ANALYSIS OF A 6×6 DIALLEL CROSS FOR HATCHABILITY IN *DROSOPHILA MELANOGASTER*

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In *Drosophila* there have been few detailed genetic investigations on quantitative characters like egg production which have low values of heritability and high environmental effects. Bell, Moore and Warren (1955) tested four methods of selection on egg production and egg-size and Rasmuson (1956) employed the "recurrent reciprocal" selection method on egg production and hatchability. Both these investigators were chiefly interested in testing the efficacy of the newer methods of selection in plant breeding introduced by Hull (1945) and Comstock, Robinson and Harvey (1949) for making maximum use of both general and specific combining abilities for use in animal breeding. The results were not as encouraging as the theoretical expectations. Though the senior author's interest in egg production dates from the year 1939, when he accidentally discovered an egg mutant "Filament" in *Drosophila pseudo-obscura* (Prabhu, 1944) and using X-ray technique showed the existence of a highly potent region affecting fertility and confined to a small region (between the mutants *garnet* and *forked*) on the X-chromosome of *Drosophila melanogaster* and covering a cross-over length of 12·3 units (Prabhu, 1939), the rest of the authors came on the scene when the Indian Council of Agricultural Research, New Delhi, sanctioned a scheme for fundamental investigations on quantitative inheritance at the Indian Veterinary Research Institute, Izatnagar, U. P., in the year 1956. The work started under the scheme is now continued as a regular activity of the Division of Animal Genetics of the Institute. The work completed under the scheme, which consisted mostly of standardising the techniques of rearing, counting and measuring flies for studies on egg-production is detailed in the report of the scheme for the year 1958-59 (Prabhu, 1960). The medium found best for egg production studies in the fly is given in a report by Prabhu, Negi and Singh (1963). Results of two-way selection for egg production in *Drosophila melanogaster* have been published by Prabhu et al. (1964) while those concerning the effect of various levels of inbreeding on egg-size and fertility (Satya Prakash, unpublished), egg-production and hatchability (Prabhu Lal, 1962) in *Drosophila melanogaster*, and two-way selection for egg production using five methods of mating (Bhatt, 1961; Rawat, 1966) in *Drosophila ananassae* await publication. One of the reasons for our not rushing to print was that we obtained certain results that did not fall into known patterns and we naturally wished to probe further into the matter before publishing. In this connection, the technique of diallel crossing that was becoming popular in detecting the genetic architecture of quantitative traits was available and recourse was taken to this, using six inbred lines selected for high and low fecundity maintained in the laboratory. Results of that study concerning egg-

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production have been given in a separate article (Singh et al., 1964). In the present article we present our findings concerning hatchability.

MATERIAL AND METHODS

The technique of rearing flies, collecting eggs and measuring them and estimating hatchability followed here are those given by Prabhu (1960). Hatchability was determined by keeping a sample of eggs laid by the fly under observation for 24 hours at 25°C and finding the proportion of eggs that hatched during this period. As the proportions so obtained were generally high for statistical analysis the proportions were converted into angles using the transformation $\sin^{-1}\sqrt{p}$, where p is the proportion of hatched eggs, as recommended by Snedecor (1951). Full particulars regarding crosses are given in the earlier paper (Singh et al., 1964). Data were analysed following the method described by Hayman (1954). There were four replications of each cross.

RESULTS

Means

Table 1 gives the transformed values of hatchability averaged over all the four replications for the six parents along with their thirty progenies.

Table 1. *Mean hatchability ($\sin^{-1}\sqrt{p}$ values)*

		FEMALES					
		A	B	C	D	E	F
MALES	A	77·0	83·0	75·9	86·7	80·8	82·2
	B	85·9	78·9	78·8	78·8	87·0	86·0
	C	84·0	82·5	84·5	73·9	86·6	87·3
	D	80·0	84·9	70·0	85·9	83·1	83·9
	E	81·4	86·4	83·4	83·4	85·3	83·1
	F	86·3	82·5	86·0	80·9	78·7	77·9

An idea of the overall direction of the F_1 means from their corresponding parental means can be obtained by comparing the mean of *all* parental lines with that of *all* F_1s. A test of significance carried gave results which are summarised below:

	Hatchability
Parental mean (P)	81·6
Progeny mean (F_1)	82·4
(F_1—P)	0·8
Significance	P > 0·60

The test revealed no significant difference in the overall parental and progeny means in case of hatchability showing clearly the absence of heterosis.

Variances

The variances within families of parents and their progenies averaged over all the four replications are presented in Table 2.

Table 2. *Variances within families*

FEMALES

		A	B	C	D	E	F
	A	94·8	20·3	43·7	74·4	28·3	18·4
MALES	B	36·3	61·4	46·0	31·8	18·4	50·0
	C	103·1	45·9	46·8	97·0	27·5	22·5
	D	19·0		90·0	13·4	36·0	105·1
	E	56·0	18·1	15·3	30·5	28·2	40·1
	F	95·4	29·3	13·8	33·3	29·3	72·4

Wide variations in variances were observed which could only be due to non-heritable causes as the parental lines were highly inbred and as such practically homozygous. Bartlett's test for homogeneity of variances (Snedecor, 1956) was applied to find out whether any heterogeneity is present. The results showed the absence of heterogeneity and as such, the non-heritable variances present were assumed to be uniform over the families.

Variances of Arrays (V_r) and Covariances (W_r)

Values of variances of arrays (V_r) and those of covariances (W_r) between the parents and their offspring in the rth array, in the four replications $(R_1$-$R_4)$ are presented in Table 3.

Table 3. *V_r and W_r for hatchability in each replication*

R_1		R_2		R_3		R_4	
V_r	W_r	V_r	W_r	V_r	W_r	V_r	W_r
26·25	9·42	2·75	−2·13	7·58	2·62	21·09	2·25
11·68	−2·28	12·71	6·92	21·99	−5·45	4·59	−1·27
12·62	−7·98	31·71	−4·96	45·33	1·15	28·76	−7·43
22·43	14·06	21·36	−4·70	34·15	−4·79	25·21	−13·23
7·55	9·59	10·86	4·75	13·13	−1·25	7·61	9·30
4·42	1·72	15·43	2·30	6·76	−2·20	31·81	21·83

Analysis of variance of $(W_r—V_r)$ carried out for testing the heterogeneity of $(W_r—V_r)$ gave the following results.

	d.f.	M.S.
Lines	5	563·04*
Replication	3	116·01
Residual	15	56·54

Significant differences between lines were observed.   An examination of data showed that $(W_r—V_r)$ for the cross $C \times D$ was, on an average, more than the other line crosses. Two values of the progenies in the diallel tables corresponding to crosses $C \times D$ and $D \times C$ were excluded as advised by Hayman (1954) from each of the four replications and the data reanalysed using the missing plot technique in respect of the omitted values.   The estimated values of $C♀ \times D♂$ and $C♂ \times D♀$ were as under:

Replication	$C♀ \times D♂$	$C♂ \times D♀$
1	79.6	78.5
2	82.6	88.9
3	80.1	80.2
4	86.6	81.1

On the basis of the above estimated values, W_r and V_r were calculated afresh for each replicate and another analysis of variance performed for testing the homogeneity of lines.   Now, it was found that there was no significant difference between lines and it was possible to go further with the analysis.   Figure 1 shows the points (W_r, V_r), the limiting parabola $W_r^2 = V_{OLO} V_r$, and the line of unit slope through the adjusted mean point (V_{IL1}, W_{OLO1}).   The unadjusted points lie well off this line.

Components of Variance

After eliminating the abnormal values and substituting the same with the estimated values, the diallel tables were subjected to an analysis of variance as given by Hayman (1954) and the results are summarised in Table 4.

Tests were carried out to find out whether the six interaction variances were homogenous or not.   The value of χ^2 for 5 degrees of freedom was 5·34; and was therefore not statistically significant.   In view of this, the error variances were pooled and the effects tested against the pooled error variance mean square $(R \times (t))$.   The resulting F ratios are given in the last column of Table 4.

CONCLUSIONS

It is found that additive and maternal effects for hatchability are totally absent.   The significance of (b) indicates the presence of dominant effects, while the significance of (b_2) shows that the distribution of alleles in the parents was asymmetrical.   Significance of (d) indicates the presence of differences not ascribable to maternal effects in parental lines.
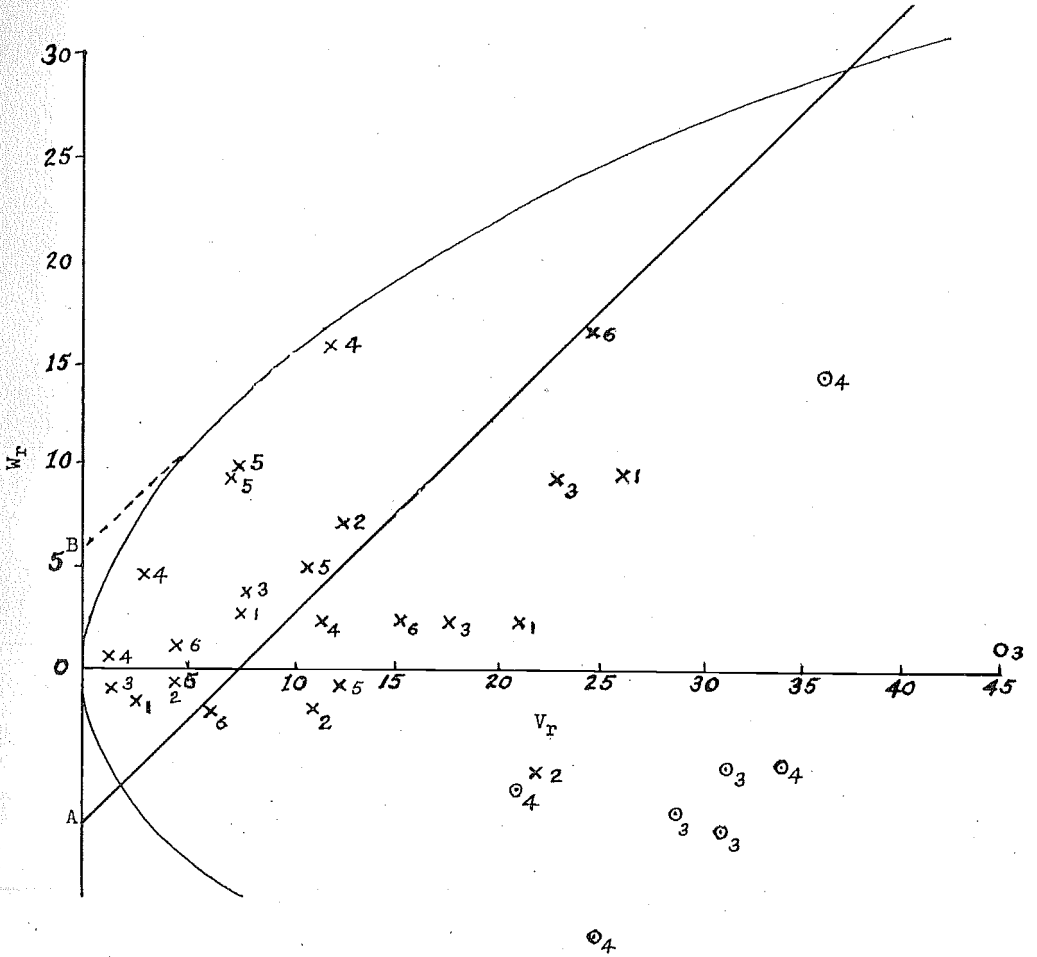
Fig. 1.

Table 4. *Components of variance*

Source of variation	d.f.	M.S.	F-ratio
(a) $D-F+H_1-H_2$	5	22·2460	1·71
(b_1)	1	48·0000	3·68
(b_2)	5	56·4140**	4·33
(b_3)	9	48·0400**	3·68
(b) H_2 (b_1, b_2, b_3 pooled)	15	50·8287**	3·90
(c) Reciprocal	5	28·5840	2·19
(d) Differences	10	33·6840*	2·59
(t) Total	35		
R (Replications)	3	12·3300	
R × (a)	15	18·0120	
R × (b_1)	3	10·0167	
R × (b_2)	15	11·9633	
R × (b_3)	27	8·2255	
R × (c)	15	20·3053	
R × (d)	30	12·0360	
R × (t)	105	13·0203	

The hatchability data were subjected to further statistical analysis and the estimate of the various genetic and non-genetic components along with standard errors worked out are presented below.

Statistic	value	Standard error	't'
$\hat{D}$	10·4997	4·0040	2·622*
$\hat{F}$	14·3996	9·7818	1·472
$\hat{H}_1$	19·6392	10·1645	1·932
$\hat{H}_2$	13·7194	9·0802	1·511
$\hat{h}_2$	3·5665	6·1116	0·583
$\hat{E}$	13·0203	1·5135	8·602**

$\hat{H}_1$ and $\hat{H}_2$ are insignificant by this test but significant by the more reliable test provided by analysis of variance.

The mean degree of dominance over all loci present given by $\left(\dfrac{\hat{H}_1}{\hat{D}}\right)^{\frac{1}{2}}$, is found to be 1·367. The value of $\dfrac{\hat{H}_2}{4\hat{H}_1}$ (=0·174) shows that $\hat{H}_1$ is significantly different from

$\hat{H}_2$ which shows that the positive and negative alleles at loci showing dominance are not in equal proportions in the parents. The value of $\dfrac{(4D\hat{H}_1)^{\frac{1}{2}}+\hat{F}}{4D\hat{H}_1)^{\frac{1}{2}}-\hat{F}}$ works out to 3·011 which indicates that there are about three dominant genes for every one recessive gene. The order of dominance of the parents is $D\ E\ C\ B\ F\ A$, the D line having the highest and A line the least hatchability.

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