Selection using assortative mating in *Drosophila melanogaster*

By GLENORCHY McBRIDE* and ALAN ROBERTSON

Institute of Animal Genetics, Edinburgh, 9

1. INTRODUCTION

The term 'assortative mating' implies that after the selection of individuals to be parents of the next generation, they are not, in fact, mated to one another at random. The classical paper on this problem is by Wright (1921), in which he is not concerned with selection but solely with the effect of the imposition of a correlation between the phenotypic values of individuals mated to one another. More recently Reeve (1953 and 1961) showed that phenotypic assortative mating increased the accuracy of estimation of genetic parameters by the regression of the performance of offspring on the mean performance of their parents.

Two recent papers, Breese (1956), and James & McBride (1958) have drawn attention to the possibility of increasing the response to selection by the use of assortative mating. After the selection of an extreme set of males and females as parents of the next generation, they are mated together according to their rank in the character under selection.

Wright (1921) showed that a phenotypic correlation between mates will also lead to a genetic correlation between them (depending upon the heritability of the character concerned) and this will cause an increase in the variance between families. Reeve (1953) gave an explicit expression for the variance between full-sib families in the more general case.

In selection, assortative mating might then be expected to increase the genetic variance available to selection by increasing the component between families. The picture is, however, not entirely one of advantage. It has been shown (Robertson, 1960) that individual selection for a character will lead to a greater rate of inbreeding than would be expected from the number of chosen parents each generation. The decrease in the effective size of the population is related to the intra-family correlation in the character under selection. The use of assortative mating in a selection programme would then be expected to increase the immediate response to selection by making more genetic variation available to selection pressure, but perhaps to reduce the total advance under selection by an increase in the rate of inbreeding.

Since selection involving the use of family means increases the intra-family correlation in the index of selection, there should be not only an increased initial

* Present address: Department of Animal Husbandry, University of Queensland, Brisbane, Australia.

response to selection but perhaps a lowered total advance because of the increased inbreeding.

Experiments were designed to give practical evidence on these points. Variation in response between replicated selection lines is generally high (see, for instance, Clayton *et al.*, 1957) and presumably much of this derives from the initial sampling of the base population. To minimize this, selection techniques were compared using lines derived from the same initial sample.

All experiments described here were carried out on the standard Kaduna strain of *Drosophila melanogaster* (used by Clayton *et al.*, in their experiments), which had been maintained with a population size of about 5000 at 25° C. for some seven years. The character measured was the sum of the numbers of abdominal bristles on the fourth and fifth sternites. In this population, the heritability of this character was found by Clayton *et al.* to be 0·52.

2. THE EFFECT OF ASSORTATIVE MATING WITHOUT SELECTION

A preliminary experiment was carried out to investigate the effect of imposing a correlation between mates on the analysis of variance of their progeny within and between families. Three groups of matings were made of flies from ten full-sib families in the base population. The matings, as described by the pedigree of the parents, were exactly similar in each group. The groups differed, however, in bristle score of mates. In the random mating group no attention was paid to the bristle score.

In the other two groups, a correlation was imposed on the scores of mates. However, because of the decision to make the pedigree in the three groups of matings identical the correlation had to be based not on the individual's absolute score, but on its deviation from the family mean. The overall results for nine replicates are shown in Table 1.

Table 1. *The effect of a correlation between mates in an unselected population*

Mating scheme	Total variance	Between full-sib family component	Full-sib correlation
Assortative	12·17	5·87	0·48 ± 0·050
Random	11·65	3·45	0·30 ± 0·041
Disassortative	9·18	1·78	0·19 ± 0·035

Although the increase in total variance is not significant, the assortative mating has had an effect which would give an increased selection differential and heritability in the next generation of selection. The differences in variance components and in full-sib correlations form a regular pattern according to theoretical expectations.

3. THE DESIGN OF THE SELECTION EXPERIMENTS

Three samples of flies (C, D and F) were taken from the Kaduna population at different times. From each sample two selected lines were developed, one (R) by

mating selected parents at random, the other (A) having a positive correlation between mates with respect to bristle score. In the initial generation, flies were taken at random from the sample and mated at random. In the first generation of selection, care was taken to balance both the selection differentials and the contributions of the initial families to the two selected lines.

An even number of flies was therefore selected from each family and these were equally divided to form the parents of the two lines. In two sets of lines (C and D) selection was based on individual measurements and in the third (F) it was based on an index combining individual measurement and family average (Lush, 1948). The lines in this set had twice as many families as those in the other two sets because higher levels of inbreeding were expected.

The C set of individual selected lines was started some time after the sampling of the base population and after some slight inbreeding had occurred. This created a set in which heritability was lowered and in which the rate of response and the level at which response to selection ceased might be affected. The three sets of lines are summarized in Table 2.

Table 2

	Set		
	C	D	F
	Individual	Individual	
Basis for selection and mating	score	score	Index
Matings	10	10	20
Males and females scored per mating	10	10	10
Selection intensity	1/10	1/10	1/10
Inbreeding at start of selection	0·092	0	0

Within each set, there was one random and one assortatively mated line, in the C set labelled CR and CA, for example.

The six lines were all made up on the same day as individual matings in freshly prepared vials and full pedigrees were kept. Spare matings were kept so that enough families would be produced to keep the population size constant. Up to 30 matings in the individual selection lines and 50 in the index lines were needed for this. A successful mating was defined as one which produced 10 males and 10 females.

In the random mated lines, the main series of matings were made at random between the 10 selected males and females (20 in the F lines) and the flies chosen for the spare matings were then in their turn mated at random. There are thus two strata of parents. Any loss in the main series of matings thus entails, firstly, a reduction in the selection differential and secondly, the generation of a positive correlation between mates for those matings whose progeny were measured. Though the large numbers of spare matings were seldom all used, losses of half the main series were common in all lines after generation 10. This loss did not create a problem in assortatively mated lines, since both selected and spare flies were mated according to their rank in bristle score and those fertile matings with highest

parental score were taken. Loss of matings would, however, increase the observed correlation. In the index lines (F) the parents were selected on the basis of a combined index of individual scores and family mean. The weight given to the family mean relative to individual score was calculated by the method of Lush (1948) to give the maximum correlation between the breeding value of an individual and its index. The value of the weight, calculated from the data of Clayton *et al.* (1957), was 1·16. Since Dempster & Lerner (1947) have shown that the selection response is not sensitive to slight errors in the weighting factor, it was decided to use the operationally more convenient value of 1·0. With this heritability and family size, index selection with random mating should in theory (Lush, 1948) give a rate of response greater by about 8% than individual selection.

4. THE SELECTION RESULTS

(i) *The relationship between pairs of lines*

The technique of James & McBride (1958) was used to estimate the percentage of genes in each line at generation 4 from each mating in the initial generation. The results are shown in Table 3. After generation 4 the contribution of the initial families to the selected lines had become fairly stable.

Table 3. *The percentage of genes in each line at generation 4 derived from families in the initial generation*

C base families		1	2	3	4	5	6	7	8	9	10
Percentage genes,	A	0	0·6	0	0	45·0	11·3	13·8	6·9	0	22·5
	R	0	3·1	0	0	36·9	1·3	45·6	0	0	13·1
D base families		1	2	3	4	5	6	7	8	9	10
Percentage genes,	A	16·9	0	16·9	0	0	0	21·9	8·1	33·1	3·1
	R	20·6	0	15·6	16·9	0	0	29·4	0	0	17·5
F base families		1	2	3	4	5	6	7	8	9	10
Percentage genes,	A	0	0	0	1·6	1·6	0	0	45·3	50·0	1·6
	R	10·9	0	0	0	0	0	0	8·4	34·4	31·6
		11	12	13	14	15	16	17	18	19	20
Percentage genes,	A	0	0	0	0	0	0	0	0	0	0
	R	0	4·7	2·5	0·9	0	0	6·6	0	0	0

It will be recalled that, in the first generation of selection, the contribution of any family to the two lines of the set was made equal.

In both the sets with individual selection it will be seen that only about one-half of the initial matings made any permanent contribution to the line. In the index selected set, the proportion is even smaller. Out of the 20 initial families, only 5 made a permanent contribution in the A line and 7 in the R line.

From these figures, the average genetic relationship between individuals from the two different lines within a set can be calculated as 0·13, 0·06 and 0·11 respectively. These relationships obviously apply only to genes not affecting the character

under selection. At loci affecting the character, individuals from the different lines would probably be more alike genetically than the above relationships would suggest.

(ii) *Response to selection*

Figures 1 and 2 show the response to selection. All points shown are the average score of males and females. As the response is plotted against the cumulative selection differential, the slope of the curve is an estimate of the realized heritability and the expected slopes for the heritability of 0·52 found by Clayton *et al.* (1957) are
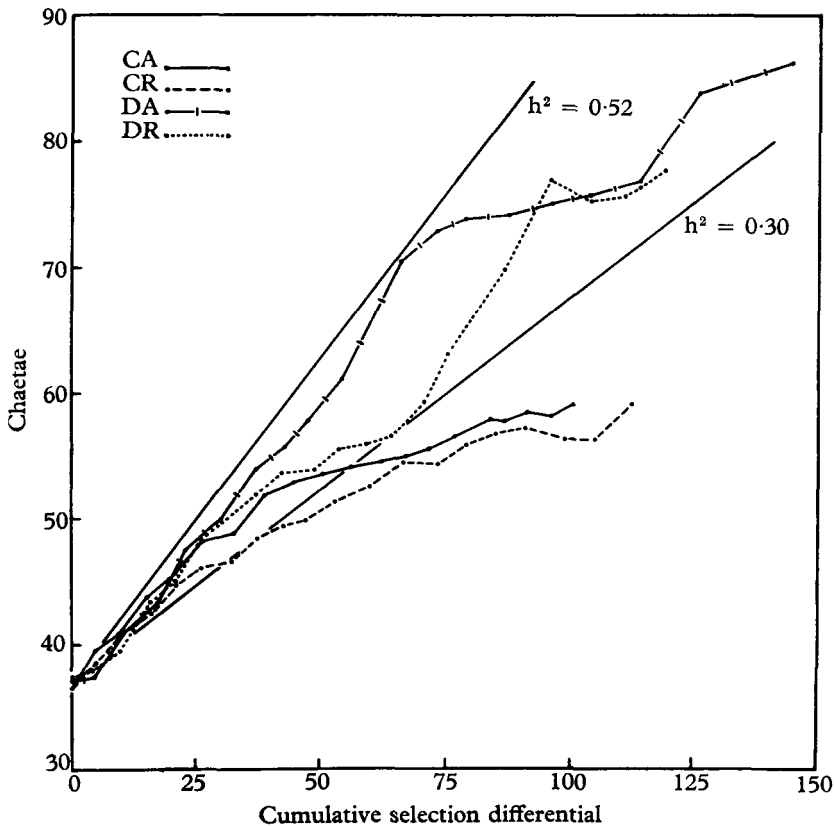
Fig. 1. The response to selection on individual score (A, assortative mating; R, random mating).

shown. The larger responses obtained in the D lines were due to the fixation of a major gene, *scabrous*, which will be referred to in more detail later.

In all sets, assortative mating led to a greater response to selection than did random mating (Fig. 3). In the earlier generations, the selection differential was greater in the assortative lines though in set C losses of extreme selected matings reduced the selection differential below that of the random line. The loss of matings, leading to a reduction of the selection differential, was low at first and increased in all lines.

Table 4 shows the correlation between mates in the separate lines. In the F series the correlations are given in terms of the individual's own measurement as well as its index value. The correlations between mates in the random lines caused by loss of matings can be seen in the later generations. Figure 4 shows the ratio of the scores of males to the scores of females. The largest changes in these ratios occurred in the
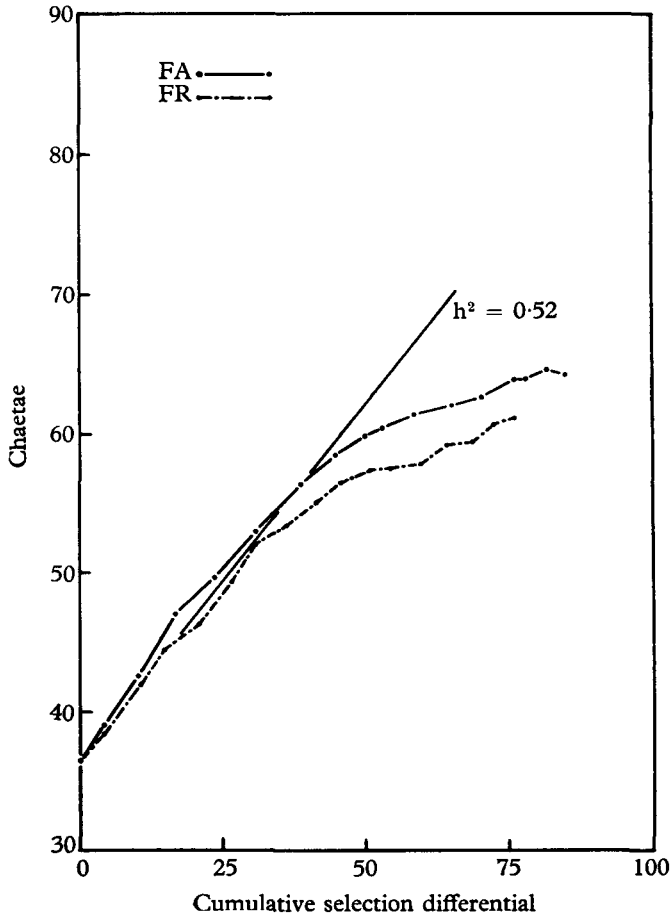

Fig. 2. The response to selection on an index including family mean. (A, assortative mating; R, random mating).

D lines and were due to the effect of the gene *scabrous*. However, smaller changes occurred in the ratio in all lines and these suggest differences between the lines in the genes selected, responsible for the high bristle number.

There is little doubt about the effect of assortative mating as compared with random mating. Since in theory the effectiveness of assortative mating should depend on the heritability of the basis of selection, it would be expected to be greater in the F lines.

This is obviously so from Fig. 3 although the D set comparison is later complicated by the effect of the scabrous gene. Again the D line difference should be greater than that in the C lines, because of the initial inbreeding in the latter. The observed effect is small but in the right direction in the early generations.
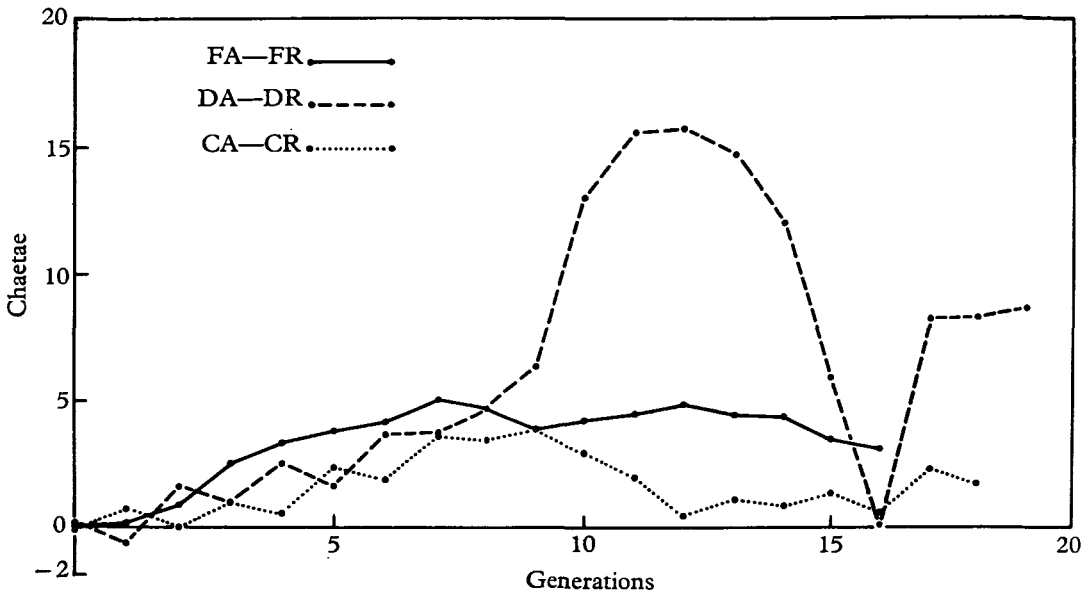

Fig. 3. The increase in response produced by assortative mating.

Table 4. *Mean correlation between mates*

Generation	CA	CR	DA	DR	FA	FR	FA	FR
					Individual score		Index	
0–3	0·89	0·03	0·09	−0·04	0·52	0·08	0·87	0·13
4–7	0·85	0·06	0·78	0·12	0·38	−0·02	0·92	0·18
8–11	0·95	0·44	0·77	0·29	0·60	0·01	0·97	−0·21
12–15	0·88	0·38	0·84	0·61	0·61	0·16	0·97	0·44
16–18	0·93	0·20	0·95	0·68				

(iii) *Variances of selected lines*

Analyses of variance were made within each generation in each line. Figure 5 shows the between-family and phenotypic variances in the six lines. The pooled within generation full-sib correlations are shown in Table 5.

As would be expected from Table 1, the between-family component tends to be greater in the assortatively mated lines. But the full-sib correlations are not significantly greater, as the phenotypic variance has increased almost in the same

proportion. But in fact the situation is vastly different in the two cases. Table 1 refers to assortative mating of the whole population whereas we are here discussing the progeny of a highly selected group, in which the parental variance has already been reduced to about one-fifth of the population value. The considerable increase in variance in the later generations of the D line is due to the segregation of scabrous.
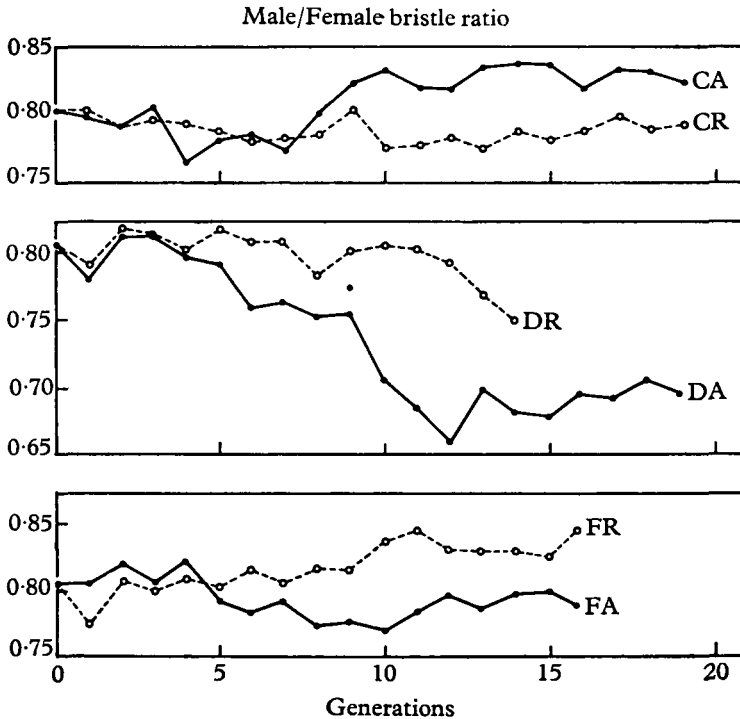

Fig. 4. The ratio of male score to female score.

(iv) *Inbreeding*

The method of Emik & Terrill (1949) was used to compute inbreeding coefficients (F) for all families in all generations. The average values are shown in Fig. 6 (lower). The upper graph shows $\log(1-F)$, since the transformed data should be linear if the effective population size remains constant. For comparison, the expected inbreeding curves for effective population sizes of 5 and 10 pairs of parents are shown. The rapid initial rise in CR was caused by a family in generation 1 with a mean score 5 bristles above the line mean. This family contributed 10 out of the 20 flies selected in this generation and caused a high rate of inbreeding for several generations. CR thus had a higher rate of inbreeding than CA although, in the other sets, the assortative lines were higher.

The decrease of $\log(1-F)$ with time was significantly non-linear only in lines FA and CR. The effective population size averaged 7·4 pairs of parents in the
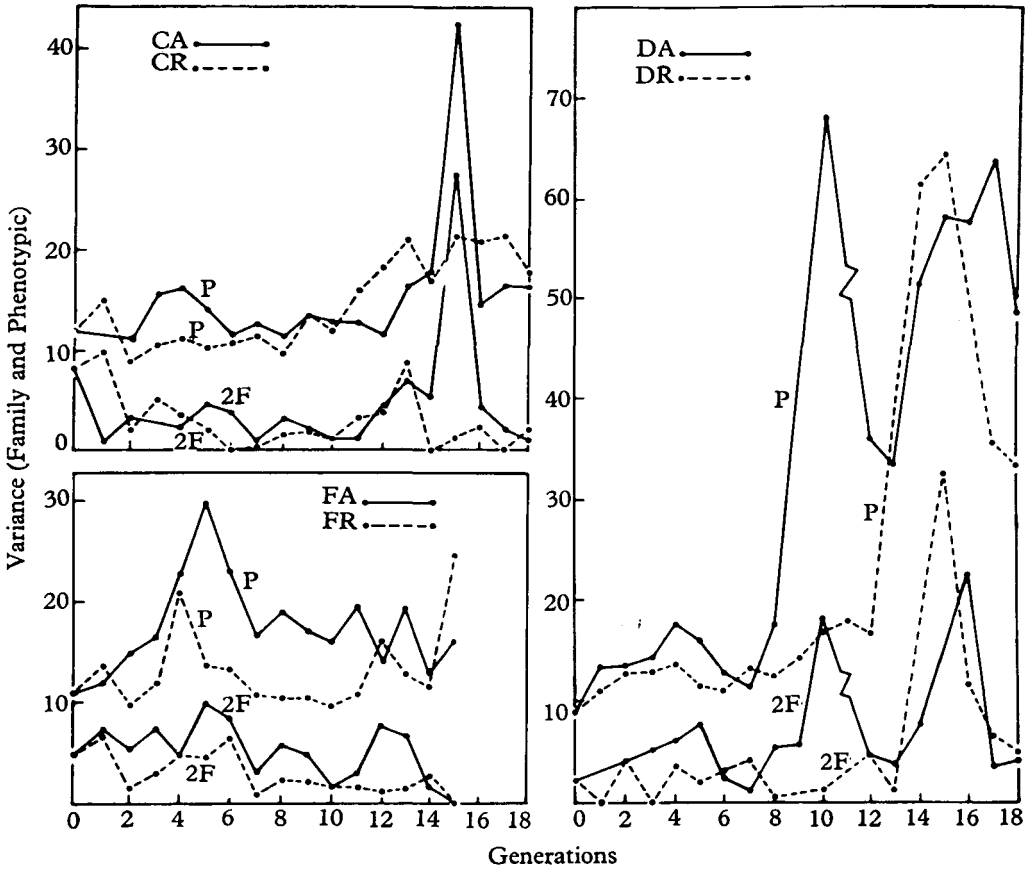
Fig. 5. The phenotypic (P) and family (F) variances in the selected lines. For clarity,
the family variance is plotted as $2F$.

Table 5. *Full-sib correlations*

	Generations 1–8	8 to end
CA	$0\cdot123 \pm 0\cdot031$[1]	$0\cdot104 \pm 0\cdot029$
CR	$0\cdot160 \pm 0\cdot040$	$0\cdot068 \pm 0\cdot019$
DA	$0\cdot140 \pm 0\cdot035$	Not computed because of scabrous gene
DR	$0\cdot086 \pm 0\cdot024$	,, ,, ,, ,, ,, ,,
FA	$0\cdot172 \pm 0\cdot033$[2]	$0\cdot111 \pm 0\cdot02$
FR	$0\cdot145 \pm 0\cdot028$[3]	$0\cdot068 \pm 0\cdot018$[4]

Pooled within generation estimates of full-sib correlations:

(1) Generations 15 and 17 omitted.
(2) Generation 5 omitted.
(3) Generation 4 omitted.
(4) Generation 15 omitted.

(Generations omitted from analysis on ground of non-orthogonality or abnormal variances
or both.)

individual selected lines compared with the actual number of 10, and 7·0 pairs in the index selected lines compared with the actual number 20. Here we see the expected reduction in effective population size below the actual size due to selection and the proportionately greater reduction with index selection.
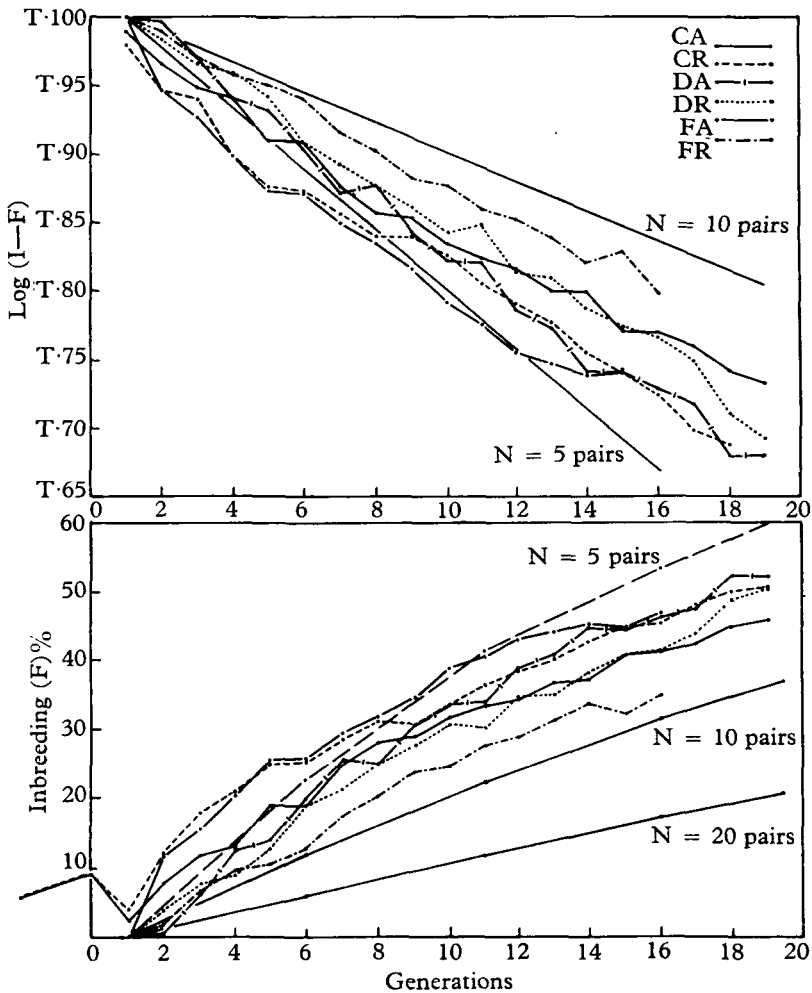

Fig. 6. Inbreeding in the selected lines, showing the expectations for different effective population sizes N.

If, as postulated, the selection is effective in increasing the level of inbreeding, this should be further reflected in an association between the level of inbreeding in a family and its mean bristle score. As Morley (1954) pointed out, the families in the parental generation with the highest score will tend to have the greatest representation amongst selected animals and thus an individual in a high family will have a greater chance of being mated to a relative than will a member of a low scoring family. As a consequence, the progeny families with the highest mean performance

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will tend to have the highest level of inbreeding. The correlations between family mean score and inbreeding coefficients were calculated within lines and generations. Of the 100 correlations obtained, 73 were positive—a significant deviation from a correlation of zero. Two other associated phenomena have been noted. When high positive correlations have been found, there is generally a drop in the rate of inbreeding in the next generation and a large drop in the selection differential, both presumably due to the lower vigour of the more highly inbred high-scoring families.

(v) *The gene scabrous*

The high selection differentials and rates of response in DA from generations 8 to 11 in DR from generations 12 to 16 were the result of the appearance and fixation of a recessive gene *scabrous*. Although the gene was not identified by crossing it to known *scabrous* stocks, its phenotype and map location fit exactly the published description of the gene. In view of the large effect that it was found to have in the selected line, its relative effect in different backgrounds was examined. The F_1 flies were crossed to the selected line and the wild-type flies were then re-crossed to it again to give two segregations in a relatively high background. An F_2 was made

Table 6. *Results of crosses between line DA, carrying the gene 'scabrous', and the Kaduna population*

	Wild type				Scabrous				Difference in Mean
	♂	♀	Mean	♂/♀ ratio	♂	♀	Mean	♂/♀ ratio	
F_1	47·2	60·1	53·7	0·785		None			
F_2	45·8	62·2	54·0	0·736	58·8	87·6	73·2	0·671	19·2
Kaduna backcross 1 F_2	41·2	50·7	45·9	0·813	51·9	71·9	61·9	0·723	16·0
Kaduna backcross 2 F_2	35·6	48·1	41·8	0·740	51·5	73·6	62·5	0·700	20·7
DA backcross 1	49·5	61·4	55·4	0·806	59·5	88·1	73·8	0·675	18·4
DA backcross 2	51·4	66·1	58·7	0·778	68·2	97·7	82·9	0·698	24·2

and the scabrous flies from this were mated to the Kaduna population. A second intercross was made and *scabrous* flies again mated to Kaduna flies. We thus have measures of the effect of the gene in five different backgrounds and these results are shown in Table 6. Two obvious points should be noted. Firstly, the background genotype does not greatly influence the effect of *scabrous* on score. Thus the effect of the segregation does not appear to have been magnified during selection. The second point of interest is the change in the male-to-female score ratio. This is normally about 0·8 but in scabrous it is about 0·7.

Clayton (personal communication) found *scabrous* phenotypes in one of his lines selected for sternital bristles from the same base population. However, he found it impossible to make his stocks homozygous for the gene and the segregation was maintained. It seems probable that the gene is present at a low frequency in the

base population. A point of interest then arises as to why the gene was not observed in these selected lines until after approximately 10 generations of selection. The results of backcrossing would suggest that this was not due to the gene having a small effect in the background of the base population. Perhaps the most probable explanation is that the gene was present at a very low frequency in the initial sample from which the D lines were taken and that it has only a very small effect on bristles in the heterozygotes.

5. DISCUSSION

The results of these experiments are more or less in line with expectation. Quite clearly the use of assortative mating led to an increase in the rate of response in the early generations, and a detailed analysis showed that this was due to an increase in the genetic variance available to selection and to an increase in the selection differential. Analyses of variance of the three sets of lines in the first eight generations of selection showed that of the 24 comparisons of genetic variance, 18 showed a higher value in the lines with assortative mating. It had been suggested that the use of assortative mating might lead to a higher degree of inbreeding and might therefore reduce the total advance under selection. In fact, measurements of the rate of inbreeding show that although this tended to be slightly higher in the assortative mating lines, it was not significantly so, and the total advance under selection was, if anything, slightly higher in the assortative mating lines.

This is one of the first experiments in which selection in Drosophila has been carried out with detailed pedigrees and with a large population size. It therefore provides, for the first time, factual evidence that the effective population size in a selection programme based on the individual's own phenotype may be much less than the actual population size, even though care is taken to breed from the same number of pairs of parents each generation. This decrease is roughly in agreement with expectation (Robertson, 1961).

In many generations the selection differential achieved did not reach that expected. This is largely a consequence of producing a constant number of families each generation and using families from reserve matings of inferior means when selected matings failed. Within each generation the matings which failed had a higher coefficient of inbreeding than those which succeeded in reproducing. However, the means of the main series of matings which failed did not differ significantly in bristle score within generations from the means of those which succeeded.

Perhaps the main consequence of this work lies in the fact that in assortative mating we have a new aid to selection which has its maximum value when the heritability is high, in distinction to aids such as progeny and family selection, which are more effective when the heritability is low. On the other hand, the results do emphasize the danger that intense selection applied to a character with higher heritability may lead to a considerable reduction in the effective population size below expectation and therefore to a rate of inbreeding higher than expected. This is particularly true if selection is at all based on family means. The effective

population size in the two index selected lines was almost as low as one-third of the actual population size.

Some evidence on the effectiveness of selection on an index of individual and weighted family mean performance was also obtained. In the random mating comparison (FR and DR) index selection gave an 11% increase in response in the first 5 generations compared with an expected increase of 8%.

One interesting feature of these experiments is that the differences between the lines in the various comparisons did not increase after the first 6 to 9 generations. This may have been due to higher rates of inbreeding in the superior lines though, if so, this was not reflected in any tendency to show a lower selection limit.

6. SUMMARY

The effectiveness of the assortative mating of selected individuals in increasing selection response was tested, using abdominal chaeta score in *Drosophila melanogaster*. Three paired comparisons were made. In two sets of lines with 10 matings per line, individual score was used for selection and as the basis for the assortative mating. In the third set with 20 matings per line an index of individual and family score, designed to maximize rate of response, was used.

The intensity of selection was one in ten in all lines. Flies were raised in vials and individual pedigrees were kept.

In all comparisons, assortative mating gave a greater selection response, this being partly due to a greater realized heritability and partly to a greater selection differential. The effect of the assortative mating was largest in the index selected lines. With random mating, the effectiveness of the index selection itself when compared to individual selection was in accordance with theory.

In two comparisons, assortative mating increased the rate of inbreeding. The highest rate of inbreeding was observed with index selection and assortative mating, even though there were here twice as many matings as in the individually selected lines.

In the individual selection lines, the effective population size was 7·4 pairs of parents, compared to the actual value of 10 and in the index lines 7·0 compared to 20. In the former, only one-half of the matings in the initial generations made any permanent contributions to the line and in the index lines only one-third. Within generations and lines, there was a significant positive correlation between the mean score of a family and its inbreeding coefficient.

It is suggested that assortative mating is a method of increasing selection response in some situations. Its particular characteristic is that it becomes more powerful when the heritability is high whereas all of the other environmental aids to individual selection are more effective when the heritability is low.

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