

FECUNDITY, EGG-SIZE, AND HATCHABILITY
IN
Drosophila Melanogaster
WITH III CHROMOSOME HELD UNCHANGED

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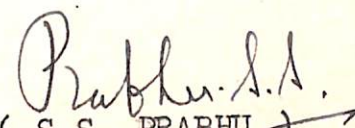
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C E R T I F I C A T E

Certified that Shri Ashok Kumar Gore of Post-Graduate College of Animal Sciences, Indian Veterinary Research Institute, Izatnagar, a candidate for M.V.Sc. (Final) Examination of 1968 in Animal Genetics and Breeding has been working under my supervision during the year 1967-68 and that the accompanying thesis entitled "Fecundity, egg size and hatchability in Drosophila melanogaster with III chromosome held unchanged" which he is submitting is his authentic original work.


(S.S. PRABHU)

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INTRODUCTION

INTRODUCTION

A laboratory for studying the inheritance of quantitative characters was established at the Animal Genetics Division of the Indian Veterinary Research Institute, Izatnagar, U.P. in the year 1956. To facilitate quick results and also for understanding the basic nature of the quantitative character studied in as much detail as possible, a Drosophila laboratory was set and most of the early studies conducted on this fly. The characters selected for study were fecundity, hatchability, egg size, and fertility. Reports of the early experiments to standardise work procedures and methods of rearing and testing flies are contained in Prabhu (1960). Results of early experiments to separate out high and low lines of Drosophila for fecundity are reported by Prabhu et al. (1964). The nature of the character egg production and its genetic architecture was given by Singh et al. (1964). That of hatchability was reported by Prabhu et al. (1967). The contribution of the X chromosome towards fecundity and hatchability in Drosophila melanogaster was investigated by Mazumdar and Prabhu (1967) and that of the II chromosome on the same characters and same flies was looked into by Win Moi Tait and Prabhu (1967). The present investigation was an extension of the same problem in which the III chromosome was kept unchanged and its effect on fecundity, egg size and hatchability was studied.

REVIEW OF LITERATURE

EGG PRODUCTION

Egg production is primarily related to the fitness of population and is highly variable and very sensitive to environmental changes. A variety of ecological factors determine the phenotypic expression of fecundity.

Cogan (1934) reported that *Drosophila* egg production presented a single cycle as contrasted with the series of cycles or egg clutches observed in the egg production in certain other forms like domestic fowl and the house fly, *Musca*. This fact made *Drosophila* egg production an easier character to study.

REVIEW OF LITERATURE

Isaacs (1934) studied the effect of temperature on egg size and variation in *Drosophila melanogaster* and reported that size of the flies did not affect the egg length and its variability under controlled environmental conditions. He showed that temperature did affect the egg length, when flies were transferred to another temperature at the time of mating during first day of egg production.

Isaacs (1934) studied the effect of ultraviolet radiation upon *Drosophila melanogaster* and reported that irradiation of females reduced the length of life and suggested

REVIEW OF LITERATURE

EGG PRODUCTION

Egg production is primarily related to the fitness of population and is highly variable and very sensitive to environmental changes. A variety of ecological factors determine the phenotypic expression of fecundity.

Gowen (1934) reported that Drosophila egg production presented a single cycle as contrasted with the series of cycles or egg clutches observed in the egg production in certain other forms like domestic fowl and the fungus fly, Sciara. This fact made Drosophila egg production an easier character to study.

Imai (1934) studied the effect of temperature on egg size and variation in Drosophila melanogaster and reported that age of the flies did not effect the egg length and its variability under controlled environmental conditions. He showed that temperature did affect the egg length, when flies were transferred to another temperature at the time of mating, during first day of egg production.

Stern (1934) studied the effect of ultraviolet radiation upon Drosophila melanogaster and reported that irradiation of females reduced the length of life and suppressed

egg laying. Five minutes' exposure brought fecundity to the level of 50% of the normal, while 8 minute exposure resulted into complete sterility. Younger flies and females were more susceptible than older flies and males as regards longevity and fertility.

Straus and Gowen (1943) studied heterosis in terms of chromosome unit in egg production of Drosophila and found that crosses between two inbred strains of Drosophila melanogaster showed 100% increase of egg production above the average of its parents. Analysis revealed that the total heterotic increase equalled the sum of the individual chromosome effects i.e. no interaction or combination effects could be detected, therefore the relationship between vigour (as measured by egg production) and chromosomal heterozygosis was linear. The heterotic effect due to the individual chromosomes proved to be proportional to their active lengths as measured by their band number in the salivary gland chromosomes and crossover units. By the chromosomal assay technique all possible homozygous and heterozygous combinations of the first 3 chromosomes from 2 inbred lines were obtained forming a balanced 3 x 3 x 3 factorial design. A randomised complete block experiment was designed to test all chromosomal types at the same time to detect environmental differences.

Robertson and Sang (1944) studied 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 changes due to genotype, temperature, humidity, nutrition, oviposition stimuli and the presence of other individuals. Dead yeast slowed down the rate of egg production and this was correlated with the longevity.

Gowen (1945) formed Drosophila races of different origin by continued brother sister mating. The life time egg production varied from 263-1606 eggs. The hybrids of 389 x 1000 egg races produced an average of 2034 eggs. The hybrids individually were not better than the best individuals of inbred. He reported that hybrid vigour was genetic in origin. Certain inbred strains contained genes which were generally effective in causing heterosis in their crosses, whereas, others contained genes which were specific to particular inbred combinations. The hybrid effect was due to a fairly large number of genes distributed at random over the chromosome pairs.

Burdick and Bell (1954) did not find any significant difference in fecundity of flies reared at different pH

levels. These results were unexpected since it was well known fact that egg production was highly variable trait.

Bell, Moore and Warren (1954) studied the effect of following four methods of selection on egg production and egg size in Drosophila melanogaster namely

- (1) Selection within a close population on the basis of individual and family merit.
- (2) Recurrent selection within a closed population for specific combining ability with an inbred tester line (Hull, 1945).
- (3) Reciprocal recurrent selection within two closed populations for specific combining ability with each other (Comstock et al., 1949).
- (4) Inbreeding and hybridisation egg production was recorded over the peak period of 4 to 7 days of age and egg size was measured as length of eggs in millimetre units.

In the first experiment, they studied high egg production and egg size for 16 generations. Selection was based on an index giving equal weight to these two traits
$$\bar{I} (\text{performance index} = 4 \text{ days' egg production} + 10 \times (\text{total of 5 egg lengths}) \bar{I}.$$

Selection within closed population was superior to the other methods for improving the highly heritable trait - egg size. During early selection individual and family selection method increased egg production more rapidly than either of the recurrent methods. The recurrent methods were more effective towards the end of experiment. At the end of experiment, the highest performance was obtained from single crosses of inbred lines followed in order by recurrent selection to the inbred tester, reciprocal recurrent selection and closed population.

They reported that fecundity was a highly heterotic trait with low heritability, while egg size showed little or no heterosis with relatively high heritability ranging between 30 to 60%.

Early testing of combining ability, for egg size provided better information on predicting subsequent combining ability than those of fecundity.

In the second experiment, selection was practiced only for egg production. It increased initially in the closed population by individual and family selection. Selection response ceased fairly soon and was surpassed by the lines selected for specific combining ability, especially that involving reciprocal recurrent selection. Crossing randomly

bred inbred lines was found to be superior as highest yield was achieved in a cross between inbred lines.

Bell, Moore and Warren (1955) noted while studying egg production and egg size in Drosophila melanogaster the high heterotic nature of fecundity with very low heritability. No significant differences for fecundity existed among the initial non-inbred stocks, but a positive genetic environmental interaction was revealed for fecundity.

Rasmuson (1956) studied the value of recurrent reciprocal selection as a method of breeding by conducting three experiments. Selection was only on the basis of progeny tests of males. From two heterogenous stocks, four lines were developed by selected males and a random sample of females from the same line and next cycle of selection was started for this purebred progeny. Fecundity, hatchability and body weight were the three characters taken for study.

She concluded the results of all the three experiments as follows. The crossbred produced by the reciprocal recurrent selection method were superior to purebred of the control lines in all the three experiments. In the first experiment, the advantage was 6% and was significant. In the other two experiments it was less than 2% and not significant.

She argued that advantage of RRS method should be more whenever overdominance is present, but in these experiments the advantage was very small and this was explained as the loci with overdominance were scarce with limited number of favourable alleles, while the epistatic interaction were striking. She discussed that epistatic interactions must be important mechanism (a) for the determination of specific and general combining ability and (b) for the formation of genetically conditioned ceilings and thus might explain the failures of selection improvements.

Brown and Bell (1957) studied the lethal and sterility genes in Drosophila melanogaster under reciprocal selection for higher fecundity and observed the plateau at 7th generation. They concluded that neither lethal nor sterility genes contributed to the lack of response for selection. The plateau was caused by an exhaustion of genetic variation.

Robertson (1957) studied genetic variation of ovary size in Drosophila melanogaster and found that body size was reduced by under feeding with a proportional decrease in ovariole number and also egg production but the eggs produced per ovariole is unaffected even by striking changes in body size. No correlation was observed between body size and ovariole number of egg production. He reported that the rate

at which eggs were laid might be affected by the supply of nutrients available and this in turn affected size.

Maynard-Smith (1958) studied the effect of temperature and egg laying on the longevity of Drosophila subobscura. The ovariless females and virgin females lived for longer period than normal mated females. The expectation of life of ovariless females at 20°C was not changed by exposure to 30.5°C. It was concluded that egg laying accelerated the aging of females at 20°C and the prolongation of life of females exposed to 30.5°C was due to the reduction in the rate at which such females lay eggs.

Mitchell (1958) reported in Drosophila melanogaster the positive association of multiple inversion heterozygosity with increased fecundity and male developmental rate.

Prabhu (1959-60) studied the genetic variability for egg production in Drosophila melanogaster and reported heritability for egg production to be 0.26 ± 0.09 by intra-sire regression method with 11 sires and 240 dam pairs. Realised heritability by Falconer's method was 0.11. The average 10 day egg production of early emerging females was 533.4 ± 18.5 eggs and in late emerging females was 501.6 ± 19.8 eggs. The difference was not significant statistically.

Bhat (1961) conducted two way selection experiment for a metric character in Drosophila and correlated responses in other non-selected metric characters. He followed six methods of selection - (1) mass selection, (2) cyclic system with 4 pair matings, (3) cyclic system with 3 pair matings, (4) cyclic system with 2 pair matings, (5) half sib mating and (6) sib mating. Cyclic system with two pair mating was found to be superior to all other methods. The mean daily egg production did not increase in any system after 5 generations of selection. Phenotypic variance showed an initial decrease in most of the selected lines followed by gradual increase in later generations.

Brown (1962) selected two population of Drosophila melanogaster for high egg production for 40 generations based on individual and family selection. Each population had attained a level and crosses between them showed heterosis which indicated that these populations were not identical genetically. The heritabilities of egg production were 0.08 ± 0.09 for 'R' population and 0.30 ± 0.12 for 'T' population. The heritability of egg production in the crosses of lines was 0.19 ± 0.06 .

Prabhu Lal (1962) studied the effect of inbreeding at different rates on egg production and hatchability in Drosophila.

Four systems of mating - full sib mating, half sib mating, cyclic system with 3 pair and 2 pair mating were used.

There was curvilinear decrease in egg production along with an increase in inbreeding in both full sib and its replication. The sharp decline of egg production was observed after 60% inbreeding. Phenotypic variance and variance between pairs showed irregular trend but variance within pair showed decreasing trend. Decline in egg production was more in rapid system of inbreeding and it was shown that egg production was highly influenced by environment, than hatchability. The heritability of hatchability was approximately 30% higher than that of egg production.

Prabhu et al. (1964) studied egg production in Drosophila melanogaster using three sets of two way selection experiment.

In Experiment I, sib mating and selection was done in either direction in 3 stocks of Drosophila for 24-26 generations. In Experiment II, the experiment was repeated by practising individual selection but avoiding inbreeding. In Experiment III, again the experiment was repeated by practicing family selection and avoiding inbreeding. The later two experiment was done for 10-12 generations with controls, but in experiment I there was no control. Distinct phenotypic response to selection which followed systematic trend in the

upward direction irrespective of direction of selection. This response was due to partly segregation of dominant genes affecting egg production.

Response to selection was erratic in experiment II. The additive portion of the genetic variance was reduced to 2-6 per cent from the initial 21% as seen from the values of realised heritability with rounds of selection. In III experiment, maximum response to selection was obtained and was possible to separate high and low line of egg production. In this experiment large proportion of the initial 24% genetic variance could be maintained at a level of 12-14% upto 9 generation, when it got reduced to 9%.

The results of these three sets of experiment have been interpreted as due to existence of four times the dominant than recessive genes affecting egg production in these stocks as established by Singh et al. (1964) by a separate study.

Singh et al. (1964) studied a 6 x 6 diallel cross for egg production in Drosophila melanogaster. They reported that :

- (1) A considerable amount of genetic and environmental interaction factors controlled egg production.

- (2) The genes affecting egg production exhibited mainly additive genetic effects and dominant deviations and showed non-allelic interaction.
- (3) The asymmetrical distribution of positive and negative alleles existed in the parents was explained as out of the selected six lines, three were of low and three were of high egg production.
- (4) They suggested that probably more dominant genes than recessive ones affected the egg production in the parental stock. The ratio of the recessive to dominant genes was 1:4.
- (5) Low egg production was due to recessive genes while high egg production to their dominant alleles.
- (6) Dominance deviations present were largely unidirectional of the order of D, B, E, C, A, F. The highest D and lowest F.

Richardson and Kojima (1965) studied the kinds of genetic variability in relation to selection responses in Drosophila egg production. Crossbred selection using reciprocal recurrent selection and purebred selection using full sib family selection were compared by Kojima and Kelleher (1963) for their relative effectiveness in increasing fecundity in

two populations of Drosophila pseudo-obscura. Their results indicated crossbred superiority where about 25% increase in egg production was obtained contrasted to almost no change for purebred selection.

For the purpose of elucidating the genetic characteristics of these populations a pair of intermix populations were formed

- (1) from the cross of initial populations in the selection experiments of Kojima and Kelleher, termed as base intermix, and
- (2) from the cross of final population from the crossbred selection scheme, termed as RRS intermix.

Two way selection was initiated on each of these intermix populations. Some unexpected results appeared during random mating phase. It was suggested that two initial populations were near their own points of adaptive maxim in the wrightian sense with intermediate gene frequency for mean performance in fecundity. Such situations could be expected with non-allelic interactions. Each population went essentially the same peak, with a majority of interacting loci in the RRS intermix populations indicating that the final populations were being fixed in a complementary fashion with respect to these alleles.

Tano and Allen Burdick (1965) reported female fecundity of various 2nd chromosome recessive lethal heterozygotes was measured in order to study the effect of genetic background on fecundity. 18 lethal stocks were selected at random. Six of the 18 lethal heterozygotes in homozygous genetic background showed significantly higher female fecundity than homozygous wild type (mean f value 1.280; all f values greater than 0.985). The mean f values in heterozygous background was 0.961, and 11 were less than 1.000. None was significantly different from the control. No correlation was found between f values obtained from homozygous and heterozygous background.

No relationship was found between progeny viability and degree of female fecundity of the mother. Thus, female fecundity of the lethal heterozygotes were influenced by the degree of heterozygosity of genetic background.

Rawat (1966) studied five systems of mating viz. mass, full sib, cyclic 2, cyclic 3, cyclic 4 for two way selection of egg production in Drosophila ananassae and correlated responses in hatchability, viability, egg length, egg volume and wing length were obtained. Selection was done for females only and experiment was continued for 13-20th generation.

1. Response to selection was low in all the types of selection except mass mating and cyclic-2 mating. This was probably

due to breaking up of existing linkage associated with high genetic variability in mass mating and cyclic-2 mating.

2. A phenomena of 'ebb and flow' was observed which indicated that additive genes played a minor role in determining egg production and much of variability was produced by non-additive gene effects.
3. The estimate of realised heritability was found to be 18.7% in the low line of cyclic-3 pair matings.
4. Asymmetry of response was in the downward direction of egg production, but the selection differential was more for upward direction.
5. The non-significant correlation of egg production with hatchability and hatchability with viability indicate the presence of lethals.
6. In the high lines the progressive reduction of egg number may be due to the presence of subvitals. The upward thrust for a few generations was attributed to the release of fresh genetic variability due to the breaking of existing linkages and short stability seemed to be due to new homeostatic stabilisation.

Chakrabarti (1966) studied relative merits of heritability estimates computed by two different methods in Drosophila viz. (1) component analysis method and (2) linear estimation procedure. The correlation between egg production-wing size and egg production-bristle number were less but not negligible.

Mazumdar and Prabhu (1967) studied the polygenic activity of X chromosome for egg production, egg size, hatchability and wing size in Drosophila melanogaster. Reciprocal crosses and their comparison with basic stock showed that in respect of egg production the bar chromosome appeared to contain a few genes that enhanced egg production but in case of hatchability it appeared to retard it. In case of egg size results indicated the presence of effective genes in both the bar and normal stock X chromosome that improved egg size, similar results to those of egg size were obtained for wing size.

Win Moi Tait and Prabhu (1967) studied polygenic activity of 2nd chromosome for egg production, egg size and hatchability in Drosophila melanogaster. They reported that curly stock had more dominant genes for egg production than in normal stock and the chromosome homologous to curly in curly stock had lesser number of dominant genes. The normal

stock chromosome contained more effective genes for hatchability than curly stock chromosomes. Results were similar to those in egg production for egg size.

Marinkovic (1967) studied the genetic loads affecting fecundity in natural populations of Drosophila pseudo-obscura.

A total of 211, 2nd chromosomes taken from five populations were studied for their effect on the fecundity of homozygous females. 118 heterozygous combinations of the second chromosome were also studied for comparison. The mean 10 days egg production by a homozygous female was 260.4 ± 6.8 while in heterozygous female it was 322.2 ± 8.3 . Some of homozygous female were found which deposited no eggs at all, although some deposited less than 10% of the mean number. The correlation between viability, fecundity and rate of development were low disregarding lethals and semi-lethals. The fecundity of heterozygous females was positively correlated with the fecundities of the females homozygous for the chromosomes present in the heterozygotes.

Jayaramakrishna (1967) studied the nature of genetic response in two-way selection for egg production in Drosophila melanogaster. A 3 x 3 diallel test was set up to find out genetic architecture of egg production, hatchability and wing length in the 3 selected lines obtained after 5-8 generations

of selection. Significant additive genetic effects were present for all the three characters studied. No asymmetry was present for dominant and recessive genes in parental lines for egg production. Asymmetry was observed for hatchability. Large portion of variability was due to dominance and in particular due to over-dominance for both egg production and hatchability. The dominant recessive ratio was 2:1. Dominance deviation was unidirectional. Four homozygous recessive arrays for low egg production and one homozygous recessive array for lower hatchability were detected. Only a few genes governing egg production were having pleiotropic effects on hatchability. He suggested that diallel analysis of quantitative characters seemed to be a very powerful tool, in order to analyse the genetic architecture of the trait in the shortest time and with maximum precision and in turn aided to lay out a very effective breeding plan for bringing out rapid progress.

EGG SIZE

Warren (1924) used egg size as a character for his studies because it was less influenced by environment as well as size and age of fly. He reported that neither the homozygosity nor heterozygosity could introduce any correlation between body size and egg size. There was no significant

difference in size between the egg laid by early and late emerging flies.

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

Bell, Moore and Warren (1955) studied egg size in Drosophila melanogaster and reported that it showed little or no heterosis with relatively high heritability of 30% to 60%. Early testing of combining abilities for egg size provided better information on predicting subsequent combining ability.

Satya Prakash (1962) studied the effect of various levels of inbreeding on egg size and fertility in Drosophila melanogaster. He reported that natural selection in favour of homozygotes reduced the rate of fixation at a few or many loci. Certain decline in mean egg size might be expected, because genetic background was homologous.

Mazumdar and Prabhu (1967) concluded that active genes were present in both bar and normal stock X chromosome that improved egg size.

HATCHABILITY, FERTILITY AND DEVELOPMENT TIME

These are some of the quantitative characters on which comparatively less work has been done.

Zarapkin (1934) conducted experiments to study duration of development in Drosophila funebris and concluded that larger flies developed 2.5 days later than smaller flies, due to the delay occurring during larval stage. No sex dimorphism was detected.

L'Heritier (1937) studied larval competition in Drosophila and reported that any inbred line was inferior in vigour to a mixed population from all inbred lines.

Maynard-Smith and Maynard-Smith (1954) reported that flies with heterozygous chromosome developed more rapidly than homozygotes and this was measured as the time taken from egg laying to eclosion in Drosophila subobscura.

Clarke and Maynard (1955) while studying the effect of hybridisation on longevity, discussed the length of imaginal life for two inbred lines of Drosophila melanogaster and for the reciprocal hybrids between them. The expectation of life at eclosion of hybrids was approximately twice that of inbred flies.

The life span of females in the B inbred line was 1.6 times that of males; in the K line the average life span of males was 1.8 times more than that of females. Hybrid males and females did not have marked difference, but B/K females

(hybrid females with B mothers) lived longer than K/B females ($P = 0.05$) and a larger proportion of old B/K females continued to lay fertile eggs. The difference between the two types of hybrid males was not significant.

Hollingsworth and Maynard-Smith (1955) studied effects of inbreeding on rate of development and fertility in Drosophila subobscura. Two sib mated lines O and NF were established from wild females. In each generation fast and slow developing flies were selected and mated together. They observed a rapid decline in the percentage egg hatch from 20% to 50% after 7 generations in their O line, NFF and NFS lines.

Infertility developed in all the inbred lines, but its appearance was most rapid in the slow selected O sub-lines. All four such sub-lines were lost in the first 5 generations. This association between slow development and infertility in 'O' line, probably explained the absence of any response to selection for rate of development. In all the three lines, the major cause of the failure of eggs laid by fertilized females to hatch was the infertility of male i.e. the inadequacy of proportion of sperm produced by inbred males. Female infertility and zygotic inviability, also contributed to the failure of eggs to hatch. Analysis showed that male infertility was not due to the segregation of a recessive

mutant. In NF line there was no significant difference between the fertility of the fast and slow selected lines. Rapid decline of fertility was observed in slow selected 'O' line.

The fertility of two brother sister mated lines, B and K, derived from structurally homozygous stock did not decline significantly. In these lines, the males were almost fully fertile and female infertility was due to failure of eggs to hatch due to zygotic inviability, but this cannot be due to the segregation of recessive which would be lethal in homozygous condition.

The data on the rate of development confirmed the hypothesis that most of the genetic variance for this character was due to chromosome regions with heterotic effects.

In O line marked correlation between development and infertility was noted. This is regarded as a result of association between slow development and infertility as a form of pleiotropism.

Buzzati Traverso (1955) studied the evolutionary changes in the components of fitness and other polygenic traits in Drosophila melanogaster population. Four parallel populations were maintained for 100 generations using Pearl's

technique, it consisted of equal numbers of males and females of a wild type oregon R strain and of another strain homozygous for white and bar. The result showed :

1. Heritability of females of the original two strains disappeared.
2. The average fecundity increased.
3. The rate of development increased.
4. Length and width of wings decreased.
5. The average body weight of the flies increased.

Maynard-Smith (1956) studied the effects of various factors like the age at which the male was mated, the number of occasions on which the male had mated previously and the period elapsing between mating and collection of eggs. The eggs laid by outbred females were collected from the time of mating until death of the females and the proportion of hatched eggs recorded. For first few days about 99% eggs hatched after mating to outbred males but after about 30 days a few or no egg hatched. On mating to inbred males, the initial hatch varied from 43% to 84% and it declined after 10 days. Thus inbred males were inferior, both in quality and quantity of sperm produced.

Sang and Clayton (1957) carried out two way selection experiment to study the heritability of 'rate of larval

development' in Drosophila from (a) outbred population (b) F_2 of inbred line crosses. Realised heritability of 20-25% was estimated in outbred stock lines. However, from an F_2 of two inbred lines, progress observed was in the direction of slower growth. The character like many of economic importance, showed hybrid vigour, so that selection for rapid growth, was mainly selection for heterozygotes and progress in this direction tends to be ineffective or negative. The situation was complicated by the slow growth of one parent due to an interaction between a homozygous loci in F_2 and backcross generations. There might be some ecological interaction between larvae of different genotypes as they develop together.

Bonnier et al. (1957) studied the rate of development of viability of heterozygous larvae with regard to the autosomal set of genes developed faster than homozygous ones. The wild type homozygous larvae with regard to the X chromosome usually grew faster and had a higher competing ability than heterozygous for one wild type 'W' allele and another non-wild type 'W' allele. Thus no signs of overdominance was detected in their experiment.

Marein (1958) conducted selection experiment for developmental rate in 30 lines of Drosophila melanogaster.

He reported that there was no appreciable changes in the rates of development in the unselected lines, with the exceptions of some of the fast lines which showed significant response to selection and in some slow lines, increased development time was also observed. Thus, in complex genetic situations, where many segregating genes were involved, the result of selection might be variable even when replicate lines kept under reasonable uniform conditions.

Vetukhiv and Beardmore (1959) studied larval viability fecundity and asymmetry of the wings. They showed that F_1 hybrid were heterotic at 25°C but not at 22°C or under fluctuating temperature. F_2 hybrid breakdown occurred in the same traits at 25°C but not in the other environments.

Mukai and Burdick (1959) studied single gene heterosis for viability associated with 2nd chromosome lethal in Drosophila melanogaster.

Bonnier et al. (1959) studied the competing ability of larvae of the pure strain which indicated a seriation following the degree of deviation of eye colour from the wild type red colour.

Parson (1959) studied variable viabilities and showed that it was due to competition with other genotypes, the

proportion of the genotype differing in coupling and repulsion. Thus the viability of a genotype was dependent on a proportion of other genotypes co-existing with it.

Walter (1959) reported the possibility of detecting differences between multiplicative and additive gene action on viability.

Parson (1959) studied the genotypic and environmental interaction for various temperatures using three inbred lines of Drosophila melanogaster. These three inbred lines were crossed in all possible combinations and the F₂ generation was raised.

The hatchability of the eggs of F₁ flies showed heterosis and less variability than the inbred lines, indicating homeostasis superiority over the inbred lines which was confirmed by the variable response to temperature treatment as measured by the emergence of 150 larvae as adult and the larger genotype environmental interaction of the inbreds than the hybrids. The hybrids therefore have a better homeostatic mechanism than the inbred line.

Two of the inbred lines were mated by sib mating and the third by mass mating. The later inbreds were almost equal to hybrids in homeostatic ability, probably due to greater opportunity for the unconscious selection of favourable

heterozygotes.

Vander Veen (1960) studied the heterozygote superiority and selection intensity plateauing and concluded that viability and fecundity are affected via linkage, or pleiotropy, and that the release of variability from residual blocks of closely linked plus and minus genes was very low.

Hiraizumi and Crow (1960) studied the heterozygous effects on viability, fertility and rate of development and longevity of Drosophila chromosomes that are lethal when homozygous and found that there was no significant difference in the heterozygous effect of lethals and semi-lethals, but these collectively caused a reduction of 2.6% in pre-adult viability. The lethal heterozygotes were slightly slower in developing. Female heterozygous for a lethal or semi-lethal produced fewer eggs at an early age than the controls but there was not a significant difference in the total lifetime production. The longevity of males heterozygous for lethals or semi-lethals from a natural population have an appreciable deleterious effect on pre-adult viability and component of adult fitness.

Gilbert (1961) analysed Karp's data on the genetical determination of viability, longevity and fertility in Drosophila melanogaster. The results showed that these

characters are usually affected alike by the substitution of chromosome segments, and heterozygosity was not always advantageous.

Hiraizumi (1961) studied the rate of division and female fertility for chromosome II and III of Drosophila melanogaster and found (a) no detectable maternal effect in the two components, (b) chromosome II and III contributed to each components in a very simple multiplicative fashion although significant but small deviations from the rate were observed, (c) development was negatively correlated with female fertility when the development rate was faster than a certain level but positively when the rate was slower than this level.

Dobzhansky (1961) studied the experimental population, which were made polymorphic and monomorphic for the AR and CH gene arrangements in their IIIrd chromosomes. In contrast to the previous experiments of Beardmore, Dobzhansky and Pavlovsky (1960) in which the larvae were crowded and adult flies relatively uncrowded, in the present study, the adult were crowded and the larvae relatively uncrowded. The chromosomally polymorphic populations proved to be superior to the chromosomally monomorphic ones, the former produced more flies and greater biomass, although the average weights of the individual flies were almost alike. In the studies of Beardmore, Dobzhansky and Pavlovsky (loc. cit.) the monomorphic AR/AR

were superior to the monomorphic CH/CH populations. In the present experiments, this order was reversed. The bearing of this reversal on the seasonal changes in genetic constitution which the populations undergo in their natural habitats was pointed out.

Battaglia and Smith (1961) reported that polymorphic population produced more, and with equal population densities heavier flies than do the monomorphic one; the polymorphic population produced greater biomass; the mean length of the wings did not differ significantly in polymorphic and monomorphic populations, the variabilities of numbers, weight and wing length in flies showed no consistent differences and the asymmetry of the wings was significantly greater in monomorphic population than in polymorphic ones.

Bonnier (1961) studied 3 unrelated wild type stock population of Drosophila melanogaster. From each of these stock populations, homozygous population was derived. Viability experiments were made with flies taken directly from the stock ('pure' flies) and the six possible F₁ hybrids between them. The viability studies included egg laying capacity, capacity of larvae to survive to the adult age in 25°C and 30°C. Hybrids showed superiority in majority of cases in all the three characters studied. The hybrids have better competing ability and they resisted the stress of 30°C better than

the pure ones and thus supported the overdominance hypothesis.

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

- a) Incompatability between eggs with 'O' cytoplasm and sperm of type B or B0 (the F₁ hybrid with B as the female parent).
- b) Homozygosity of females laying the eggs.
- c) Though B and B0 sperm showed an overall similarity, B sperm gave more unhatched eggs with B cytoplasm but B0 sperm gave more unhatched eggs with O cytoplasms.

The following variables have no detectable effect on egg hatching.

- (1) Ratio of O genes to B genes in females (and in the unfertilized egg).
- (2) Ratio of O genes to B genes in the fertilized egg.
- (3) Heterozygosity of the fertilized egg.

Saxena (1962) studied the correlations between egg production, egg size, hatchability and wing size with emergence time and reported that there was no correlation in emergence time and other metric traits.

Ayala (1965) studied the relative fitness of Drosophila serrata and Drosophila birchii and their intraspecific hybrids. Biomass (the number of flies produced per unit) was studied. Both production and population size increased rapidly during first few weeks and reached an equilibrium between 8th and 15th week. Number of flies per culture bottle was more in Drosophila serrata and considerably less in Drosophila birchii. The hybrid population of Drosophila serrata performed better than parental lines whereas the hybrids of Drosophila birchii were intermediate to their parental lines.

Allen (1966) studied the effects of recombination on quasi-normal second and third chromosome of Drosophila melanogaster. A natural population was sampled and simultaneous tests for 2nd and 3rd chromosome viability were made using a balanced marker technique. The population showed a high degree of variation for viability values of homozygous chromosome using six quasi-normal strains chosen from these tested chromosomes, investigations were made on the effects of recombination within chromosomes and/or rearrangement.

There was no difference in the amount of variation produced by recombinations within chromosomes and that produced by reassortment. Second chromosome showed an increase in variation, over the control values but none was observed for third chromosomes. Similar tests on a laboratory population by Spiess and Allen (1961) contrasted in these results that second chromosomes were less affected than third. Analysis of variance showed significant epistatic interaction, within variance was significant but additive effects of chromosomes were not significant. Based on the high F values in those categories that were significant it was concluded that quasi-normal chromosomes from the natural population seem to fit a balanced more nearly than a classical condition. The expression of recombination and reassortment was probably not great enough to show extremes for there was little evidence for the production of synthetic lethals.

Terrin (1966) studied homozygous viability and fertility loads in Drosophila melanogaster. In continuation of a study of Drosophila melanogaster population by Grunberg and Crow (1960) a total of 1083 second chromosomes were studied and analysed for their effects on viability. When homozygous these chromosomes caused an average viability reduction or load of 40.9% in comparison with a group of random heterozygotes for these chromosomes.

in almost every case. It was concluded that recessive lethal genes had little or no effect on the viability of heterozygotes carrying them while subvitals do.

A tentative biochemical interpretation of the results was given that recessive lethals might produce an inactive gene product or none at all and sub-vital produced a damaged but still partly functional gene product. These later might interfere with normal development in the heterozygote, while the completely inactive products of lethal mutation might not.

Prabhu et al. (1967) studied 6 x 6 diallel cross for hatchability in Drosophila melanogaster and concluded that additive and maternal effects for hatchability were totally absent. The significance of (b) indicated the presence of dominant effects, while the significance of b₂ showed that the distribution of alleles in the parents was asymmetrical. Significance of (d) indicated the presence of differences not ascribable to maternal effects in parental lines.

The hatchability data were subjected to further statistical analysis.

Roberts (1967) studied a positive correlation between the amount of crossing over within pericentric inversions and the degree of egg hatch reduction of heterozygous females

A comparison of lethal heterozygotes with non-lethal heterozygotes suggested a slight decrease in viability of the former.

Fertility effects on the male and females were studied for 240 of the above chromosomes. The total load due to complete sterility, partial sterility and infertility based on adult mortality was 14.2%. Thus one fourth of the entire inbred loads measured was due to impairment of fertility.

Correlation between viability and fertility suggested that some of the partial sterility might be due to a reduction in general fitness of the organism. Complete sterility was due to some specific defects in the reproductive system. There was a significant association between complete sterility and low viability. Homozygous chromosomes leading to complete sterility in both sexes were rare.

Wills (1966) examined two populations, one structurally monomorphic and one polymorphic for the IIIrd chromosome to study whether there was a correlation between homozygotes and heterozygotes viability and there was no significant difference in the viability of heterozygotes for chromosomes not carrying a lethal compared with those in which one of the chromosomes carried a lethal, but there was a significant positive correlation between viability of the homozygotes and the heterozygotes

in almost every case. It was concluded that recessive lethal genes had little or no effect on the viability of heterozygotes carrying them while subvitals do.

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suggested that embryonic death is caused by duplication-deficiency chromosomes formed as a consequence of crossing over within inversions. Drosophila females heterozygous for pericentric inversions in which there is appreciable recombination should be at a pronounced selective disadvantage.

MATERIALS AND METHODS

STOCK

The investigations were carried out with the following stocks of *Brachyphala melanogaster*:

1. 1931

2. Half alb-high line - 1.

The stock 1931 was obtained from U.S.A. It had a dominant character 'D' (Dichaeta) placed on 3rd chromosome with inversions. It also had *Xol* (*X*) and *Sh* (*S*) which were not considered in the present investigation. The half alb-high line was obtained in the laboratory from the hundred flies which were trapped in Indian Veterinary Research Institute campus in the month of March 1950. This was a wild stock.

GENETIC MEDIA

Media of *Brachyphala melanogaster* (1931) is known to be suitable for the purpose of the present investigation. The media used throughout the investigation were of the type described here. This medium was used throughout for these investigations.

TEMPERATURE FOR REARING THE STOCK

All operations were conducted in an air cooled room.

MATERIALS AND METHODS

STOCK

The investigations were carried out with the following stocks of Drosophila melanogaster :

1. h₁₂₁
2. Half sib-high line - 1.

The stock h₁₂₁ was obtained from U.S.A. It had a dominant character 'D' (Dicheate) placed on 3rd chromosome with inversions. It also had Moire (Me) and Stubble (Sb) which were not considered in the present investigation. The half sib high line - 1 stock was maintained in this laboratory from the hundred flies which were trapped in Indian Veterinary Research Institute campus in the month of March 1966. This was a wild stock.

CULTURE MEDIA

Prabhu et al. (1963) tested different kinds of media (Banana, Burdick's, Molasses and Yeast) and found Burdick (1954) media most suitable after some modifications for studies of the type undertaken here. This medium used throughout for these investigations.

TEMPERATURE FOR REARING THE STOCK

All operations were conducted in an air cooled room

and the cultures were throughout maintained at $25^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ in a thermostatic cabinet kept in this room.

COLLECTION OF VIRGINS

This was the most important step of the experiment since it involved operational problems of experiment with its genetic consequences. The life cycle of Drosophila melanogaster at 25°C is about 192 hours. Majority of larvae hatch between 20-22 hours after laying (Demerec, 1950). If any old males are present they mate with emerging females. To ensure that virgin females were available in sufficient number, their collection was done every 6 hours and males and females kept in different food vials.

ETHERISATION OF FLIES

It is necessary that flies should be made unconscious for ease of handling and to avoid contamination in laboratory (i.e. avoiding mating at random of the flies of one stock with another). Etherisation was done by etherisor specially made for this purpose.

TESTING OF EGG PRODUCTION, HATCHABILITY AND EGG SIZE

Egg production

Eggs were collected as per the technique described

by Prabhu et al. (1952) and in general use in this laboratory. The same Burdick medium was used with the addition of apple green powder, an edible dye ("Permicol" by Bush) which provided a soothing background for counting eggs and had a restful effect on the eyes. This coloured media was then poured upto 1 cm thickness on a thick glass plate (18" x 12") surrounded by different L shaped metal blocks forming a square. Then this whole plate was removed to the refrigerator at 5°C so that the food got solidified. The set food was then cut into equal sized square slabs (1 cm x 1 cm) using a cutter specially devised for the purpose. Each piece of food was then placed on a paraffin impregnated long cardboard piece (8 cm x 1 cm) that went neatly in a test tube. Impregnation of these cardboard pieces in hot paraffin was necessary to prevent absorption of moisture from food kept on it and to give proper support to it. A drop of live yeast was seeded on each slab and allowed to dry so that the flies did not get stuck up while taking food or oviposition. It acted as food supplement and flies did not lay eggs without addition of live yeast, so proper precautions about it was taken during the whole experiment. The females to be tested were introduced singly in each test tube with a male and food chips were kept. These test tubes were then kept in boxes in chronological order and kept in the temperature cabinet. The food was replaced first

at 72 hours and then at every 24 hours. The number of eggs laid by each fly was counted by the aid of a binocular microscope using 10 X eyepiece and 3 X (fixed) objective. Eggs were counted for 4th, 5th and 6th days.

DETERMINATION OF HATCHABILITY

After the last count (i.e. 6th day count), the eggs on food chips were transferred to temperature cabinet (since all eggs of Drosophila hatch out within 24 hours - Demerec, 1950). After 24 hours the unhatched eggs were counted, since it is difficult to count hatch eggs and deducted from 6th day egg count from which hatchability per tube was estimated. Hatchability was measured as the percentage of eggs that hatched from the number of eggs kept for incubation, after 24 hours of incubation. It is important that the male is present in the tube to ensure that the eggs tested were not unfertilized ones.

DETERMINATION OF EGG SIZE

On 7th day the food chips supplied on 6th day were removed, marked and kept in a refrigerator to prevent hatching. With the help of moistened fine brush five unhatched eggs were taken randomly on a clean glass slide. The length and

width of the eggs were measured with an ocular micrometer fitted in a monocular microscope with a magnification of 10 X. The length was measured as the distance between two ends of the egg and width was measured at the broadest part of egg. The volume was calculated by using the formula.

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

where,

$$II = \frac{22}{7}$$

$$l = \text{length of the egg}$$

$$w = \text{width of the egg.}$$

EXPERIMENTAL DESIGN

The experiment was designed to investigate the effect of third chromosome on egg production, egg size and hatchability in the stocks used. For this purpose, replacement of all the chromosomes of *M.* except the one containing D (Dichaete), by the chromosomes from the *H₁* (half sit half line) stocks through repeated selection of Dichaete and backcrossing to the *H-1* stock, was done. On the other hand, replacement *H-1* chromosome by D was done. Simultaneously control were run by both the stocks. In the present investigation *H-1* $\sqrt{\text{designated as Dichaete (D)}}$ and half sit line $\sqrt{\text{designated for seventeen generations}}$ designated as Normal $\sqrt{\text{(N)}}$ were used.

From original stocks of *H₁* Dichaete (D) and Normal (N) 50 pairs of flies were taken from each randomly and were transferred into 8 culture bottles each having 15 pairs of flies and kept them in constant temperature cabinet adjusted to $25^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ and allowed to mate for 72 hours. After 72 hours mating, these flies were again transferred to fresh bottles (separately for each stock) and kept for 24 hours. After 24 hours, the flies were removed, but bottles were retained till the new flies emerged and were collected at 2 hourly interval to get the virgin flies. These virgin flies

EXPERIMENTAL DESIGN

The experiment was designed to investigate the effect of IIIrd chromosome on egg production, egg size and hatchability in the stocks used. For this purpose, replacement of all the chromosomes of M, except the one containing D (Dicheate), by the chromosomes from the H₁ (half sib half line) stocks through repeated selection of Dicheate and backcrossing to the H-1 stock, was done. On the other hand, replacement H-1 chromosome by M was done. Simultaneously control were run of both the stocks. In the present investigation h-121 $\overline{\text{D}}$ designated as Dicheate (D) $\overline{\text{D}}$ and half sib high line inbred for seventeen generations $\overline{\text{H}}$ designated as Normal (H) $\overline{\text{H}}$ were used.

From original stocks of h₁₂₁ Dicheate (D) and Normal (H) 50 pairs of flies were taken from each randomly and were transferred into 5 culture bottles each having 10 pairs of flies and kept them in constant temperature cabinet adjusted to $25^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ and allowed to mate for 72 hours. After 72 hours mating, these flies were again transferred to fresh bottles (separately for each stock) and kept for 24 hours. After 24 hours, the flies were removed, but bottles were retained till the new flies emerged and were collected at 6 hourly interval to get the virgin flies. These virgin flies

were used for 50 pair matings from each stock separately.

Base population was set with 50 pair matings for each stock, followed by a food chip and kept for 72 hours to allow them to mate. After 72 hours, the food chips were replaced by fresh food chips and records were taken for egg production, hatchability and egg size as per the detailed methods already described.

1. Egg production records were taken for 4th, 5th and 6th day.
2. Sixth day egg production batch were tested for hatchability.
3. After recording the egg production on 4th day, chips were transferred to separate food vials for collection of virgins for next generation.
4. Seventh day batch of eggs were measured for egg volume.

P₁ Generation

For P₁ generation following matings were set :

1. D ♀♀ x D ♂♂ (Control) - 20 x 5 = 100 pairs
2. D ♀♀ x H ♂♂ - 20 x 5 = 100 pairs
3. H ♀♀ x D ♂♂ - 20 x 5 = 100 pairs
4. H ♀♀ x H ♂♂ (Control) - 20 x 5 = 100 pairs

Ten virgin flies were collected from each of the vials from D and H-1 stocks of P_1 mating and males were kept separately from females. Out of 10 flies from D stock, 5 females were mated separately to their vial mates and 5 females were mated to 5 males of H-1 stock. The same was repeated for H-1 flies also. Fourth egg production batch chips were kept separately in food vials for next generation virgin collection. Records of egg production, hatchability and egg size were noted as mentioned.

First Generation

For F_1 matings - virgins were collected and males and females were kept separately, and then mixed, so that at random flies could be collected from each line. Now 50, 50 pair mating for controls for each stock and 100, 100 pair matings of Dicheate flies collected from these two were kept, with males of high line-1 and Dicheate respectively for backcrossing.

Second Generation

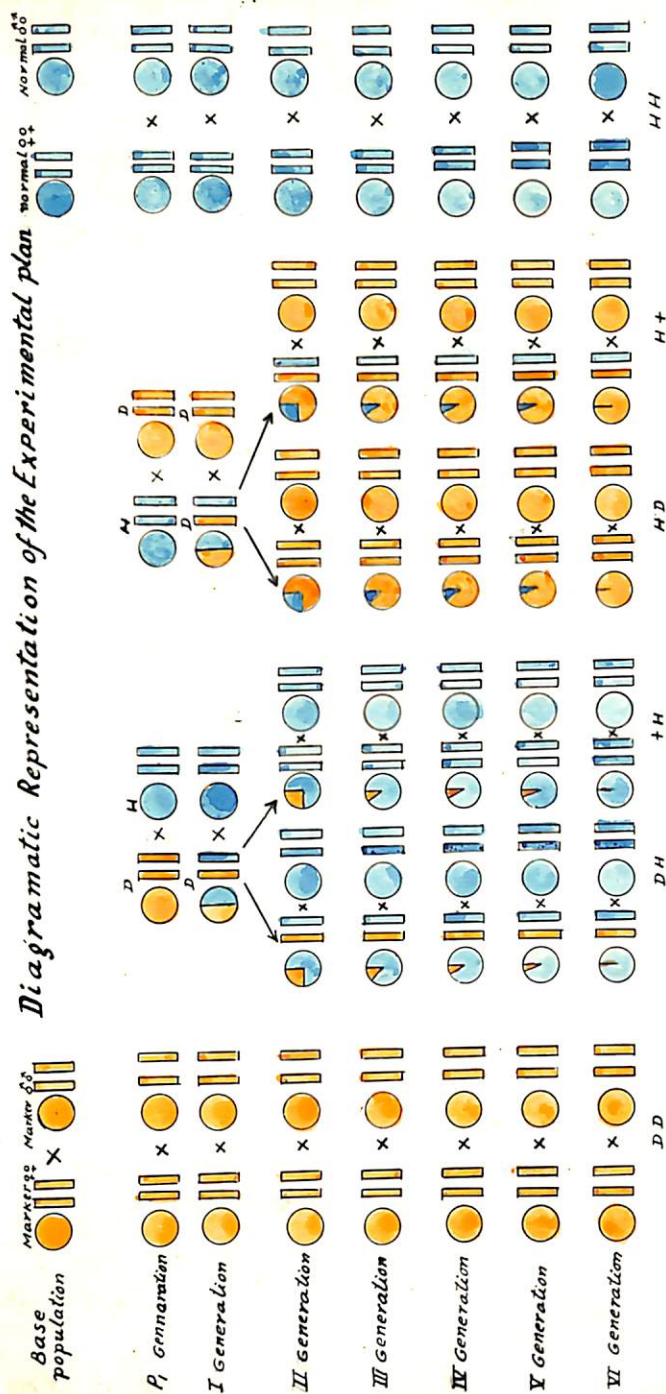
For F_2 matings - controls were maintained as before. From reciprocal cross D x H, 50 non-dicheate and 50 dicheate flies were taken at random and pair mated to H-1 males and

designated as $\pm H$ and DH for convenience. Similarly, from H x D cross, 50 non-dicheate and 50 dicheate flies were pair mated to DD males and designated as $H\pm$ and HD respectively (150 pair matings).

Third and other Generations

For F_3 and further crosses virgin flies were collected and pair mated similarly as F_2 matings.

The following chart represents the schematic plan of the experiment.



Note ① Bars represent III chromosome. Circles represent rest of chromosome

② DH: dichete ♂ from D x H cross mated to normal ♂

+H: non-dichete ♀ from D x H cross mated to normal ♂

HD: dichete ♀ from H x D cross mated to dichete ♂

H+: non-dichete ♀ from H x D cross mated to dichete ♂

SCHEMATIC PLAN OF THE EXPERIMENT

| | M 00 x M 00 | M 00 x H 00 | H 00 x M 00 | H 00 x H 00 |
|----------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|
| F ₁ | 5000 x 5000 (5 x 20 = 100) | 5000 x 5000 (5 x 20 = 100) | 5000 x 5000 (5 x 20 = 100) | 5000 x 5000 (5 x 20 = 100) |
| F ₂ | 5000 x 5000 | 100D00 x 10000 | 100D00 x 10000 | 5000 x 5000 |
| F ₃ | 5000 x 5000 | 50D00 x 5000 | 50D00 x 5000 | 5000 x 5000 |
| F ₄ | 5000 x 5000 | 50ND00 x 5000 | 50ND00 x 5000 | 5000 x 5000 |
| F ₅ | 5000 x 5000 | 50D00 x 5000 | 50D00 x 5000 | 5000 x 5000 |
| F ₆ | 5000 x 5000 | 50D00 x 5000 | 50ND00 x 5000 | 5000 x 5000 |
| F ₇ | 5000 x 5000 | 50D00 x 5000 | 50D00 x 5000 | 5000 x 5000 |

D = Dicheate

ND = Non-dicheate

ANALYTICAL PROCEDURE

Analysis was done to test the effects of IIIrd chromosome on fecundity, egg size and hatchability.

1. Generation Mean

- (1) Egg production : Total of the data recorded for 4th, 5th, 6th day per individual was averaged and then overall average for all individuals in a cross was calculated.

$$(X) = \frac{\sum X}{n}$$

- (2) Egg size : ANALYTICAL PROCEDURE length and width of eggs were recorded and volume was calculated by the formula :

$$\text{Egg volume} = \frac{\pi}{6} l w^2$$

where,

$$\pi = \frac{22}{7}$$

l = length of egg

w = width of egg

An overall mean for each cross in a generation was calculated.

- (3) Hatchability : Proportion of eggs hatched was expressed in percentage hatched eggs.

ANALYTICAL PROCEDURE

Analysis was done to test the effects of IIIrd chromosome on fecundity, egg size and hatchability.

1. Generation Mean

(A) Egg production : Total of the data recorded for 4th, 5th, 6th day per individual was averaged and then overall average for all individuals in a cross was calculated.

$$(N) = \frac{X}{n}$$

(B) Egg size : For each individual length and width of eggs were recorded and volume was calculated by the formula :

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

where,

$$II = \frac{22}{7}$$

$$l = \text{length of egg}$$

$$w = \text{width of egg}$$

An overall mean for each cross in a generation was calculated.

(C) Hatchability : Proportion of eggs hatched was expressed in percentage hatched eggs.

2. Standard error : was calculated with the help of the formula :

$$SE (\bar{X}) = \sqrt{\frac{(\sum X - \bar{X})^2}{n(n-1)}}$$

(Snedecor, 1961)

3. Analysis of variance : Simple analysis of variance technique was applied to test the differences between the different crosses and the differences tested by critical difference test as given by Snedecor (1961).

RESULTS AND DISCUSSION

The present experiment was aimed at finding the effect of the cytoplasm on egg production, egg size and hatchability. This cytoplasm was introduced in normal stock through both the male and female side in reciprocal crosses and through repeated backcrossing. The effects were seen when present along with the rest of the normal stock, or the rest (Dichoste) chromosomes.

EGG PRODUCTION

In Table I are presented the mean daily egg production of the various crosses of *D. obscura* and *D. dichoste* in 3 generations. In Table II are shown the different frequencies of mean daily egg production between flies of different genetic constitution in different generations.

Discussion

The normal females mated by normal males ($D. obscura \times D. obscura$) gave a mean daily egg output of about 25 eggs. As compared to this the marker females mated by marker males ($D. obscura \times D. obscura$) gave about 25 eggs. The marker females mated by normal males ($D. obscura \times D. obscura$) and the other females gave about 25 eggs which was different from $D. obscura \times D. obscura$. The normal females

RESULTS AND DISCUSSION

The present experiment was aimed at finding the effect of III chromosome on egg production, egg size and hatchability in Drosophila. This chromosome was introduced in Normal stock through both the male and female side in reciprocal crosses and through repeated backcrossing, the effects were seen when present along with the rest of the Normal stock, or its own (Dicheate) chromosomes.

EGG PRODUCTION

In Table I are presented the mean daily egg production of the various crosses of normal and marker flies in 6 generations. In Table II are shown the critical differences of mean daily egg production between flies of different genetic constitution in different generations.

P₁ generation

The normal females mated by normal males (H ♀♀ x H ♂♂) gave a mean daily egg output of about 32 eggs. As compared to this the marker females mated by marker males (D ♀♀ x D ♂♂) gave about 26 eggs. The marker females mated by normal males (D ♀♀ x H ♂♂) on the other hand gave about 24 eggs which was not different from D x D production. The normal females

Table I

Mean daily egg production in six crosses in different generations
with their standard error

| Crosses | GENERATIONS | | | | | | | | | | | | | |
|--------------|----------------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| | P ₁ | | I | | II | | III | | IV | | V | | VI | |
| | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. |
| D x D (a) | 26.2 | ±0.7 | 43.3 | ±1.6 | 51.9 | ±1.8 | 42.9 | ±1.9 | 32.5 | ±1.4 | 56.2 | ±1.7 | 64.7 | ±2.7 |
| DH (b) | 24.3 | ±1.1 | 35.0 | ±1.5 | 60.6 | ±2.0 | 37.2 | ±1.5 | 34.4 | ±2.2 | 46.2 | ±3.0 | 60.7 | ±2.8 |
| HD (c) | 32.7 | ±1.1 | 41.6 | ±1.6 | 52.7 | ±2.0 | 43.4 | ±1.4 | 42.0 | ±1.8 | 46.8 | ±2.6 | 57.4 | ±3.1 |
| H x H (d) | 32.1 | ±0.9 | 57.0 | ±2.6 | 52.2 | ±1.5 | 52.7 | ±1.5 | 57.9 | ±1.4 | 63.1 | ±1.3 | 72.5 | ±3.2 |
| +H (e) | - | - | - | - | 70.0 | ±1.4 | 47.8 | ±1.1 | 46.7 | ±2.0 | 55.8 | ±2.8 | 74.1 | ±1.8 |
| H+ (f) | - | - | - | - | 68.3 | ±1.3 | 45.8 | ±1.0 | 42.5 | ±1.3 | 55.8 | ±2.3 | 71.6 | ±1.5 |

D x D = Dicheate ♂ x Dicheate ♂ (Control)

D x H = Dicheate ♀ x Normal ♂

H x D = Normal ♀ x Dicheate ♂

H x H = Normal ♀ x Normal ♂ (Control)

+H = Non-dicheate from (D x H) cross x Normal ♂

H+ = Non-dicheate from (H x D) cross x Dicheate ♂

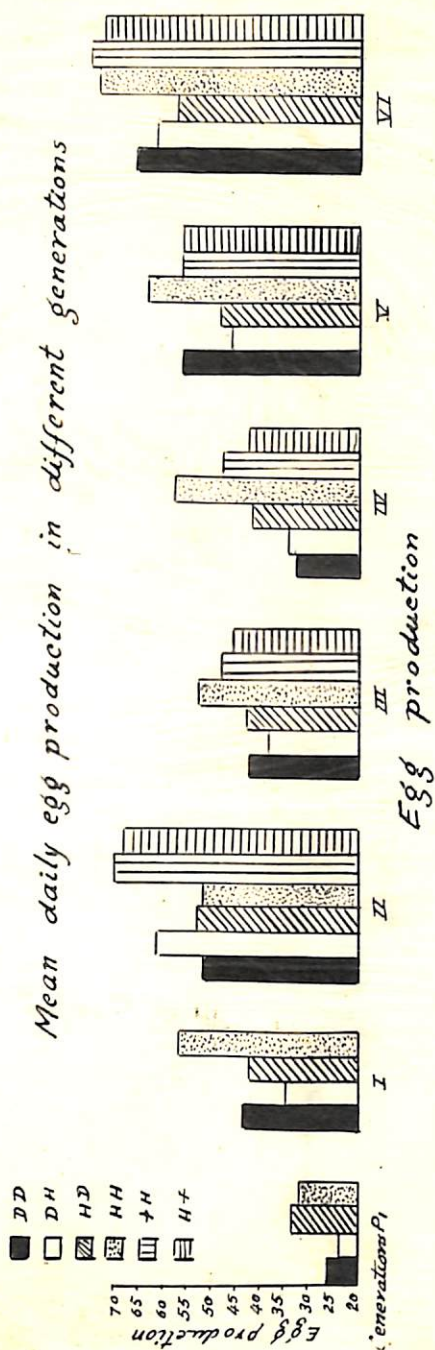


Fig-1.

mated to marker males (H ♀♀ x D ♂♂) gave about 33 eggs which was not different from the production of normal control females.

First generation

In the first generation, the females from marker control (DD ♀♀) gave 43 eggs as opposed to the production of normal controls (HH ♀♀) which gave 57 eggs. The difference was statistically significant and in favour of normals.

The heterozygous DH females gave 35 eggs and the heterozygous HD females gave 42 eggs. The differences between these two females and the marker flies' production were 8 and 2 eggs respectively. The former was statistically significant, while the latter was not. In case of the difference between these two and the normal flies, however the differences were statistically significant in both cases, showing that the heterozygous marker x control females produced significantly lesser number of eggs than the normal females.

Further the two heterozygous females too differed significantly in their production. Those which had marker as father gave less than those which had marker as the mother. These results are contrary to the findings of Mazumdar and Prabhu (1967) and Win Moi Tait and Prabhu (1967) who studied

the effect of X and II chromosome on egg production. The former found no difference in the egg production of heterozygous females, irrespective of the fact whether it was the male or female that introduced the chromosome from normal or marker stock. Win Moi Tait and Prabhu's (1967) finding was contrary to what was observed here. In case of II chromosome, when the II chromosome of the Normal marker (heterozygous) females came from the marker stock, they gave less number of eggs than when the same came from Normal stock males. Our finding was opposite to those reported by Win Moi Tait and Prabhu (1967) for the effect of II chromosome on egg production.

Second generation

In the second generation, the marker stock (DD) ♀♀ gave about 52 eggs per day, which was the same as given by the normal HH ♀♀. The Dicheate ♀♀ in second generation were from two crosses. One arising from crossing of F₁ Dicheate ♀♀ to normal (HH) males, and the other arising from crossing of F₁ Dicheate females to Dicheate (DD) males. The former gave about 61 eggs and the latter about 53 eggs. The difference between the two (61-53 = 8 eggs) was statistically significant, showing that the increase in the genes from HH stock had brought about an increase in the number of

egg production. The role of III chromosome could be determined by comparing the Dicheate females production with the non-Dicheate females production from the same cross. In the present instance it was 70 eggs. Thus $70 - 61 = 9$ eggs worked out to be the mean effect of substitution of a Dicheate chromosome by a normal III chromosome.

The difference between the Dicheate females arising out of the cross of $F_1 H \phi \times D \sigma$ backcrossed to $DD \sigma\sigma$, and the normal or non-Dicheate females from the same cross, gave an estimate of the substitution of the Dicheate chromosome by a normal III chromosome, the rest of the genes being more of Dicheate than of normal stock. The difference worked out to $68 - 53 = 15$ which was slightly less than what was seen in the earlier case. The reason was in the earlier instance, the rest of the chromosomes had more normal (H) genes than in the latter instance and the result actually obtained was expected on that score alone.

Mazumdar and Prabhu (1967) who carried out similar studies with X chromosome, found in the second generation, the difference in the egg production of females having like appearance and containing each a marker and a normal X-chromosome, but in one more of the normal genes in the autosomes and in the other more of the genes from marker

stocks in autosomes, a difference of 10 eggs, which was not different from the 8 eggs found here. More eggs were found in the females containing greater number of normal genes in the autosomes. In case of substitution of II chromosome normal in marker stocks, work carried out by Win Moi Tait and Prabhu (1967) obtained a difference of 11 eggs between the production of heterozygous II chromosome females one carrying higher and the other lower number of normal stock genes in the autosomes and the difference was in favour of the flies containing lesser number of genes of normal stock in the autosomes. This was contrary to the findings reported here and that of Mazumdar and Prabhu (1967).

Third generation

In the third generation, the marker stock females (DD) produced about 43 eggs daily which was about 10 eggs less than the production of normal stock females (HH). The two types of Dicheate females - one arising through backcrossing with Dicheate stock and another through backcrossing with normal stock showed a difference of 6 eggs in favour of the latter. Comparison of these flies' production with their normal looking sibs showed further that there was hardly any difference between the two normal looking females, with regard to their production, but there was a difference of

about 11 eggs between the Dicheate flies with higher percentage of normal autosomal genes for egg production and non-Dicheate flies with like constitution. In case of Dicheate and non-Dicheate females from crosses involving Dicheate male, the difference was small being only 2 eggs.

The results obtained by Mazumdar and Prabhu (1967) for X chromosome at this stage differed from the findings here. There they obtained higher production in the F₃ females obtained by backcrossing F₂ marker females to normal male than like F₂ females backcrossed to marker males. The difference was of the order of 6 eggs in favour of the former. Further, the latter differed from the marker stock females by about 24 eggs. In other words, the production of F₃ females obtained through crossing of F₂ marker showing flies with marker males was nearer the normal than marker stock production.

In case of the second chromosome, Win Moi Tait and Prabhu (1967) did not find any significant difference between the two F₃ cross females and between them and the normal stock. All the three types however differed by about 10-12 eggs from the marker stock females.

Fourth generation

The results were practically the same as found in the

third generation. DH females differed from HD females by about 8 eggs - the higher production being in HD females. Comparison of HD with H+ showed that the performance was about the same level, while that between DH and +H females gave a difference of about 13 eggs in favour of non-Dicheate females.

In the X-chromosome substitution work, carried out by Mazumdar and Prabhu (1967) at this generation, there was a sharp difference in the production of females backcrossed repeatedly to normal and marker males. While the former continued to show production of about the same level as normal stock females, the latter, approached that of the marker stock females, the actual difference between the marker stock and the backcrossed stock was about 7 eggs. These results are contrary to the findings in the present investigation.

In case of the II chromosome, in the 4th generation of replacing II chromosome by marker or normal chromosome through repeated backcrossing, Win Moi Tait and Prabhu (1967) observed that the results were different in some respects from that obtained by Mazumdar and Prabhu (1967) for the X chromosome. They found that the production of 4th generation of backcrossed females backcrossed to marker

males gave as high a production as found in normal stock females. In fact the difference in these flies and the marker stock was as high as 20 eggs. On the other hand there was hardly any difference between the two heterozygous females and homozygous normal flies.

Fifth generation

In this generation, the egg production in DH and HD females was found to be about the same and that between +H and H+ also about the same. There was however, a slight increase in HH flies.

Sixth generation

As in fifth generation though the actual production level was higher throughout than in the fifth generation. Thus DH females gave 61 eggs and HD females 57 eggs. The two normal flies (+H and H+) gave about the same number of eggs as the HH stock flies.

The results of analysis of variance showed that in all generations, the between group variance was significant. The results are summarised in Table II, using critical difference test and bar notations.

Table II

Critical difference test between mean egg production of different groups

| Generations | | | | | | |
|----------------|-----------|-----------|-----------|-----------|-----------|-----------|
| P ₁ | | HD (c) | HH (d) | DD (a) | DH (b) | |
| | | 32.7 | 32.1 | 26.2 | 24.3 | |
| <hr/> | | | | | | |
| I | | HH (d) | DD (a) | HD (c) | DH (b) | |
| | | 57.0 | 43.3 | 41.6 | 35.0 | |
| <hr/> | | | | | | |
| II | +H (e) | H+ (f) | DH (b) | HD (c) | HH (d) | DD (a) |
| | 70.0 | 68.3 | 60.6 | 52.7 | 52.2 | 51.9 |
| <hr/> | | | | | | |
| III | HH (d) | +H (e) | H+ (f) | HD (c) | DD (a) | DH (b) |
| | 52.7 | 47.8 | 45.8 | 43.4 | 42.9 | 37.2 |
| <hr/> | | | | | | |
| IV | HH (d) | +H (e) | H+ (f) | HD (c) | DH (b) | DD (a) |
| | 57.9 | 46.7 | 42.5 | 42.0 | 34.4 | 32.5 |
| <hr/> | | | | | | |
| V | HH (d) | DD (a) | +H (e) | H+ (f) | HD (c) | DH (b) |
| | 63.1 | 56.2 | 55.8 | 55.8 | 46.8 | 46.2 |
| <hr/> | | | | | | |
| VI | +H (e) | HH (d) | H+ (f) | DD (a) | DH (b) | HD (c) |
| | 74.1 | 72.5 | 71.6 | 64.7 | 60.7 | 57.4 |
| <hr/> | | | | | | |

The means within the same bars are not significantly different and are arranged in descending order.

DD = Dicheate ♀♀ x Dicheate ♂♂ (a)

DH = Dicheate ♀♀ x Normal ♂♂ (b)

HD = Normal ♀♀ x Dicheate ♂♂ (c)

HH = Normal ♀♀ x Normal ♂♂ (d)

+H = Non-dicheate ♀♀ from (b) x Normal ♂♂ (e)

H+ = Non-dicheate ♀♀ from (c) x Dicheate ♂♂ (f)

EGG SIZE

In Table III, the mean egg size with their standard errors for the various crosses of normal and marker flies in six generations are presented. In Table IV, the critical differences in mean egg size of the flies of different genetic constitution in different generations are shown. The figures are proportional values and have not been reduced to true values for sake of convenience in calculation.

P₁ generation

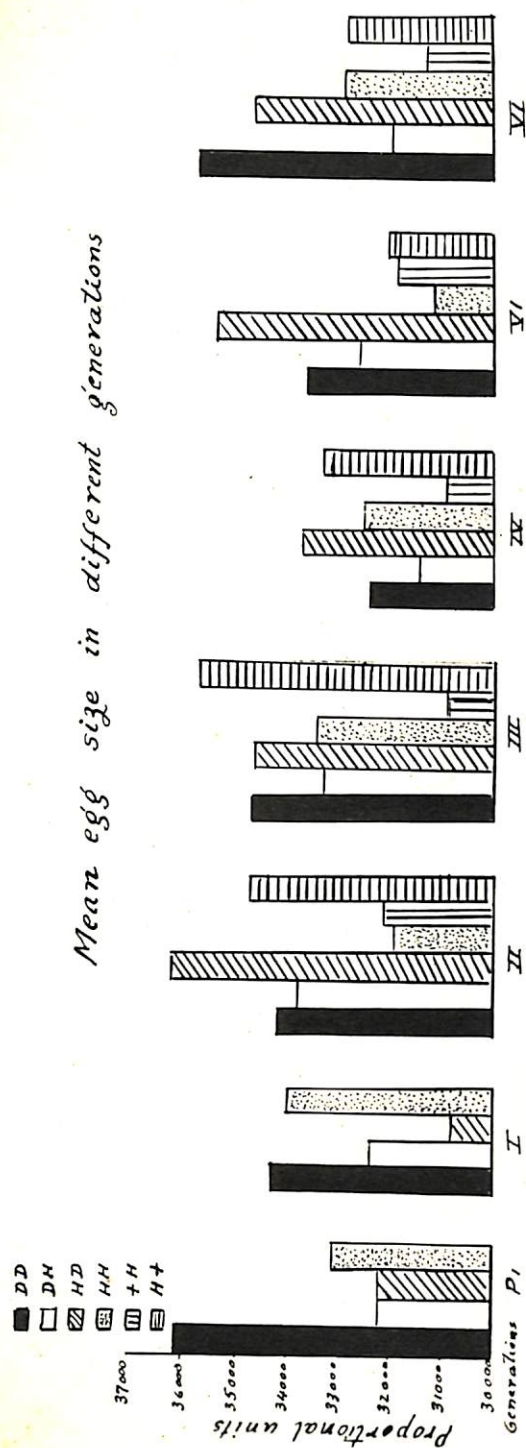
The egg size of the normal females mated by normal males (H ♀♀ x H ♂♂) was 33057 ± 301 (in proportional units) whereas, the eggs of the marker females mated to marker males were of 36131 ± 293 size. The difference of 3074 was statistically significant. The marker females mated by normal males (D ♀♀ x H ♂♂) gave eggs of 32211 ± 282 unit size, which was statistically significant when compared with DD ♀♀ x DD ♂♂ stock. The egg size of the normal females mated to marker males (H ♀♀ x D ♂♂) was 32224 ± 241 which was not different from the egg size of normal control females.

First generation

In the first generation, the egg size of the female of marker stock (D ♀♀ x D ♂♂) was 34329 ± 444 per egg as

Mean egg size (in proportional units) in six crosses in different generations with their standard error

| | | | |
|-------|---|---------------------------|---------------------|
| D x D | = | Dicheate ♀♀ x Dicheate ♂♂ | (Control) |
| D x H | = | Dicheate ♀♀ x Normal ♂♂ | |
| H x D | = | Normal ♀♀ x Dicheate ♂♂ | |
| H x H | = | Normal ♀♀ x Normal ♂♂ | (Control) |
| +H | = | Non-dicheate from (D x H) | cross x Normal ♂♂ |
| H+ | = | Non-dicheate from (H x D) | cross x Dicheate ♂♂ |



Egg size
Fig. 2.

compared to the egg size of the females of Normal stock (H ♀♀ x H ♂♂) which was 34029 ± 333 . The difference was not significant. The size of the heterozygous DH female's eggs was 32425 ± 339 per egg, whereas, in case of heterozygous HD females it was 30732 ± 287 . The difference between the egg size of these two females and marker females were 1904 and 3597 units respectively and were significant in both the cases, indicating that heterozygous females mated by any of the two control stock males produced eggs of smaller size than that of marker females. When compared with normal stock females, the differences were significant in both the cases. The difference between the two heterozygous females^w was 1693 units and was significant. Females which had marker father gave larger eggs as compared to the females which had normal father. These results were contrary to the findings of Mazumdar and Prabhu (1967) who found that females with normal fathers gave larger eggs. Similarly Win Moi Tait and Prabhu (1967) found that curly x normal gave larger eggs. Both these studies claimed that the normal chromosome had more dominant genes for egg size than marker (Bar or curly) which was contradictory to the findings here, where results indicated that marker chromosomes had more genes for larger egg size.

Second generation

In the second generation, marker females gave eggs of

34152 \pm 366 size which were larger than the eggs of the normal females (i.e. 31893 \pm 386). The difference of 2259 units was statistically significant. The Dicheate flies in this generation were from two reciprocal crosses - one arising from the cross of F₁ Dicheate females to normal males (DH) and the other from the cross of F₁ Dicheate female to Dicheate males (HD). The DH gave eggs of 33773 \pm 278 and the HD of 36212 \pm 352 size. The difference of 2439 units was significant, showing that the increase in genes of DD stock had brought about an increase in the egg size. The effect of III chromosome could be shown by comparing the Dicheate females egg size with the non-dicheate females egg size from the same cross. In the present case, it was 33773 \pm 278 and 32055 \pm 366 units respectively. The difference of 1718 units indicated that substitution of Dicheate chromosome by a normal III chromosome did not effect the size of the eggs of Dicheate females.

The egg size of the Dicheate females (progeny of DH) was 33773 \pm 278 and the normal or non-dicheate females from the same cross was 32055 \pm 366 units. The difference of 1574 units was statistically significant. The egg size of the Dicheate females (progeny of HD) was 36212 \pm 352 and the normal looking or non-dicheate females from the same cross was 34738 \pm 321. The difference 1474 units was

significant. It gave an estimate of substitution of normal chromosomes by a Dicheate III chromosome. The difference was the mean effect of substitution and showed that when the Dicheate chromosomes were more, the size also increased. Mazumdar and Prabhu (1967) who conducted similar experiments with X chromosome found in the second generation the difference in egg size of females having each a normal and a marker X chromosome but in one more normal genes in autosomes and in other more of marker genes in autosomes. Larger eggs (323 cu.mm. large) were laid by females containing more normal genes in autosome which was contrary to the findings here. Win Moi Tait and Prabhu (1967) carried out similar studies with II chromosome and obtained a difference of 2291 units between the egg size of heterozygous II chromosome females, one carrying higher and other lower number of normal stock genes in autosomes and the difference was in favour of the flies containing more of normal stock genes in the autosome. This was contrary to the findings here where difference was in favour of the flies containing more genes of Dicheate stock.

Third generation

In the third generation, the marker stock females (DD ♀♀) produced eggs of 34741 ± 381 size which was 1386 units more than the production of normal stock females (HH ♀♀).

Two types of Dicheate flies arising from backcrossing with normal stock and the another with Dicheate stock showed a size difference of 1261 units in favour of latter. Comparison of the egg size of their normal looking sibs showed significant difference between them. This indicated that the normal looking progeny of HD crossed with Dicheate produced larger eggs (i.e. H+) than the normal looking females from DH (+H). Again, there was difference of 2374 units between the Dicheate flies with higher percentage of normal autosomal genes for egg size and 1057 units between Dicheate flies with more of Dicheate genes. The latter difference was not significant.

The results obtained by Mazumdar and Prabhu (1967) for X chromosome in the 3rd generation differed from the findings here. There, they found larger egg size of F₃ female obtained by backcrossing F₂ marker females to normal males than like F₂ female backcrossed to marker males. The difference of 101 units was in favour of the former.

Win Moi Tait and Prabhu (1967) found similar results as in this study. They found significant differences between the egg size of the two F₃ cross females and between them and normal control stock. Results obtained in the present study were similar to these findings.

Fourth generation

In the fourth generation, differences between Dicheate and Normal controls were not significant. DH females gave eggs of smaller size than that of HD. The difference of 2271 units was significant. Comparison of HD with H+ and DH with +H both showed significant differences. Results indicated that where proportion of Dicheate chromosomes were increased, egg size also increased.

Mazumdar and Prabhu (1967) at this stage of their study found that the egg size almost approached to Normal level in both the reciprocal crosses and marker differed significantly with both reciprocals and N x N control. In the present study also, HD and H+ exceeded the level of Dicheate control. In case of II chromosome, Win Moi Tait and Prabhu (1967) found significant difference between the two F₃ cross females, and between them and normal stock, whereas in the present study, there was hardly any difference between two control but there was significant difference between DH, +H and H+ with Normal control stock.

Fifth generation

In the fifth generation the difference between two controls was 2520 units, which was highly significant. There was significant difference between egg size of two Dicheate

females (from DH and HD). Differences between two normal looking F_4 flies was not significant. Comparison of these two (+H and H+) with Normal control stock showed very slight difference.

Sixth generation

Again in the sixth generation, Dicheate flies gave 2793 units larger eggs than normal stock flies. Comparison of DD with DH showed that they differed significantly; whereas, DD with HD showed very little difference, HD being larger than DD.

The difference between +H and H+ was also significant, H+ being 1311 units larger than +H. Both differed highly with that of DD. When compared with normal control (HH), +H differed significantly whereas H+ was almost of the same size.

These results confirmed the previous view that Dicheate chromosome had more genes for egg size than Normal chromosomes. The results of analysis of variance showed that in all generations the between group variance was significant. The results are summarised as follows, using critical difference test and bar notations.

Table IV

Critical difference test between mean egg size of different groups

Generations

| P ₁ | DD (a) | HH (d) | HD (c) | DH (b) | | |
|----------------|-----------|-----------|-----------|-----------|-----------|-----------|
| | 36131 | 33057 | 32224 | 32211 | | |
| I | DD (a) | HH (d) | DH (b) | HD (c) | | |
| | 34329 | 34029 | 32425 | 30732 | | |
| II | HD (c) | H+ (f) | DD (a) | DH (b) | +H (e) | HH (d) |
| | 36212 | 34738 | 34152 | 33773 | 32055 | 31893 |
| III | H+ (f) | DD (a) | HD (c) | HH (d) | DH (b) | +H (e) |
| | 35624 | 34741 | 34567 | 33355 | 33306 | 30932 |
| IV | HD (c) | H+ (f) | HH (d) | DD (a) | DH (b) | +H (e) |
| | 33657 | 33246 | 32452 | 32422 | 31386 | 30896 |
| V | HD (c) | DD (a) | DH (b) | H+ (f) | +H (e) | HH (d) |
| | 35338 | 33600 | 32582 | 32025 | 31809 | 31080 |
| VI | DD (a) | HD (c) | HH (d) | H+ (f) | DH (b) | +H (e) |
| | 35611 | 34525 | 32818 | 32766 | 31909 | 31455 |

The means within the same bars are not significantly different and are arranged in descending order.

DD = Dicheate ♀♀ x Dicheate ♂♂ (a)

DH = Dicheate ♀♀ x Normal ♂♂ (b)

HD = Normal ♀♀ x Dicheate ♂♂ (c)

HH = Normal ♀♀ x Normal ♂♂ (d)

+H = Non-dicheate ♀♀ from (b) x Normal ♂♂ (e)

H+ = Non-dicheate ♀♀ from (c) x Dicheate ♂♂ (f)

HATCHABILITY

In Table V are presented the mean hatchability percentage in various crosses of normal and marker flies in different generations. In Table VI are shown the critical differences in mean hatchability between flies of different genetic constitution.

The percentage of hatchability was maximum in normal control stock in all the generations, except in third generation where it was highest in +H.

P₁ generation

The hatchability in normal females mated to normal males (H ♀♀ x H ♂♂) was $97.4 \pm 0.7\%$ as compared to marker females mated to marker males where it was $71.9 \pm 2.8\%$. The marker females mated to normal males (D ♀♀ x N ♂♂) had mean hatchability of $86.6 \pm 1.8\%$ which was 7.9% less than the normal female mated to marker males, which had $94.5 \pm 1.1\%$ hatchability and was not different significantly from normal control.

First generation

In the first generation eggs from the marker stock (DD ♀♀) had hatchability of $76.8 \pm 2.9\%$ as against $86.1 \pm 2.3\%$

Table V

Mean egg hatchability in six crosses in different generations with their standard error

| Crosses | GENERATIONS | | | | | | | | | | | |
|--------------|----------------|------|------|------|------|------|------|------|------|------|------|------|
| | P ₁ | | I | | II | | III | | IV | | V | |
| | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. |
| D x D (a) | 71.9 | ±2.8 | 76.8 | ±2.9 | 69.2 | ±3.1 | 67.4 | ±2.2 | 62.6 | ±4.0 | 64.5 | ±2.9 |
| DH (b) | 86.6 | ±1.8 | 66.4 | ±8.4 | 91.4 | ±2.0 | 92.0 | ±1.3 | 85.4 | ±3.3 | 76.3 | ±4.4 |
| HD (c) | 94.5 | ±1.1 | 76.4 | ±3.8 | 66.6 | ±3.7 | 67.7 | ±2.4 | 58.5 | ±3.3 | 68.6 | ±3.0 |
| H x H (d) | 97.4 | ±0.7 | 86.1 | ±2.3 | 95.7 | ±1.3 | 90.2 | ±1.5 | 96.1 | ±0.8 | 95.0 | ±1.9 |
| +H (e) | - | - | - | - | 94.9 | ±1.8 | 95.7 | ±2.0 | 91.2 | ±2.2 | 89.5 | ±2.1 |
| H+ (f) | - | - | - | - | 94.3 | ±1.9 | 90.5 | ±1.9 | 85.0 | ±4.1 | 82.3 | ±3.3 |

D x D = Dicheate ♀♀ x Dicheate ♂♂ (Control)

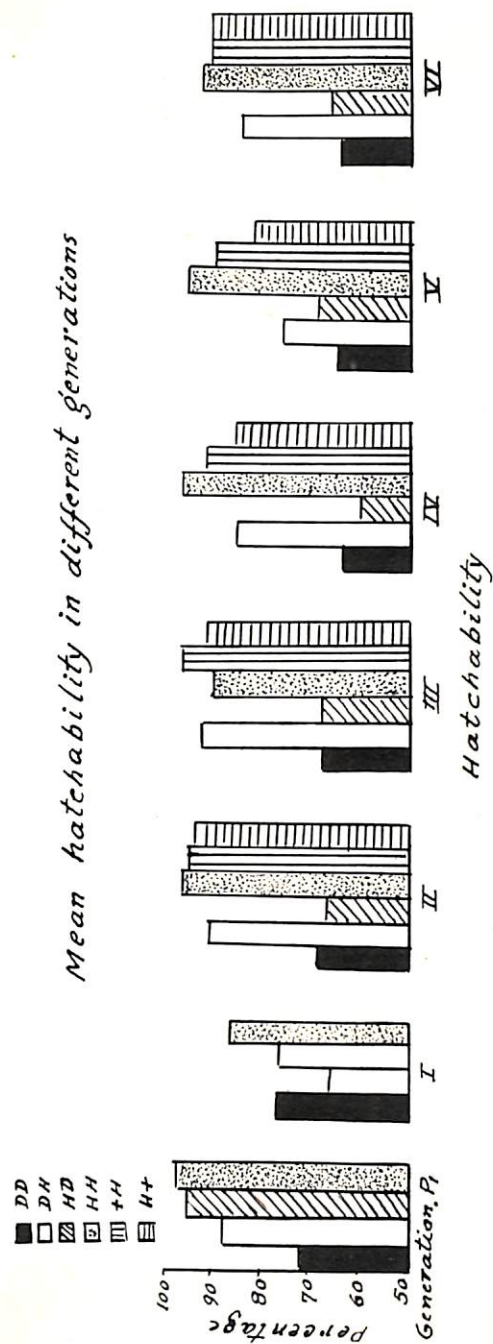
D x H = Dicheate ♀♀ x Normal ♂♂

H x D = Normal ♀♀ x Dicheate ♂♂

H x H = Normal ♀♀ x Normal ♂♂ (Control)

+H = Non-dicheate from (D x H) cross x Normal ♂♂

H+ = Non-dicheate from (H x D) cross x Dicheate ♂♂



of Normal stock. The difference was not significant though Normal flies had higher hatchability.

The eggs of heterozygous DH female had $66.4 \pm 8.4\%$ and heterozygous HD females had $74.4 \pm 3.8\%$ hatchability. The difference between hatchability of eggs of these two types of females and the marker flies hatchability was 10.4 for former and 0.4 for latter. These differences were not statistically significant. When these two were compared with normal flies, DH differed significantly whereas no marked difference was seen with HD. When the two heterozygous females were compared for their egg hatchability percentage they showed no significant difference. These results corresponded with the findings of Mazumdar and Prabhu (1967) who studied this character in their study of the role of X-chromosome and found significant difference between the two reciprocals. The one having Normal genes in higher proportion had higher hatchability but the one which had Bar chromosome had lower hatchability. Similar results were recorded by Win Moi Tait and Prabhu (1967) in their study involving the effect of II chromosome.

Second generation

The hatchability in the second generation marker stock was $69.2 \pm 3.1\%$, while the hatchability of Normal (HH) stock

was $95.7 \pm 1.3\%$. The difference of 25.5% was statistically significant. The Dicheate female in second generation were from two crosses DH and HD - the former was the female offspring of F_1 Dicheate female mated to Normal (HH) males, whereas, the latter was the female offspring of F_1 Dicheate females mated to Dicheate (DD) males.

The hatchability percentage of DH and HD were $91.4 \pm 2.0\%$ and $66.6 \pm 3.7\%$. The difference of 24.8% was highly significant which indicated that the increase in the genes from Normal (HH) stock resulted in an increase in the hatchability percentage. To determine the role of III chromosome comparison between the hatchability of Dicheate female was made with the normal or non-dicheate females from the same cross, i.e. between DH and H^+ which was 3.5 and was not significant. The difference between the Dicheate females from HD cross and normal or non-dicheate (H^+) females from the same cross was 27.7% , HD and H^+ being $66.6 \pm 3.7\%$ and $94.3 \pm 1.9\%$ respectively. The difference was highly significant. The hatchability of HD was less as compared to previous generation, which might be due to the fact that in previous generation less number of genes of Dicheate stock were present than in the present generation.

When HD and H^+ were compared with normal stock control the former showed significant difference of 29.1% and the

latter showed insignificant difference of 1.4%.

These results suggested that when Dicheate chromosome replaced Normal stock chromosome, the hatchability percentage decreased but when Dicheate was replaced by normal stock chromosome it increased. This increase was significant suggesting that normal stock chromosomes had more dominant genes for hatchability.

Mazumdar and Prabhu (1967) found in the second generation of their study higher hatchability in the eggs of the females having greater proportion of normal genes than the bar genes. The present study gave similar results.

Win Moi Tait and Prabhu (1967) studied the effect of II chromosome and found no significant difference among different crosses in second generation. The results were contrary to the findings here and that reported by Mazumdar and Prabhu (1967).

Third generation

In this generation, hatchability of marker (DD) stock was $67.4 \pm 2.2\%$, whereas of the Normal (HH) stock was $90.2 \pm 1.5\%$. The difference of 22.8% was highly significant. Two types of Dicheate flies arising from the backcross with Normal stock and another with Dicheate stock showed difference among

them, of 24.3% in favour of former. Further comparison of these flies with their normal looking sibs showed no significant difference between them. Further the difference between HD and H+ - both of them had Dicheate father - was 22.8% which was statistically significant. These results indicated that whenever proportion of normal chromosome increased irrespective of which male was used for mating, the hatchability percentage was higher.

The results obtained by Mazumdar and Prabhu (1967) in third generation of their experiment were similar to the findings here. When proportion of normal chromosome in a cross increased, hatchability also increased. The results also corresponded with the findings of Win Moi Tait and Prabhu (1967) where they found that the substitution by normal stock chromosome resulted in high hatchability.

Fourth generation

In the fourth generation, results were almost similar to third generation. An overall reduction in hatchability was observed in all, except HH stock where slight increase than in previous generation was seen. The difference between DH and HD was significant and DH had 24.3% higher hatchability. Comparison of DH and +H showed difference of 5.8% which was not significant, whereas, the difference of 26.5% between HD

and H+ was significant and in favour of non-dicheate H+.

In a similar study Mazumdar and Prabhu (1967) found that after continued backcrossing with normal male percentage of hatchability increased but repeated backcrossing with marker stock resulted into lowering of hatchability. In the present study, repeated backcrossing of Dicheate flies with normal males resulted into gradual increase in hatchability upto third generation, corresponding with that of Mazumdar and Prabhu's findings but an overall fall in hatchability was observed in fourth generation. Dicheate fly from HD backcrossed to Dicheate (DD) maintained almost same level as previous generations. In the normal looking sibs of these flies (i.e. +H and H+), the hatchability was maintained to almost same level in former, but slight decrease was observed in the eggs of the flies mated to Dicheate males.

Win Moi Tait and Prabhu (1967) noted same results. The present findings corresponded with the previous findings for the similar study carried out for X and II chromosome.

Fifth generation

The results were similar as previous generations except that a slight decrease was observed in DH cross mated to normal. All other crosses maintained almost same level as previous generations.

Sixth generation

In the sixth generation, the hatchability trend was found to be same as previous generations, except that the hatchability of DH which was decreased in fifth generation was again improved.

These results indicated that after fourth generation, there was no marked change in the hatchability levels of different crosses but only some fluctuations. Further from these results, it is clear that wherever Dicheate chromosomes were replaced by normal stock chromosomes, improvement in hatchability was observed, but when normal chromosomes were replaced by Dicheate stock, slight decrease in hatchability was seen.

Analysis of variance showed that between group variance was statistically significant in all the cases and the results are summarised using critical difference test and bar notation in Table VI.



Table VI

Critical difference test between mean egg hatchability of different groups

Genera-
tions

| | | | | | | |
|----------------|-----------|-----------|-----------|-----------|-----------|-----------|
| P ₁ | HH (d) | HD (c) | DH (b) | DD (a) | | |
| | 97.4 | 94.5 | 86.6 | 71.9 | | |
| I | HH (d) | DD (a) | HD (c) | DH (b) | | |
| | 86.1 | 76.8 | 76.4 | 66.4 | | |
| II | HH (d) | +H (e) | H+ (f) | DH (b) | DD (a) | HD (c) |
| | 95.7 | 94.9 | 94.3 | 91.4 | 69.2 | 66.6 |
| III | +H (e) | DH (b) | H+ (f) | HH (d) | HD (c) | DD (a) |
| | 95.7 | 92.0 | 90.5 | 90.2 | 67.7 | 67.4 |
| IV | HH (d) | +H (e) | DH (b) | H+ (f) | DD (a) | HD (c) |
| | 96.1 | 91.2 | 85.4 | 85.0 | 62.6 | 58.5 |
| V | HH (d) | +H (e) | H+ (f) | DH (b) | HD (c) | DD (a) |
| | 95.0 | 89.5 | 82.3 | 76.3 | 68.6 | 64.5 |
| VI | HH (d) | +H (e) | H+ (f) | DH (b) | HD (c) | DD (a) |
| | 92.4 | 90.0 | 90.0 | 83.8 | 65.5 | 63.8 |

The means within the same bars are not significantly different and are arranged in descending order.

DD = Dicheate ♀♀ x Dicheate ♂♂ (a)

DH = Dicheate ♀♀ x Normal ♂♂ (b)

HD = Normal ♀♀ x Dicheate ♂♂ (c)

HH = Normal ♀♀ x Normal ♂♂ (d)

+H = Non-dicheate ♀♀ from (b) x Normal ♂♂ (e)

H+ = Non-dicheate ♀♀ from (c) x Dicheate ♂♂ (f)

Above results clearly showed that there was significant difference in egg production between the marker and Normal stocks. Except in second generation, this difference continued. Crosses with larger proportions of marker genes gave less number of eggs as compared to the crosses with more number of normal genes, except in H+ cross, where III chromosome was from Normal and the rest were from marker stock. Still production was high in this case indicating that Normal stock had more dominant genes for egg production than marker stock. These findings corresponded with the findings of Majumdar and Prabhu (1967) and Win Moi Tait and Prabhu (1967) and others. This showed that III chromosome enhanced egg production in Drosophila melanogaster due to the presence of more number of dominant genes effecting the character.

In case of egg size it was found that the marker stock produced considerably larger eggs in all generations as compared to those of normal stock. Reciprocals produced considerably smaller eggs than both marker and normal stocks. This indicated that marker stock had genes for large egg size, and the Normal stock had genes for small egg size; because when normal chromosomes were introduced into marker stock, egg size was either reduced or was brought down to the level of normal stock. In all the generation HD and H+ lines (backcrossed with Diccheate males) were more inclined towards

the Dicheate control stock whereas DH and +H lines (backcrossed with normal males) had more inclination towards normal stock. These results suggested that III chromosome of Dicheate (Marker) stock had more genes effecting large egg size whereas normal III chromosome produced small eggs.

As for hatchability was concerned it was found that the difference between Dicheate control and normal control stock were highly significant. The percentage of hatchability was maximum in all cases in normal stock or in the cross where the genotype was almost similar to normal (+H) - normal looking females backcrossed to normal. Minimum hatchability was in Dicheate stock or in the cross where genotype was almost similar to Dicheate control stock (HD = Dicheate females backcrossed to Dicheate males). Hatchability percentage was significantly higher in +H, DH (both backcrossed to normal). These results showed that wherever Dicheate chromosomes were replaced by normal stock chromosomes, the hatchability increased considerably but when normal chromosomes were replaced by Dicheate chromosomes, hatchability decreased. However this decrease was insignificant in H+ cross, where non-dicheate females were mated with Dicheate females.

Strauss and Gowen (1942) in case of egg production

found that activity of II, III and X chromosome was in proportion of 4:2:1 whereas Robertson and Reeve (1955) found this proportion to be 3:5:1 respectively. Mather and Harrison (1949) studied two way selection for bristle number and reported that selection of infertility genes were linked to the polygenes and responsible for high bristle number. These polygenes behaved as unit because these were tightly linked. With the chromosomal assay technique, it was found that all the three major chromosomes were involved for selection of high bristle number. The results were interpreted in terms of Mather's theory of polygenes (1943, 1949). According to him (1943) polygenes were genes which had individually small effects, but these effects were cumulative in nature and controlled continuous variation. A heterozygous III chromosome of the isogenic line was substituted in an otherwise inbred line genotype. By combining selection to recessive inbred parents, an attempt was made to study any major gene present on these chromosomes (Purser, 1954). Clayton and Robertson (1957) discussed that the high line variability was apparently due to continued selection of heterozygotes for a lethal gene. Such genes were present in II and III chromosomes. Genetic differences in the III chromosome of two selected lines of Drosophila melanogaster were discussed by Breese and Mather (1957). They suggested

that the correlated response in the one to selection for the other must be depended on linkage relation and not on pleiotropy of gene action. Further they suggested (1960) that the pleiotropic effects of the chromosome segments are due to linkage within them. Hiraizumi (1961) suggested that II and III chromosomes contributed in a very simple multiplicative fashion. Seiger (1966) reported that the substitution of III chromosome of Canton-S for the III chromosome of P_1 -Oregon resulted in a lower body weight.

In the present study, Dicheate stock had less number of genes or gene blocks effecting egg production and hatchability, whereas it had more genes effecting egg size as contrasting with normal stock III chromosome which had more dominant genes effecting egg production and hatchability but less genes effecting egg size.

SUMMARY

1. The experiment was aimed to study the effect of III chromosome on egg production, egg size and hatchability in *Drosophila melanogaster* by the chromosome substitution technique. The stocks used for the experiment were:

(i) m_{11} - containing *Dichmate* wings which are extended uniformly at 45° from body axis and elevated 30° above, associated with m_{11} (32).

(ii) m_{11} - half m_{11} high line - 2 flies killed for seventeen generations, raised from 100 flies captured in WML traps in March.

SUMMARY

2. The experiment was started with 50 pair matings of pure line stocks in base generation. F_1 generation was raised from the progeny of these pair matings and two reciprocal lines and two controls were set. In first generation phenotypically *Dichmate* flies were selected from each reciprocal and mated to males of other line. The second generation consisted of 4 lines apart from the two controls. These four lines were raised by selecting *Dichmate* and non-*Dichmate* flies from each reciprocal and mating them in reciprocal and *Dichmate* males. This was continued upto sixth generation. At each generation, reciprocal crosses were so made that through the stock chromosomes were

SUMMARY

1. The experiment was aimed to study the effect of III chromosome on egg production, egg size and hatchability in Drosophila melanogaster by the chromosome substitution technique. The stocks used for the experiment were :
 - (i) h_{121} - containing Dicheate wings which are extended uniformly at 45° from body axis and elevated 30° above, associated with In (3L).
 - (ii) H_1 -Half sib high line-1 flies inbred for seventeen generations, raised from 100 flies captured in IVRI campus in March 1966.
2. The experiment was started with 50 pair matings of both the stocks in base generation. P_1 generation was raised from the progeny of these pair matings and two reciprocal lines and two controls were set. In first generation phenotypically Dicheate flies were selected from each reciprocals were mated to males of other line. The second generation consisted of 4 lines apart from the two controls. These four lines were raised by selecting Dicheate and non-dicheate flies from each reciprocal and mating them to normal and Dicheate males. This was continued upto sixth generation. At each generation, reciprocal crosses were so made that normal (H) stock chromosomes were

introduced into the Dicheate (D) stock by backcrossing, but keeping the Dicheate (marker) III chromosome constant, and the Dicheate (D) stock chromosomes were introduced into normal (H) stock keeping normal III chromosome constant.

3. Results of egg production indicated that the Dicheate with rest of the chromosome from normal stock produced similar effect as normal stock III chromosome with rest from Dicheate stock showing Dicheate stock had less dominant genes for egg production than normal stock.
4. In case of egg size, it was noticed that the normal stock chromosomes contained less factors effecting egg size. Dicheate stock, or other lines with Dicheate chromosomes had significantly larger eggs.
5. As regards hatchability, results showed that normal stock chromosome contained more dominant factors for hatchability than Dicheate stock. In case where Dicheate was replaced by normal stock hatchability was high. Only where all the chromosomes were of Dicheate stock, hatchability got reduced considerably.

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