

5. SUMMARY

1. In *Dactylis glomerata* subsp. *lusitanica*, the effect of extra heterochromatin on the inter-relationships of chiasma frequency in the normal complement was studied. In the diploids with no extra heterochromatin there was a negative correlation in the normal set. In a plant with 3 extra heterochromatic supernumeraries there was also a significant negative correlation, while in the group of plants with two supernumeraries there was a significant positive correlation. In plants with 1 and 4 supernumeraries there was no correlation. This seems to be one more role which heterochromatin plays in cellular processes.

2. In the trisomic plant, there was no correlation of chiasma frequencies, and there was no increase in the upper limit of chiasma formation. Data are compared with the earlier work on maize trisomics.

3. In the asynaptic plant, the total variance increased considerably. However, the variance components are not significantly different.

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EFFECTS OF INBREEDING AND BRISTLE NUMBER ON REPRODUCTIVE SUCCESS IN SELECTED LINES OF *DROSOPHILA MELANOGASTER*

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1. INTRODUCTION

WHEN populations of plants or animals are selected for a metric trait, a number of changes usually occur: in particular, the mean of the metric trait is altered, the coefficient of inbreeding rises (Robertson, 1961) and

reproductive capacity falls. It is well known that in normally outbreeding species reproductive capacity declines as inbreeding increases. Furthermore, there is considerable evidence, reviewed by Lerner (1954) that fecundity declines as the population mean for a metric trait deviates from an optimum value. When information of this kind is obtained by comparison of different generations of selected populations, however, the effects of population mean and inbreeding are confounded. A definitive analysis of these effects therefore requires special experimentation.

When evidence is available on the reproductive success of each mating, together with the metric trait phenotypes of the parents and the inbreeding coefficient of their offspring, it is nevertheless possible to learn something of the scales on which these variables should be measured to obtain the greatest correlation with reproductive success.

TABLE 1
List of transformations

Scale	Chætae score	Curvature value	Inbreeding	Curvature value
1	$\log (M-\bar{f})$	-0.039	\sqrt{F}	-1.62
2	$\sqrt{(M-\bar{f})}$	-0.019	F	0.00
3	M	0.00	$\exp (F)$	1.00
4	$\exp (M/\bar{f})$	0.028	$\log_e (1-F)$	1.44
5	$(M-\bar{f})^2$	0.039	F^2	3.25

2. MATERIAL AND METHODS

Six lines of *Drosophila melanogaster* (Kaduna strain) were selected for high abdominal chætae score (fourth and fifth segments) by McBride and Robertson (1963). Three samples of the Kaduna strain each produced two lines, one selected with random mating, and one selected with assortative mating. Two pairs of lines, DA and DR, CA and CR were selected on individual scores with ten pairs of parents in every generation. One pair of lines, FA and FR, were selected on an index combining individual and family scores, with twenty matings per generation. In the above designations, the letters A and R represent assortative and random mating respectively.

The size of each line was kept constant by drawing upon reserve matings where necessary. All matings were of single pairs and full pedigrees were kept. Selection intensity was 1/10 so that a successful mating was defined as one which produced 10 male and 10 female offspring. The success or failure of mating was the only information on reproductive performance kept. Wright's (1921) inbreeding coefficient (F) and the mean parental chætae score (M) were also available for each mating.

To study the effects of F and M on reproductive success of a mating, discriminant function analyses (Fisher, 1948) were carried out. In this, all matings carried out in each line, regardless of generation, were considered as a single series differing in M and F. Five transformations of each of the F and M scales were used in the analyses, all 25 combinations being tested. The transformations are listed in table 1, the listing being in order of increasing "concavity" over the relevant range of each variable.

The curvature of the transformations is measured by $\left(\frac{d^2f}{dx^2}\right) / \left(\frac{df}{dx}\right)$ evaluated at the average of x , the untransformed variable. Positive curvature values indicate

concave scales and negative values convex scales. \bar{f}_i is the mean of the unselected population.

The analyses were carried out on each line separately, on combined C lines, D lines and F lines, on combined C and F lines, and all 6 lines pooled. The D lines were omitted from one set of analyses because the gene *scabrous* appeared and was fixed in these lines and had a large effect on both bristle number and reproductive performance.

The criterion used to judge effectiveness of discrimination was R^2 , the squared multiple correlation between reproductive performance of matings scaled zero (failed) or one, and the calculated discriminant function. In a rough sense it measures the proportion of variation in reproductive success which can be accounted for in terms of the discriminant function. A simple transformation converts this to the generalised distance between populations of Mahalanobis (Rao, 1952).

These R^2 values were subjected to a factorial analysis of variance, the factors being the 6 lines, 5 M scales and 5 F scales. These values do not, of course, meet the formal requirements of an analysis of variance, but this does not seem to be very serious. At any rate the conclusions are not altered by a variety of transformations of R^2 values, and the analysis is merely being used to indicate which of the factors are important in determining goodness of discrimination.

3. RESULTS

The analysis of variance of the R^2 values obtained for the 6 individual lines is shown in table 2.

TABLE 2

Analysis of variance of R^2 values

Effect	DF	MS $\times 10^5$
Lines (L)	5	5710.0
Chaetae scales (M)	4	51.1
Inbreeding scales (F)	4	124.0
L \times M	20	18.2
L \times F	20	33.1
M \times F	16	1.5
L \times M \times F	80	2.3

There are large differences between lines, M scales and F scales. In addition there are interactions between lines and both series of scales, but not between the scales themselves. Tukey's test (1949) carried out separately for each line gave no indication of non-additivity of M and F scales. Accordingly the mean R^2 values for each scale of M and F in the 6 lines are plotted in fig. 1.

Apart from the large differences between lines in discrimination, several facts emerge. Except for the D lines, there is a tendency for "concave" transforms to give better discrimination. For the D lines the original M scale is best, a fact almost certainly related to the presence of the *scabrous* gene. There are, however, interactions between lines and scales other than those due to the D lines which thus cannot be attributed to *scabrous*. Nevertheless it does appear that apart from the D lines the square transform of both M and F is favourable for discrimination, so the results of the discriminant function analyses using squares in the C and F lines are given in table 3.

The difficulty of separating the effects of the two factors is obvious from the high correlation between them, but some success appears to have been achieved. An interesting point emerges from comparison of table 3 with fig. 1. When $R^2(b)$ is larger for M than F it is found on the figure that the line is more sensitive to changes in M scale than in F scale and vice versa. This is true also of the results from data pooled over lines mentioned previously. However, because of the dissimilar results of the individual

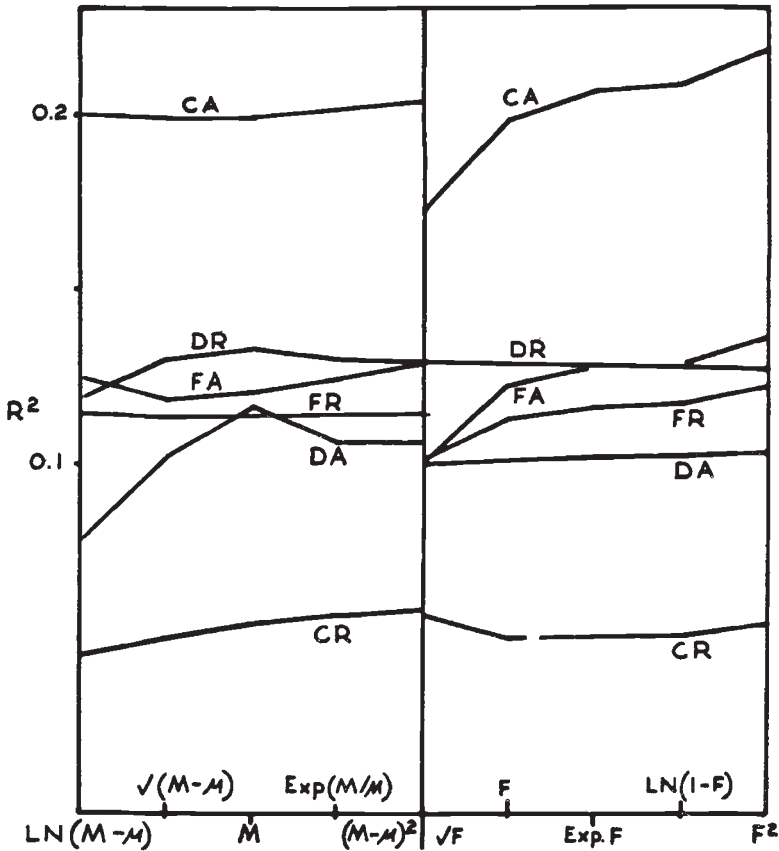


FIG. 1.—The values of R^2 for the chæta score (M) and inbreeding (f) transformations.

lines, these pooled analyses are not presented here. It appears that sensitivity of R^2 to scale changes reflects the importance of the corresponding variable in affecting reproductive success. Thus in the D lines chætae score appears more closely related to fitness than does inbreeding, whereas the reverse is true in the other lines except for CR which appears to be sensitive to both variables. This line was noted as exceptional among these four in another connection by James (1962a).

In table 4 some characteristics of the 6 lines are given.

There is a close relationship between fitness and discrimination, Kendall's (1955) rank correlation coefficient being -0.73 which is significant at the 5 per cent. level. It is thus likely that differences between lines in power

of discrimination are attributable to differences in average fitness. There is no clear relation between fitness and mean chaetae score or mean inbreeding of the various lines.

TABLE 3
Results of discriminant function analyses

Line	b	$R^2(b)$	R^2	N	r
CA	$\begin{bmatrix} M - 9.6 \times 10^{-5} \\ F - 0.43 \end{bmatrix}$	$\begin{bmatrix} 0.0013 \\ 0.0623^* \end{bmatrix}$	0.2191	289	0.802
CR	$\begin{bmatrix} M - 2.8 \times 10^{-4} \\ F - 0.40 \end{bmatrix}$	$\begin{bmatrix} 0.0047 \\ 0.0010 \end{bmatrix}$	0.0576	243	0.911
FA	$\begin{bmatrix} M - 1.7 \times 10^{-4} \\ F - 1.7 \end{bmatrix}$	$\begin{bmatrix} 0.0043 \\ 0.0205^* \end{bmatrix}$	0.1394	434	0.824
FR	$\begin{bmatrix} M - 7.1 \times 10^{-5} \\ F - 3.0 \end{bmatrix}$	$\begin{bmatrix} 0.0003 \\ 0.0222^* \end{bmatrix}$	0.1212	392	0.880

b : discriminant function coefficients.
 $R^2(b)$: improvement in R^2 due to inclusion of second factor.
 R^2 : squared multiple correlation.
 N : number of matings.
 r : correlation between $(M-fi)^2$ and F^2 .
 * : significant at 5% level.

Over the 6 lines the highest correlations between transformed values of M and F were obtained with $\log(M-fi)$ and \sqrt{F} while the most consistently low correlations were obtained with $\log(M-fi)$ and F^2 . Consistently high correlations were also found between $\sqrt{M-fi}$ and \sqrt{F} ,

TABLE 4
Characteristics of 6 lines

Line	N	Fitness *	Mean M	Mean F	Max (R^2)
DA	269	0.6840	72.87	0.3308	0.1219
DR	292	0.6541	65.37	0.3096	0.1336
CA	289	0.6505	58.45	0.3271	0.2191
CR	243	0.7778	56.36	0.3442	0.0633
FA	434	0.6613	61.43	0.3272	0.1394
FR	392	0.7296	56.97	0.2090	0.1240

* Proportion of successful matings.

and there were also consistently low correlations between $(M-fi)^2$ and \sqrt{F} . High and low are of course relative terms here as all correlations are fairly large. It appears that high correlations are found when both variables are measured on convex scales, and low correlations when one is measured on a convex scale and one on a concave scale.

4. DISCUSSION

It is perhaps not surprising that a significant degree of discrimination between successful and unsuccessful matings can be made on the basis

of chætae score and inbreeding, since all that is required for this is that the average reproductive rate should decline as selection proceeds, and it is well known that this usually occurs. It would not necessarily have been expected, however, that the "distance" between successful and failed matings should be greater in the less fit lines. This relation is not, it should be mentioned, dependent on the use of R^2 to measure distance, being still present, for example, when Mahalanobis' D^2 is used. There is no real indication here of the reason for this relationship.

Of more interest are the comparisons among the transformations of the chætae and inbreeding scales. The difference between the D lines and the other four were to be expected, and reflect the fact that the *scabrous* gene was a major determinant of reproductive success in these lines. The superior performance of the square transformation in the other lines is in accordance with predictions from theoretical models (Robertson, 1956), and while hardly to be regarded as confirmatory evidence for these models, is at least not contradictory to them.

Rather surprisingly, the square transformation of inbreeding also proved most effective, though there are some slight deviations from this pattern. The results of Latter and Robertson (1962) suggest that the square root transformation might have performed best of those used in this study. Unfortunately there are a great many reasons why this expectation might have been disappointed, and it is not possible from the data to decide among these.

The most obvious difference is that their criterion of fitness is different from the criterion used in this study. They compared competitive ability of different generations whereas we compare the successes and failures of individual matings. However, since reproductive rate declined with time, the present criterion is to a considerable extent, though by no means entirely, a comparison of different generations. On general grounds one might expect a reasonable correspondence between the criteria, though with a trait as complex as fitness general arguments are apt to be misleading in particular cases.

Another striking difference between these studies is in methodology. Latter and Robertson used an experimental plan specifically designed to study effects of inbreeding in the absence of selection, whereas we have attempted a statistical disentanglement of their concurrent effects. To this extent their results are the more soundly based. There is, however, one complicating factor. As Latter and Robertson show, the effects of fast and slow inbreeding differ in intensity, and similar results had been obtained previously. Thus inbreeding effects depend on the nature of the inbreeding. But as shown by James (1962*b*) there is reason to believe that the inbreeding obtained during selection may be of a somewhat different nature from that found without selection. If this is true it may be a contributing factor to the discrepancy.

It must be concluded that the analyses have not greatly clarified the relationships between fitness, inbreeding and metric selection. They suggest that, at least over the ranges of the variables included in the data, fitness declines at an increasing rate as both selective advance and inbreeding increase. They do not, however, provide insight into the causes of these relations.

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