *Drosophila*.

Heredity, *11*:1-107.

Bell, A.E., Moore, C.H. and Warren, D.C. (1954). A biological evaluation with *Drosophila melanogaster* of four methods of selection for the improvement of quantitative characters.

Proc. 9th intern. Congr. Gen. Caryologia, *6* Suppl., 851-853.

Bell, A.E., Moore, C.H. and Warren, D.C. (1955). The evaluation of new methods for the improvement of quantitative characters.

Cold. Spr. Harb. Symp. quant. Biol., *20*:197-211.

Bennett, J.H. (1956). Lethal genes in inbred lines.

Heredity, *10*:263-270.

Bhat, P.N. (1961). Two way selection for a metric character in *Drosophila* and correlated responses in other non-selected metric characters.

M.V.Sc. Thesis, Agra University, Agra.

Bonnier, G. and Ulla, B.J. (1957). Rate of development and viability of mutants in *Drosophila melanogaster*.

Evolution, *11*:271-279.

Bonnier, G. (1961). Experiments on hybrid superiority in *Drosophila melanogaster*. I. Egg laying capacity and larval survival.

Genetics, *46*:9.

Breese, E.L. and Mather, K. (1957). The organisation of polygenic activity within a chromosome in *Drosophila*. I. Hair characters.

Heredity, *11*:373-394.

Breese, E.L. and Mather, K. (1960). The organisation of polygenic activity within a chromosome in Drosophila. II. Viability.

Heredity, 14:375-399.

Bridges, C.B. and Brehme, K.S. (1944). The mutants of Drosophila melanogaster.

Carnegie Institution of Washington Publication 552, Washington, D.C.

Brown, W.P. (1962). Some genetic parameters of egg number in selected population of Drosophila melanogaster.

D.I.S., 34:73.

Brown, W.P. and Bell, A.E. (1961). Genetic analysis of a "Plateaued population of Drosophila melanogaster."

Genetics, 46(4):407-425.

Brown, W.P. and Bell, A.E. (1961). Control population in selection experiments for egg number in Drosophila melanogaster.

Genetics, 46:854.

Burdick, A.B. (1954). New medium of reproduceable quality, stable at room temperature.

D.I.S., 28:170.

Burdick, A.B. and Bell, A.E. (1959). Effect of medium pH on emergence time and egg production.

D.I.S., 28:112.

Buzzati-Traverso, A.A. (1952). Heterosis in population genetics.

Heterosis (Iowa State College Press Ames), 149-160.

Buzzati-Traverso, A.A. (1955). Evolutionary changes in components of fitness and other polygenic traits in Drosophila melanogaster populations.

Heredity, 9:153-186.

Carson, H.L. (1961). Relative fitness of genetically open and closed experimental populations of *Drosophila robusta*.

Genetics, 46:553-567.

Castle, W.E., Carpenter, F.W., Clark, A.H., Mast, S.O. and Barrows, W.N. (1906). The effects of inbreeding, crossbreeding and selection upon the fertility and viability of *Drosophila*.

Proc. Amer. Acad. Arts & Sci., 41.

Chakrabarti, S. (1966). Relative merits of heritability estimates computed by two different methods in *Drosophila*.

M.V.Sc. Thesis, Agra University, Agra.

Charles, D.R. and Smith, H.H. (1939). Distinguishing between two types of gene actions in quantitative inheritance.

Genetics, 24:34-48.

Clark, J.M., Maynard-Smith, J. and Sondhi (1961). Asymmetrical response to selection for rate of development in *Drosophila subobscura*.

Genet. Res. 2.

Clayton, G.A., Morris, J.A. and Robertson, A. (1957). An experimental check on quantitative genetical theory. I. Short term responses to selection.

J. Genetics, 55:131-151.

Clayton, G.A., Morris, J.A. and Robertson, A. (1957). An experimental check on quantitative genetical theory. II. Long term effects of selection.

J. Genetics, 55:152-170.

Clayton, G.A., Knight, G.R., Morris, J.A. and Robertson, A. (1957). An experimental check on quantitative genetical theory. III. Correlated responses.

J. Genetics, 55:171-180.

Cocks, B. (1954). Polygenic system controlling the expression of major mutant genes which affect chaetae number in Drosophila melanogaster.

Heredity, 8:13-34.

Crow, J.F. (1955). General theory of population genetics.

Cold Spr. Harb. Symp. Quant. Biol., 20:54-59.

Darlington, C.D. (1942). The polygenic concept.

Nature, 150:154.

Darlington, C.D. and Mather, K. (1949). The elements of genetics.

George Allen and Unwin Ltd., London. 1st edition.

Demerec, M. (1950). Biology of Drosophila.

New York John Wiley and Sons Inc. Lond.

Defries, J.C. and Touchberry, R.W. (1961). A 'maternal effect' on body weight in Drosophila.

Genetics, 46:1261.

Defries, J.C. and Touchberry, R.W. (1961). The variability of response to selection. I. Inter-line and intraline variability in a population of Drosophila affinis selected for body weight.

Genetics, 46:1519-1530.

Dobzhansky, Th. and Spassky, B. (1944). Genetics of natural population. XI. Manifestation of genetic variants in Drosophila pseudo-obscura in different environments.

Genetics, 29:270-290.

Dobzhansky, Th. (1947). Genetics of natural population. XIV. A response of certain gene arrangements in the third chromosome of Drosophila pseudo-obscura to natural selection.

Genetics, 32:142-160.

Druger, M. (1962). Selection and body size in Drosophila pseudo-obscura at different temperatures.

Genetics, 47:209-222.

Durrant, A. and Mather, K. (1954). Heritable variation in a long inbred line of Drosophila.
Genetics, 27:97-119.

Falconer, D.S. (1960). Introduction to quantitative genetics.
Oliver and Boyd. Edinburgh and London.

Fisher, R.A. (1930). The genetical theory of natural selection. Claridon Press. Oxford.

Fraser, A.S., Scowcroft, W., Nasser, R., Angles, H. and Bravo, G. (1965). Variation of scutellar bristles in Drosophila. IV. Effects of selection.
Aust. J. Biol. Sci., 18:619-641.

Gibson, J.B. and Thoday, J.M. (1963). Effects of disruptive selection. VIII. Imposed quasi-random mating. Heredity, 18:513-524.

Gibson, J.B., Parson, P.A. and Spickett, S.G. (1961). Correlation between chaetae number and fly size in Drosophila melanogaster.
Heredity, 16:349-354.

Gilbert, N. (1961). Quantitative inheritance in Drosophila.
J. Genetics, 57:77.

Gilbert, N. (1961). Polygenic analysis. II. Selection.
Genet. Res. (Camb.), 2:456-460.

Gowen, J.W. (1945). An analysis of genetic and cytoplasmic basis of heterosis. Genetics, 30:7.

Gowen, J.W. (1946). Significance of additive, dominant, complementary gene action to hybrid vigour in Drosophila.
Genetics, 31:247.

Gowen, J.W. (1952). Heterosis. Hybrid vigour in Drosophila. Iowa State College Press, Ames, Iowa.

Haskell, G.M.L. (1943). The polygenes affecting the manifestation of scute in Drosophila melanogaster. J. Genetics, 45:269-276.

Hayman, B.I. and Mather, K. (1953). The progress of inbreeding when heterozygotes are at a disadvantage.
Heredity, 7:165-183.

Hiraizumi, Y. (1961). Negative correlation between rate of development and female fertility in Drosophila melanogaster.
Genetics, 46:615.

Hiraizumi, Y. and Crow, J.F. (1960). Heterozygous effects on viability, fertility, rate of development and longevity of Drosophila chromosomes.
Genetics, 45:1071-1083.

Hollingsworth, M.J. and Maynard-Smith, J. (1955). The effects of inbreeding on rate of development and on fertility in Drosophila subobscura.
J. Genetics, 53:295-314.

Hyde, R.H. (1914). Fertility and sterility in Drosophila anapelophila.
J. Exp. Zoo. XVII:141-171, 173-212.

Imai, T. (1934). The influence of temperature on egg size and variation in Drosophila melanogaster.
Arch. Ento. Mech. Org., 132:206-219.
(A.B.A. 4:443)

Ives, P.T. (1945). The genetic structure of American population of Drosophila melanogaster.
Genetics, 30:167-196.

Ives, P.T. and Hinton, T. (1947). Second chromosome inversion in a local wild population of Drosophila melanogaster.
Genetics, 32:92 (Abstract).

Jayaramakrishna, V. (1967). Nature of genetic response to two way selection for egg production in Drosophila melanogaster.
M.V.Sc. Thesis, Agra University, Agra.

Karp, M.L. (1936). O Kooperacu Scetionoc-nyh genov u.D.m. (On the cooperation of bristle genes in Drosophila melanogaster).
Zool. Z. (Mosk), 15:604-639.
(A.B.A. 5:450).

Karp, M.L. (1936). Distribution of genes affecting the number of sternopleural bristles in the III-chromosome of *Drosophila melanogaster*.
Zoo. Z. (Mosk), *15*:26-47.
(A.B.A. 5:449)

Kearsey, M.J. and Ken-chi, Kojima (1966). The genetic architecture of body weight and egg hatchability in *Drosophila melanogaster*.
Genetics, *56*:23-37.

Kidwell, J.K. and Malick Linda (1967). The effect of genotype, mating status, weight and egg production on longevity in *Drosophila melanogaster*.
J. Heredity, *58*:169-171.

Lerner, I.M. (1954). Genetic homeostasis.
Oliver and Boyd, Edinburgh.

Lerner, I.M. (1958). The genetic basis of selection.
John Wiley and Sons, New York.

Li, C.C. (1950). Population genetics.
Chicago University of Chicago Press, Lond: Cambridge University.

Lush, J.L. (1945). Animal breeding plans.
Ames: Iowa State College Press.

Marein, D. (1958). Selection for developmental rate in *Drosophila pseudo-obscura*.
Genetics, *43*:3-15.

Marinkovic, D. (1967). Genetic load affecting fecundity in natural population of *Drosophila pseudo-obscura*.
Genetics, *56*:61-71.

Martin, G.A. and Bell, A.E. (1960). An experimental check on the accuracy of prediction of response during selection.
Biometrical Genetics. Pergamon Press, 1960.

Mather, K. (1941). Variation and selection of polygenic characters.
J. Genetics, 41:159-193.

Mather, K. (1942a). The balance of polygenic combinations.
J. Genetics, 43:309-336.
(A.B.A. 10:193)

Mather, K. (1942b). The polygenic concept.
Nature, 149:731-732.
(A.B.A. 10:193)

Mather, K. (1943). Polygenes in development.
Nature, 151:560.
(A.B.A. 11:201)

Mather, K. (1949). Biometrical genetics.
Methuen and Co. Ltd. London 1st edition, 1949.

Mather, K. (1956). Polygenic mutation and variation in population.
Proc. Roy. Soc. B., 145:293-297.

Mather, K. and Harrison, B.J. (1949a). The manifold effects of selection.
Heredity, 3:1-52.

Mather, K. and Harrison, B.J. (1949b). The manifold effects of selection.
Heredity, 3:131-162.

Mather, K. and Wigan, L.G. (1942). The selection of invisible mutations.
Proc. Roy. Soc. B., 131:50-64.

Maynard-Smith, J. and Maynard-Smith, S. (1954). Genetics and cytology of *Drosophila subobscura*. VIII Heterozygosity, viability and rate of development.
J. Genetics, 52:152.

Maynard-Smith, J. (1956). Fertility, mating behaviour and sexual selection in *Drosophila subobscura*.
J. Genetics, 54:261-279.

Maynard-Smith, J. (1958). The effect of temperature and egg laying capacity on the longevity of *Drosophila subobscura*.
J. Exp. Biol., 35:832-842.

Mazumdar, N.K. and Prabhu, S.S. (1967). Polygenic activity of X chromosome for egg production, egg size, hatchability and wing size in *Drosophila melanogaster*. J. Genetics, 61:1 (unpublished).

McBridge, G. and Robertson, A. (1963). Selection using assortative mating in *Drosophila melanogaster*. Genet. Res. (Camb.), 4:356-369. (A.B.A. 32:1629)

Mitchell, D.F. (1958). Inversion heterozygosity, recombination and variability of quantitative traits. Cold. Spr. Harb. quant. Biol., 23:279-289.

Moen Khaus, W.J. (1911). The effects of inbreeding and selection on fertility and vigour and sex ratio of *Drosophila ampelophila*. J. Morph. XXII:123-154.

Narain, P., Joshi, C. and Prabhu, S.S. (1962). Response to selection for fecundity in *Drosophila melanogaster*. D.I.S., 36:97.

Nassar, R.F. (1965). Variation of scutellar bristles in *Drosophila*. VIII. Selection and polygenes. Genetics, 52:915-923.

Parson, P.A. (1959). Genotype-environmental interactions for various temperatures in *Drosophila melanogaster*. J. Genet., 44:1325-1333.

Prabhu Lal (1962). Effect of inbreeding at different rates on egg production and hatchability in *Drosophila*. M.V.Sc. Thesis, Agra University, Agra.

Prabhu, S.S. (1960). Fundamental study of quantitative inheritance. Annual report of Animal Genetics Division, IVRI, Izatnagar.

Prabhu, S.S. and Robertson, F.W. (1961). The ecological genetics of growth in *Drosophila*. V. Gene environment interaction and inbreeding. Genet. Res. (Camb.), 2:424-430.

Prabhu, S.S., Prem Narain, Swastika Negi, Joshi, C. and Singh, H.P. (1964a). Two way selection for egg production in *Drosophila melanogaster*.
J. Anim. Morph. & Physio., **11**:199-218.

Prabhu, S.S., Swastika Negi and Singh, H.P. (1963). Quantitative studies on *Drosophila* egg. I. Selection of medium.
J. Anim. Morph. & Physio., **10**:32-46.

Prabhu, S.S., Singh, H.P., Narain, P. and Rawat, S. (1966). Analysis of a 6 x 6 diallel cross for hatchability in *Drosophila melanogaster*.
J. Genet., **60**:1 (unpublished).

Rasmuson, M. (1952). Variation in bristle number of *Drosophila melanogaster*.
Acta Zool. Stockh., **33**:277-308.

Rasmuson, M. (1956). Recurrent reciprocal selection results of three model experiments on *Drosophila* for improvement of quantitative characters.
Hereditas, **42**:397-414.

Rawat, S. (1966). Effect of different methods of selection for one quantitative character on the expression of other quantitative characters in *Drosophila ananassae*.
Ph.D. Thesis, Agra University, Agra.

Reeve, E.C.R. and Robertson, F.W. (1953). Studies in quantitative inheritance. II. Analysis of a strain of *Drosophila melanogaster* selected for long wings.
J. Genet., **51**:276-316.

Reeve, E.C.R. and Robertson, F.W. (1954). Studies in quantitative inheritance. VI. Sternite chaeta number in *Drosophila*: a metameric character.
Z. indukt. Abstamn. u. Vererblehre, **86**:269-288.

Robertson, A. (1952). The effect of inbreeding on the variation due to recessive genes.
Genetics, **37**:189-207.

Robertson, F.W. and Reeve, E.C.R. (1952). Studies in quantitative inheritance. I. The effects of selection of wing and thorax length in Drosophila melanogaster.

J. Genet., 50:416-448.

Robertson, F.W. and Reeve, E.C.R. (1953). Studies in quantitative inheritance. IV. Effects of substituting chromosomes from selected strains in different genetic background in Drosophila melanogaster.

J. Genet., 51:586-610.

Robertson, F.W. (1954). Studies in quantitative inheritance. V. Chromosome analysis of crosses between selected and unselected lines of different body size in Drosophila melanogaster.

J. Genet., 52:494-515.

Robertson, F.W. and Reeve, E.C.R. (1955). Studies in quantitative inheritance. VII. Crosses between strains of different body size in Drosophila melanogaster.

Z. indukt. Abstamn. u. Vererblehre, 86:424-438.

Robertson, F.W. and Reeve, E.C.R. (1955). Studies in quantitative inheritance. VIII. Further analysis of heterosis in crosses between inbred lines of Drosophila melanogaster.

Z. indukt. Abstamn. u. Vererblehre, 86:439-458.

Robertson, F.W. (1955). Selection response and the properties of genetic variation.

Cold. Spr. Harb. Symp. Quant. Biol., 20:166-177.

Robertson, F.W. (1956). The use of Drosophila in the experimental study of animal breeding problems.

A.B.A. 24:218-223.

Robertson, F.W. (1957). Studies in quantitative inheritance. XI. Genetic and environmental correlation between body size and egg production in Drosophila melanogaster.

J. Genet., 55:428-443.

Robertson, F.W. (1959). Gene environment interaction in relation to the nutrition and growth of Drosophila.
Biol. Contr. Uni. (Texas) Pub. No. 5914:89-98.

Robertson, F.W. (1962). Genetic correlation and environment.
Ann. Human Genet., 25:427.
(B.A., 41:4453)

Robertson, F.W. and Sang, J.H. (1944). The ecological determinants of population growth in Drosophila culture. I. Fecundity of adult flies.
Pro. Roy. Soc. B., 132:258-289.

Rokickii, P.F. (1936). Comparison of rate of mutation in X-rayed and non-X-rayed lines.
Usp. Zootech. Nauk., 2:161-202.

Sang, J.H. (1956). The quantitative nutritional requirements of Drosophila melanogaster.
J. Exp. Biol., 33:45-72.

Sang, J.H. and Clayton, G.A. (1957). Selection for larval development time in Drosophila.
J. Heredity, 48:265-270.

Satya Prakash (1962). Effect of various levels of inbreeding on egg size and fertility in Drosophila melanogaster.
M.V.Sc. Thesis Agra University, Agra.

Saxena, A.K. (1962). Correlations between egg production, egg size, hatchability and wing size with emergence time in Drosophila melanogaster.
M.V.Sc. Thesis Agra University, Agra.

Scrowcroft, W.R. (1966). Variation of scutellar bristles in Drosophila. IX. Chromosomal analysis of scutellar bristle selection lines.
Genetics, 53:389-402.

Sheldon, B.L. (1963). Studies in artificial selection of quantitative character. I. Selection for abdominal bristles in Drosophila melanogaster. II. Selection for body weight in Drosophila melanogaster.
Aust. J. Biol. Sci., 16:490-515, 516-541.

Sinnott, E.W., Dunn, L.C. and Dobzhansky, Th. (1958). Principles of genetics.
Kogakusha Co., Tokyo.

Singh, H.P., Prabhu, S.S., Prem Narain and Swastika Negi (1964b). Analysis of a 6 x 6 diallel cross for egg production in *Drosophila melanogaster*.
J. Genet., *59*(1):58-68.

Snedecor, G.W. (1956). Statistical methods applied to experiments in Agriculture and Biology.
Iowa State College Press, Ames, Iowa, U.S.A.

Spassky, B., Spassky, N., Levene, H. and Dobzhansky, Th. (1958). Release of genetic variability through recombination.
Genetics, *43*:844-867.

Stanley, W.F. (1935). The effect of temperature upon wing size of *Drosophila*.
J. Exp. Zool., *69*:459-495.
(A.B.A *3*:85-86. 1935)

Stern, E.B. (1934). The effect of ultraviolet radiation upon fecundity of *Drosophila melanogaster*.
Proc. Ind. Acad. Sci., *43*:224-227.
(A.B.A. *5*:328, 1937)

Straus, F.S. and Gowen, J.W. (1943). Heterosis: its mechanism in terms of chromosome units in egg production of *Drosophila melanogaster*.
Genetics, *38*:93.

Tait, W., Prabhu, S.S. (1966). Polygenic activity of II chromosome on egg production in *Drosophila melanogaster* (unpublished).

Tantawy, A.O. (1957). Selection limits with sib mating in *Drosophila melanogaster*.
Genetics, *44*:287-295.

Tantawy, A.O. (1961). Effects of temperature on productivity and genetic variance of body size in populations of *Drosophila pseudo-obscura*.
Genetics, *46*:227-238.
(B.A., *36*(15):47112)

Tantawy, A.O. and Reeve, E.C.R. (1956). IX. The effects of inbreeding at different rates in *Drosophila melanogaster*.
Z. indukt. Abstamn. Vererblehre, 87:648-667.

Temin, R.G. (1966). Homozygous viability and fertility loads in *Drosophila melanogaster*.
Genetics, 53:27-46.

Thoday, J.M. (1958). Homeostasis in a selection experiment.
Heredity, 12:401-415.

Thoday, J.M. (1960). Effects of disruptive selection. III. Coupling and repulsion.
Heredity, 14:35-49.

Thoday, J.M. and Boam, T.B. (1961). Effects of disruptive selection. V. Quasi-random mating.
Heredity, 16:219-223.

Vitukhiv, M.O. and Beardmore, J.A. (1959). Effect of environment upon the manifestation of heterosis and homeostasis in *Drosophila pseudo-obscura*.
Genetics, 44:759-768.

Warren, D.C. (1924). Inheritance of egg size in *Drosophila melanogaster*.
Genetics, 9:41-69.

Wentworth, E.N. (1913). The segregation of fecundity factors in *Drosophila*.
J. Genet., iii:113-120.

Wigan, L.G. (1944). Balance and potence in natural populations.
J. Genet., 46:150-160.

Wigan, L.G. (1949). The distribution of polygenic activity on the X chromosome of *Drosophila melanogaster*.
Heredity, 3:53-65.

Wigan, L.G. and Mather, K. (1942). Correlated responses to the selection of polygenic characters.
Ann. Eugen. (Camb.), 11:354-364.
(A.B.A. 12:107, 1944)

Wright, S. (1939). Genetic principles governing the rate of progress of livestock breeding.

Proc. Amer. Soc. Anim. Prod., 32:18-26.

Zarapkin, S.R. (1934). Size differences in *Drosophila funibris* due to genetic and environmental factors. II. Relation between body size and cell number. III. Duration of individual development of plus and minus cultures.

Z. indukt. Abstamn. u. Vererblehr, 68:163-171.