A COMPARISON OF PUREBRED AND CROSSBRED SELECTION SCHEMES WITH TWO POPULATIONS OF DROSOPHILA PSEUDOOBSCURA[1]

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THE methods of selection for changing the values of quantitative characters may be classified into two broad categories. One group includes a variety of methods which are aimed at changing individual population performance at the expense of additive genetic variance within the populations. Some familiar methods in this category are mass selection and family selection. Individuals or families are selected on the basis of their own performance for the propagation of the population, and they are never outcrossed with members of other populations. Therefore, this category of selection will be termed *purebred selection.*

The other category includes the methods of selection which are designed to improve hybrid or crossbred performances of lines or populations. The members of populations or lines are crossed to members of other lines or populations (testers). and are selected on the basis of the performance of their hybrid progenies. In the case of continued selection these are remated with members of their own population for the maintenance of genotypic superiority with respect to the testers. These types of selection will be called *crossbred selection.* The genetic variation utilized by crossbred selection is the genetic variance associated with members of the parent population in combination with tester genotypes.

In the present study responses in two purebred selection programs from two separate base populations are compared with responses in a crossbred selection program in which the same two populations are used as the testers and the tested reciprocally. The relative effectiveness of the two types of selection will be discussed, and the information from the present study will be compared with that from similar studies in Drosophila conducted by other investigators.

BASE POPULATIONS

The base populations used are two cage populations, called "*Mather*" and "*Mono*," of *Drosophila pseudoobscura. Mather* and *Mono* refer to two separate locations around Yosemite National Park, where the progenitors of the respective populations were collected by DR. TH. DOBZHANSKY and his co-workers. Each

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population cage was made by mixing a number of strains obtained from the respective locations, considerably prior to the start of the selection experiments (at least 20 generations), and had been maintained by standard procedures in the laboratory conditions of 19°C and high relative humidity.

The character studied is egg production. The daily egg counts per female (averaged over three days, the 12th through the 14th day of adult age) are presented in Table 1. AA and BB stand for *Mather* and *Mono*, and AB and BA for progenies from *Mather* male × *Mono* female and those from *Mono* male × *Mather* female, respectively. The figures in this table are pooled values of several separate tests. It was noted that egg production was very sensitive to rearing and testing, suggesting the necessity of unified techniques and experimental designs.

The magnitude of additive genetic variances in the base populations and their hybrids was studied by the use of full-sib and half-sib relationships. The preliminary results indicated that the additive genetic variance was very low in both base populations; the estimates from several separate tests being distributed near zero with some negative estimates. In the hybrid population the estimates were higher than in the base populations, giving, on the average, an estimate of 18.8 ± 18.1 for the crossbred additive genetic variance and of 166.6 for the total phenotypic variance from replicated tests.

EXPERIMENTAL PROCEDURES

(1) *Culture methods:* The base populations maintained in plastic cages are fed twice a week by inserting cups (one-and-a-half inches diameter × two inches deep) containing cream of wheat medium into the holes at the bottom of cages. Experimental samples are taken by inserting cups with fresh medium, removing them after two days, and transferring the surface part of the medium with a large number of eggs and larva into regular culture bottles. The culture bottles (one-half pint milk bottles) contain approximately one-eighth to one-sixth pints of fresh medium with a drop of water suspension of dry yeast. One-inch diameter vials are used for the purpose of holding, aging and mating adult flies.

To make half- and full-sib families, individual males are placed with a group of virgin females in separate vials for a period of three days. The impregnated females are then transferred individually into separate culture bottles. Thus, full-sib families are always reared in single bottles.

(2) *Egg count procedure:* During the period of peak emergence of experimental flies, all bottles are cleared of adults which emerged prior to this time. Forty-eight hours later, all new adults in a culture bottle are aspirated by air pump into a

TABLE 1

Daily egg counts of base populations and their hybrids (per female per day for the period of 12–14 day adult age

AA	BB	AB	BA
41.68	39.18	41.54	40.83

vial with fresh medium, where they are aged, males and females together, for five days. The flies are then etherized, sexed under dissecting microscopes, and the females, impregnated by this time, are placed in a vial with fresh medium. On the tenth day from the collection of adults from culture bottles, females are aspirated into empty one-half pint milk bottles (test bottles), three females per bottle.

The test bottles are plugged by paper caps (commercial milk bottle stoppers), a thin layer of two percent agar medium containing charcoal powder and molasses having been spread on the inside of each cap. The medium on caps is sprayed with water suspension of dry yeast immediately before they are used. The capped bottles are placed in wooden boxes upside down, and eggs are laid on the caps.

The caps are replaced daily with new ones for a period of five days. In the present study three-day averages or four-day averages are used for the evaluation of test bottle performance. For three-day counts the caps from the first two days are discarded, and only those from the last three days are counted. For four-day counts only the first day caps are discarded. This period of counting represents the first peak egg production time after eclosion for the present material.

(3) *Breeding schemes:* (a) FFS: The scheme used for purebred selection is a type of full-sib family selection, and it will be abbreviated by FFS in this paper. The flow diagram of the FFS scheme is given in Figure 1. *Mather* (AA) and *Mono* (BB) are the two separate selection lines, each selected in the same manner and tested simultaneously in each cycle of selection.

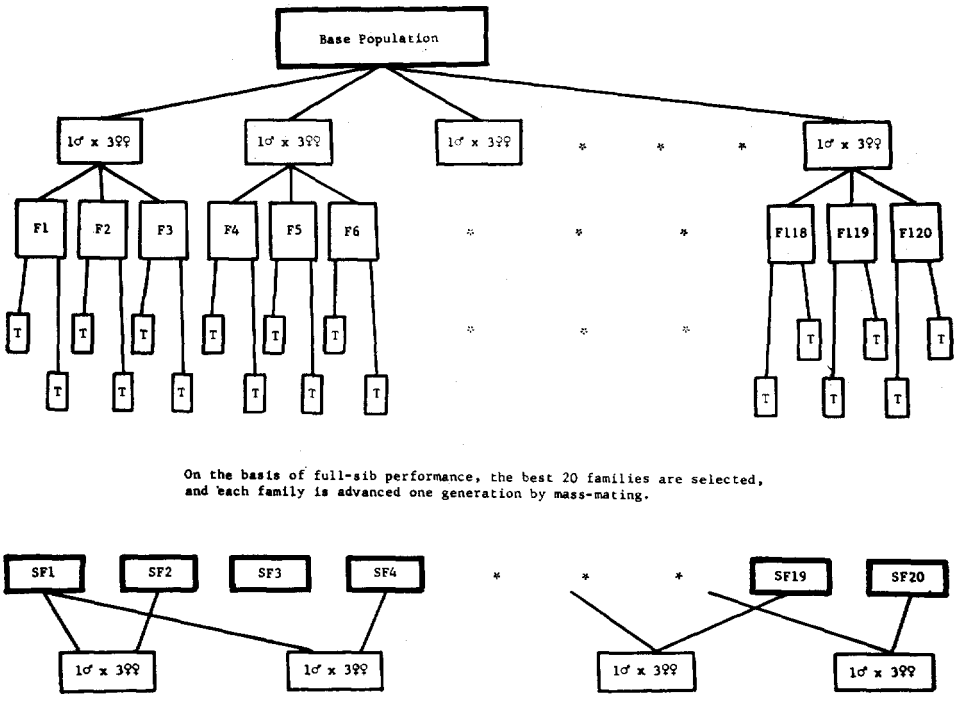

FIGURE 1.—Full-sib family selection (FFS) scheme.

At the outset of the selection experiment a sample of 40 males and 120 virgin females is taken at random from the cage population. Each of the 40 males is mated with three females, and then individual females are transferred into separate culture bottles. The offspring from each female bottle make up a full-sib family, giving a total of 120 full-sib families.

From each full-sib family six females are tested in two test bottles. Thus the egg count test in each cycle of selection includes 240 test bottles for each selection line. There are 480 test bottles for the two selection lines of AA and BB, and they are randomized together with 72 control bottles. An egg count test in each cycle consists, therefore, of two lines (AA and BB), 40 paternal half-sib families for each line, three full-sib families per half-sib, two test bottles per full-sib, and three females per test bottle, plus 72 bottles, each with three females, of control material.

On the basis of full-sib averages, the 20 families with the highest egg production are determined, and their full-sibs which emerged after the collection of test flies are selected. From each selected family about 30 sib-mated females are randomly taken and transferred into three mass culture bottles. In Figure 1, three bottles of mass culture for each family are denoted by single heavy boxes marked as SF 1, SF 2, . . ., SF 20.

When the progenies of the mass culture start to emerge, a few males and several virgin females are collected from each bottle. Out of these flies, two females from each of three bottles for each of the 20 selected families are used as the female parents of 120 families in the next cycle of selection. From the male collection from each family (usually numbering ten to 12 males), two males are randomly chosen from each selected family and these 40 males are used as the male parents of 40 half-sib families.

The pedigree of every family is kept and the inbreeding coefficients of all possible crosses are computed at each cycle before actual crosses are made. On the basis of this information, the actual crosses to be made among the selected families are determined by considering the following two points:

(i) It is desirable that the mean inbreeding of each line increases at a minimum rate over the cycles of selection.

(ii) The variation among the degrees of inbreeding of families tested in each cycle should be small, so that inbreeding depression can be ignored in the comparison of family means in a given cycle.

The optimum requirements for the two conditions contradict one another in part, particularly in the long run. Hence moderate compromise is made between the two conditions in actual crosses.

(b) RRS: The scheme employed for crossbred selection is a form of reciprocal recurrent selection which was proposed by COMSTOCK, ROBINSON and HARVEY (1949). This scheme will be denoted by RRS in this paper. The flow diagram of RRS is given in Figure 2. A and B in the diagram stand for a pair of base populations required for RRS.

A random sample of 60 males and 300 virgin females is obtained from each of *Mather* (AA) and *Mono* (BB) cages. Each of 60 males of AA is mated to two

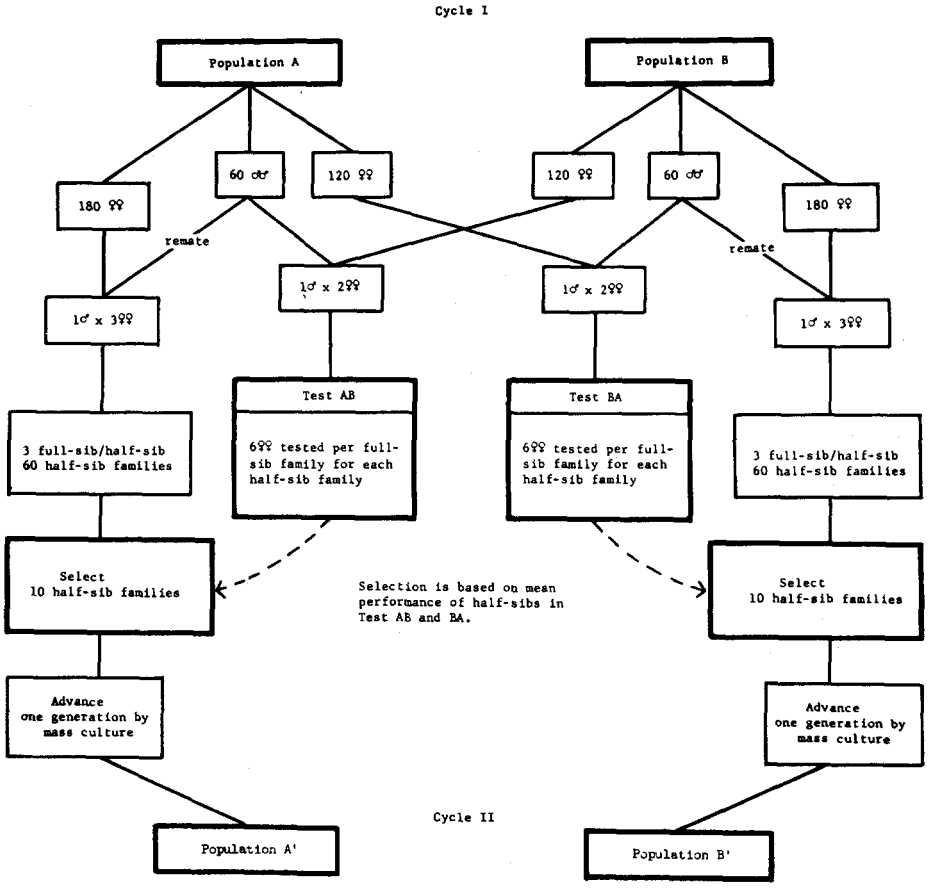

FIGURE 2.—Reciprocal recurrent selection (RRS) scheme.

females taken at random from BB. These 60 matings are called *test cross* AB. Three days later each female is transferred into single bottle cultures, and each male is remated to three virgin females from AA. The cross of these rematings is called *cycle cross* AA, which will provide individuals for the next cycle: Each female of the cycle cross is transferred into single bottle cultures. Reciprocally, test cross BA and cycle cross BB are made by the same procedure at the same time as AB and AA.

From each full-sib family in AB and BA, six females are tested in two test bottles. The entire test of one cycle is constituted by the two reciprocal test crosses, 60 half-sib families per test cross, two full-sib families per half-sib family, and two test bottles per full-sib family, and three females per bottle, plus 72 control bottles.

From the results of egg counts the ten AB and ten BA half-sib families with the highest egg production are determined. Their half-sibs in cycle crosses, i.e., 30 AA and 30 BB full-sib families, are selected for the next cycle of selection.

In RRS there was a change in the procedure for advancing selected material in one cycle to the next. From Cycle I to Cycle IV, two males and ten virgin females were taken from each selected full-sib family, giving 60 males and 300 females in total. Of the total, 120 females, four from each full-sib family, were used for test crosses, and the rest of the 180 females served as cycle cross parents of the next cycle.

This procedure was found to be difficult to follow, since males and virgin females had to be kept in all full-sib families of both cycle crosses until egg counts of test crosses were finished. Another reason that made the change in the procedure necessary was the observation that the fertility (expressed as percentages of fertile matings in test and cycle crosses) tended to decrease from 95 percent to 80 percent.

The selected cycle cross families of Cycle V were placed individually into mass culture for a period of four generations. During this period approximately 15 percent gain in fertility was observed.

The modified procedure employed after the resumption of selection is as follows. Each selected full-sib family in the cycle cross is made into mass culture for one generation, allowing intra-family recombination as in the case of FFS. This modification prolongs the time required for one cycle of selection from 55 days to 85 days. However, there has not been any substantial reduction in fertility under the new system.

(c) Control: The material for control is made up of F_1 hybrid females from nine inbred lines. Prior to selection studies, a large number of inbred lines were derived from several different locality populations by approximately 20 generations of brother-sister mating. After a series of testing for the desirability for control material (see KOJIMA and KELLEHER, in press, for the types of desirability), nine inbred lines, three lines from each of *Mather*, *Mono* and *Bryce* locality populations, were chosen and duplicated. One set was carried with FFS, and the other with RRS. Thus, the two selection experiments were to have identical control, apart from possible divergence within inbreds.

For every test, a particular line of one locality is crossed with two particular lines from the two other localities. Such a scheme produces nine different F_1's. Their reciprocal crosses are also made, giving a total of 18 crosses. Each cross is made in duplicate culture bottles, each with one male and two virgin females. From each cross, 12 F_1 females, six from each culture bottle whenever possible, are sampled, making four test bottles for each cross and 72 test bottles in all for the control.

RESULTS

(1) *Direct response to FFS:* The responses to FFS in mean egg counts are shown for the period of 13 cycles of selection in Figure 3. The ordinate is given in terms of mean numbers of eggs per female per day, and the abscissa represents the cycles of selection. The solid, broken and dotted lines are for *Mather* (AA), *Mono* (BB) and control (C), respectively. The rather distinct difference of the mean levels between the first half and the last half of the cycles is mainly due

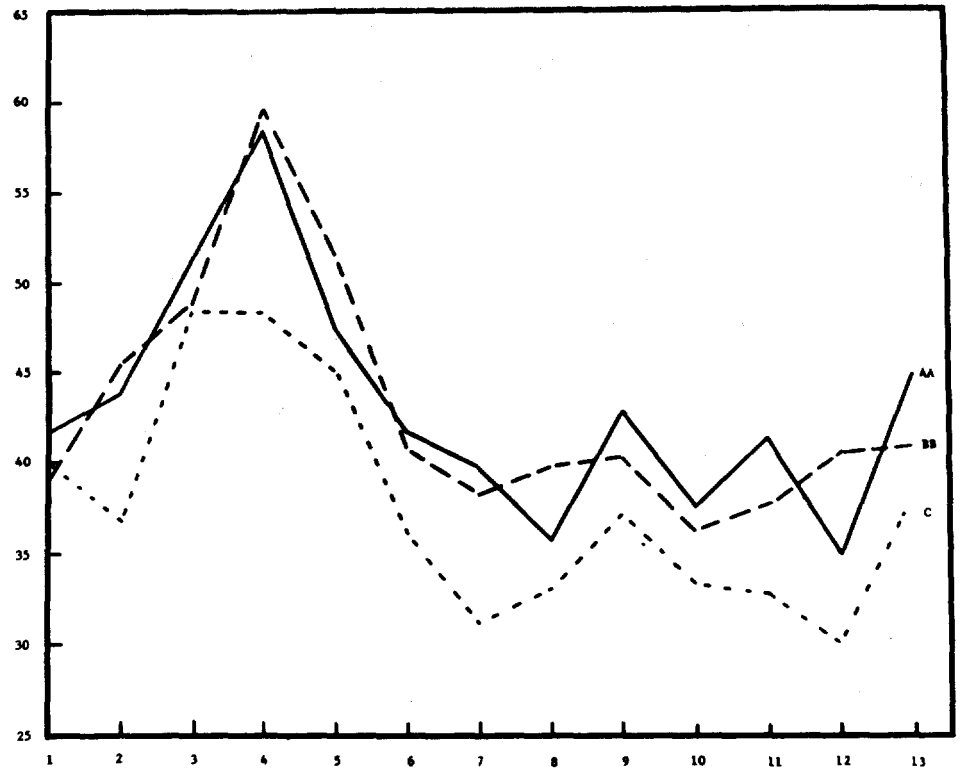

FIGURE 3.—Observed performance in FFS for *Mather* (solid line), and *Mono* (broken line). The dotted line is for control performance. Ordinate: Number of eggs per day per female. Abscissa: Cycles of selection.

to the difference in the mean number of eggs on a three-day count from that on a four-day count. The mean number of eggs on the first day of the four-day period is about 17 eggs per female, while the means of the last three days' counts is approximately 47 eggs per female per day. Hence, the means for the first six cycles (I–VI) have to be reduced by 7.5, i.e., (47–17)/4, in order to compare them with the means of the last seven cycles.

The trend of responses to selection may be seen more readily in Figure 4, in which the adjusted numbers of eggs (Y) are plotted against the accumulated selection differential at each cycle of selection. The adjustment is given by $Y_j = Y_{j-1} + (T_j - C_j) - (T_{j-1} - C_{j-1})$, where Y, T, and C stand for the adjusted means, raw test means and control means, and the subscript (j) designates the cycle of selection. $Y_1 = T_1$ is used for the first cycle. The accumulated selection differential for the jth cycle is equal to $\sum_{i=1}^{j} (T_{si} - T_i)$, where T_{si} is the mean egg count of the selected families in the ith cycle. The slope expressed by the regression value of Y's on the corresponding accumulated selection differentials is an estimate of average heritability over the 13 cycles in each of the FFS lines. The

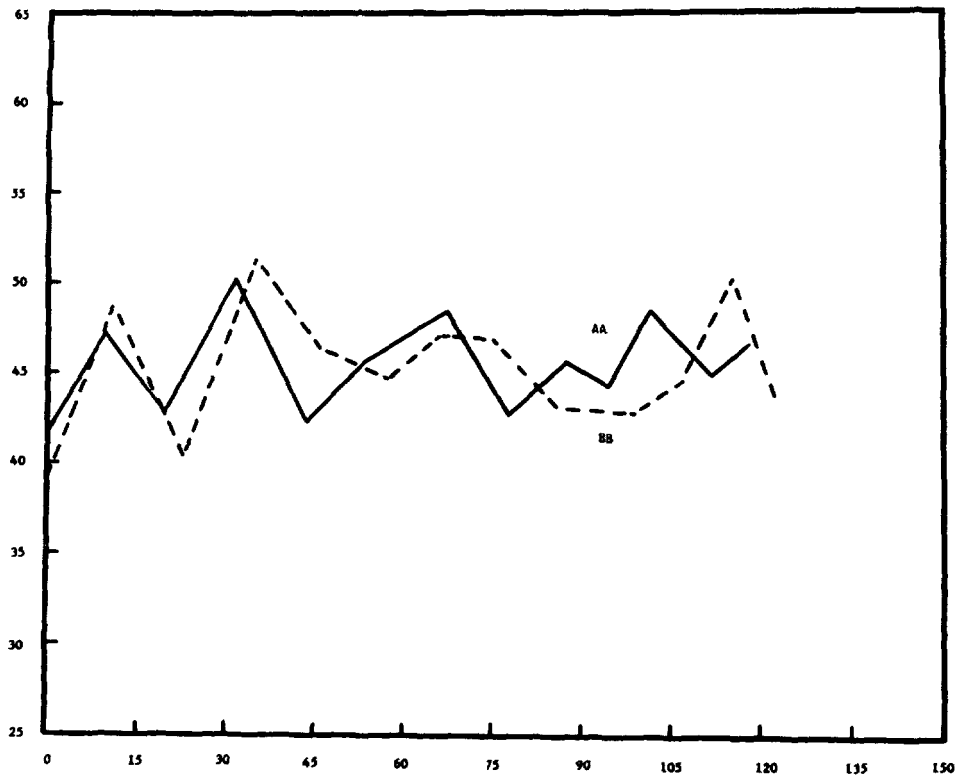

FIGURE 4.—Cumulative responses to FFS, adjusted for control values, in *Mather* (solid line) and *Mono* (broken line). Ordinate: Number of eggs per day per female. Abscissa: Cumulative selection differentials.

estimates of the slopes are 0.01 ± 0.02 and 0.02 ± 0.03 for *Mather* (solid line) and *Mono* (broken line) lines, respectively.

Since there might have been a reduction in egg counts due to inbreeding depression as generations advanced, experiments were set up to estimate such a depression effect. A combined estimate obtained from these experiments is a depression of 1.5 eggs per 0.10 increase in the inbreeding coefficient, F.

The average values of F for the *Mather* and *Mono* families tested in each cycle are given in Table 2. The maximum and minimum values in Table 2 stand for the F values of the families with the highest and lowest inbreeding values at each cycle. They show that the F values are close enough for various families tested simultaneously so that the family-to-family comparisons of egg production in each cycle can be made without serious biases due to differential inbreeding depressions. The second point to be observed is that the average of F values increases almost linearly as selection advances from the third to the 13th cycle, giving an average increase of 1.5 percent cycle. Thus, the trend of improvement in egg production given in Figure 4 can be corrected linearly by the information on inbreeding depression. The new slopes are 0.03 for *Mather* and 0.04 for *Mono*.

TABLE 2

Mean, maximum, and minimum inbreeding coefficients of 13 cycles in two lines of FFS

	Cycles	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII
	Min.	0	0	0	0	.016	.028	.042	.073	.088	.102	.113	.138	.140
AA	Mean	0	0	.003	.020	.045	.066	.070	.092	.106	.129	.132	.148	.153
	Max.	0	0	.063	.078	.102	.113	.098	.107	.125	.162	.151	.157	.163
	Min.	0	0	0	0	.006	.035	.048	.078	.085	.105	.119	.136	.157
BB	Mean	0	0	.007	.033	.038	.060	.077	.096	.106	.122	.140	.149	.165
	Max.	0	0	.063	.094	.127	.108	.132	.112	.142	.167	.173	.159	.174

At the same time, the averages of half-sib covariances (male components of variance) estimated from the analyses of variances of each cycle test are -2.16 ± 5.43 and -4.40 ± 5.24 for *Mather* and *Mono* lines, respectively. Both of these estimates suggest that their true values are probably close to zero, and it is unlikely that the genetic variances are large enough to allow the lines to respond to selection effectively. The average magnitude of the total variance among full-sib family means is about 55 in both *Mather* and *Mono* lines.

In conclusion, purebred selection such as FFS did not provide an effective means for the improvement of egg production in these two populations.

(2) *Direct response to RRS:* The unadjusted responses in test crosses, AB and BA, for 16 cycles of selection are presented in Figure 5. The solid, broken and dotted lines are for AB, BA, and control (C), respectively. Some discontinuity in control occurs at the early stage because of incomplete sets of control crosses. At two successive cycles of such cases, only those crosses grown in both cycles were used for comparison. During the period of Cycles VI through X, egg counts were made on three days, and this resulted in an upward shift of means as in the case of FFS. Four-day counts were used in all other cycles. The means of the reciprocal tests are, on the average, equal. The progress due to selection is indicated by the divergence between the test and control egg counts.

Figure 6 presents the average performance of the reciprocals adjusted for the control performance in the same manner as in the case of FFS. The response to selection is approximately linear to the 11th cycle. This part of response was previously reported by KOJIMA and KELLEHER (in press). Then positive response ceases rather suddenly, and the performance seems to be maintained at a plateaued level for the remaining cycles. The slope of the linear response for the first ten cycles is 0.16 ± 0.03 in Figure 6.

In order to estimate the heritability corresponding to this slope, the male components of variance and the variance among half-sib means were estimated for each cross in each cycle. The balance sheet of variation for test cross AB in Cycle I is given in Table 3 as an example of such analyses. The identification of symbols used is found at the bottom of the table. The statistical effects are all considered as random variables in the present analysis. The interactions of *male* × *day* or *female* × *day* actually represent the variations due to differential egg productions of half-sib families and full-sib families over days of egg counts.

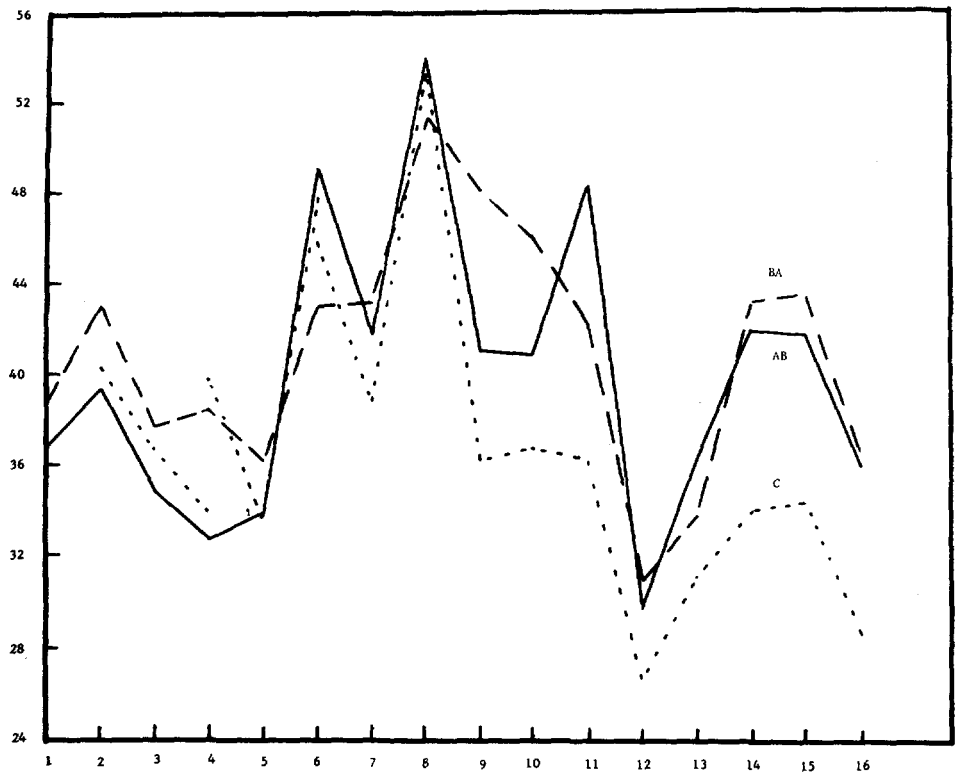

FIGURE 5.—Observed performance in RRS for *Mather* × *Mono*, AB (solid line), and *Mono* × *Mather*, BA (broken line). The dotted line is control performance. Ordinate: Number of eggs per day per female. Abscissa: Cycles of selection.

The type of data shown in Table 3 can be pooled over the cycles of selection in order to obtain average estimates. Pooling the analyses of the first ten cycles, the components necessary for the heritability estimate are

$$\sigma^2_{m1} = 8.64 \pm 5.49 \text{ and } \sigma^2_{m_2} = 3.67 \pm 9.36$$

$$\sigma^2_{F1} = 48.30 \pm 5.67 \text{ and } \sigma^2_{F2} = 44.58 \pm 9.15$$

where Subscripts 1 and 2 stand for test crosses, AB and BA, respectively. Thus, the heritability equivalent to the slope of the response in Figure 6 is given by

$$H = (\tfrac{1}{2})\ (\sigma^2_{m1} / \sigma^2_{F1}) + (\tfrac{1}{2})\ (\sigma^2_{m_2} / \sigma^2_{F2}) \doteq 0.13$$

The value of H is not too far from the estimate of the slope, and the difference is approximately of the order of one standard error of the estimate.

After the response ceased, the estimates of male component of variance drop to -0.07 ± 5.51 and 0.59 ± 2.74 for test crosses, AB and BA, respectively. Hence it is likely that the plateau attained by the RRS program represents a genetic limit for the present system.

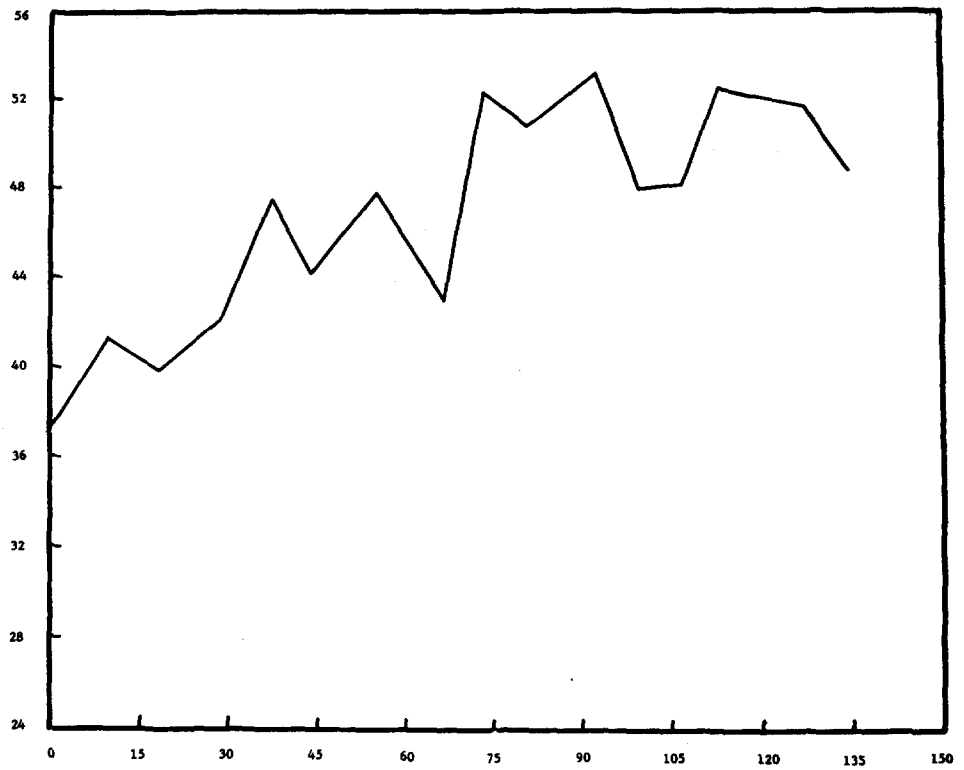

FIGURE 6.—Cumulative responses to RRS, adjusted for control values. Reciprocal crosses, AB and BA, are averaged for each cycle of selection. When compared with Figure 4, note the difference of scaling. Ordinate: Number of eggs per day per female. Abscissa: Cumulative selection differential.

TABLE 3

The components of variance in test cross AB *at Cycle* I, RRS

$$\sigma^2_m = 14.46 \qquad \sigma^2_f = 5.95$$
$$\sigma^2_{md} = 19.04 \qquad \sigma^2_{fd} = 125.67$$
$$\sigma^2_r = 197.80$$
$$\sigma^2_F = \sigma^2_m + \sigma^2_{md/d} + \sigma^2_{f/f} + \sigma^2_{fd/fd} + \sigma^2_{r/fdr} = 50.26$$

σ^2_m: due to variation among male parents

σ^2_f: due to variation among female parents mated to the same male

σ^2_{md}: due to male × day interactions

σ^2_{fd}: due to female × day interactions

σ^2_r: due to residual variations

σ^2_F: variance among half-sib family means; d=no. of egg-count days, f=no. of female parents per male parent, and r=no. of test bottles per full-sib.

(3) *Comparisons with single cross performance:* The total responses obtained by cyclic selection may be evaluated by comparing them with performances of F_1 hybrids (single cross progenies) made by crossing inbred lines derived from the base populations. A group of 12 inbred lines were chosen at random from each of *Mather* and *Mono* inbred stocks for this purpose.

Twelve lines in each group were randomly divided into three subgroups of four lines, and a given subgroup of *Mather* was matched with a given *Mono* subgroup. Within matches, each line of *Mather* was crossed to all four lines of *Mono*, and *vice versa*. Thus, one subgroup provided a set of 16 single crosses and their reciprocal crosses. Over three subgroups then there were 48 single crosses and their reciprocals. The egg laying of all crosses and control was tested by the standard procedure. The result is summarized in Table 4, along with some pertinent quantities for the comparison with the response obtained in the RRS program.

Each of the ranked values is the average egg production of 12 females tested for four days. The shape of this distribution is approximately of normal distribution. The estimate of the total genotypic variance is obtained by pooling information from the initial five cycles of the RRS experiment. The square root of 30.80 is approximately 5.55, and this would indicate that the true performances of interpopulational single crosses possible from the two base populations are distributed with the standard deviation of ca. 5.5 around mean.

The estimate of mean of single crosses is 26.99. The mean performance of RRS crossbreds during the last three cycles is 8.0 eggs over the mean of control materials. Therefore, the RRS performance is equal to 35.96 (i.e., 8.00 + 27.96), when compared with the mean of single crosses (26.99), that is to say, the RRS performance is 8.97 above the mean of single crosses. This deviation is 1.63 times the standard deviation of genotypic distribution, 5.5. One-tail normal deviate of this magnitude corresponds to probability 0.04. Thus, it may be concluded that the mean performance of the RRS crossbreed has been improved to the level which is as high as top four percent of all single crosses possible between random inbreds of *Mather* and those of *Mono*.

DISCUSSION

Other studies with similar objectives, but with somewhat different outcomes have been reported by BELL, MOORE and WARREN (1955) and RASMUSON (1956). Both of these investigators dealt with egg count selection with *D. melanogaster*. In the main, BELL and his associates found that, in a short run, purebred selection (full-sib family type reinforced by individual selection within the best families in their case) was superior to RRS; but that, in a long run, the mean performance

TABLE 4

Distribution of egg counts of F_1 hybrids between inbreds from two base populations, and its comparison with RRS mean performance

Rank	1	2	3	Mean	46	47	48
	38.06	37.08	35.19	26.99	20.64	18.98	16.93

Control mean 27.96

Total Genotypic variance*: 30.80

The deviation of RRS mean from control (the 14, 15, and 16th cycles): 8.00

* The best estimate for the crossbred progenies between the base populations.

in RRS excelled that in FFS and was approximately equal to the best single cross performance. Thus, the final outcome seems to agree with the result of the present experiment, while the efficiency of their FFS during the early stage of selection was much higher than was found in the present study.

RASMUSON's findings are that the performance in her RRS program was approximately 6–7 percent superior to the average performance of half-sib family selection lines over 20 cycles of selection. She published the data of egg counts for every cycle of selection. The overall mean egg counts are higher for the RRS line than for the half-sib selection lines in her data. However, a comparison of cycle-to-cycle gains by the two types of selection indicates that there may not have been any superiority of RRS to half-sib selection. On the contrary, the latter seems to be slightly more efficient than the former in her study.

Patterns of responses to selection, and efficiencies of different selection schemes are generally determined by the distribution and amounts of genetic variances within and between progeny groups. Hence, the likelihood of observed responses can be evaluated by examining the agreement between the actual response and the one expected from the magnitude of genetic variance relative to the total variance among selection criteria. Unfortunately, BELL and his associates did not publish the estimates of these variances in their purebred and crossbred populations. RASMUSON stated that 54 percent of observed variations was due to "hereditary variation" in her material. She did not specify, however, which populations (crossbred, purebred, or average of both) had this heritability. At any rate, the actual response observed in either selection method was much less than what was expected from this order of heritability value.

In the present study the estimates of these kinds verified the actual responses obtained in both schemes of selection. In the RRS program, the actual response to selection was within the range of predicted response which was based upon the estimate of genetic variance in the crossbred populations. Little response to selection was observed in the two purebred selection programs, where the estimates of genetic variance were extremely low within each purebred population. Such situations in *Mather* and *Mono* were probably derived through the cage culture condition over a considerable time. During this period of time natural selection in cages had probably favored genotypes for relatively high egg production under uniform and constant laboratory conditions, and this process must have led each population to unique equilibrium where selection pressure on individual genes is nearly balanced. Consequently the (additive) genetic variances in the cages were reduced considerably more than what might happen in nature. The genetic divergences between the two populations were, however, maintained or possibly increased.

If theoretical consideration on the relationship between the response observed and the heritability is applied, both purebreds and crossbreds used by BELL and his associates must have had fairly high and equal heritability values. This speculation is plausible, when the origin of their base populations is considered. The base for their FFS was a composite population made from eight unselected stocks. For their RRS, the eight stocks were randomly grouped into two sets, and

two composites were made from each set. Such operations often result in the situation where the diversity between the two composites is not large as compared to the variabilities within the composites. Thus, it is not difficult to visualize that the heritability in the purebred used for FFS was high, and that the purebreds and crossbreds for RRS also had high heritability values. Thus, one of the most logical explanations for the difference in the relative efficiency of the two schemes of selection observed by BELL *et al.* and by the present authors, is given by the difference in the distribution of genetic variances in purebreds and crossbred progenies.

In conclusion, the genetic circumstances where systematic crossbred selection such as RRS is superior to purebred selection may be summarized as follows. The first is the condition of low heritability within purebred populations. Such a condition may be a result of either previous purebred selection or natural selection due to the close relation of the character to fitness scale. The second possibility is the situation where the genetic structures of individual populations are so integrated that crossing them destroys existing epistatic gene complexes favorable to desirable performance in purebreds. Such situations may exist in the characters which have been under selection for a considerable time. KOJIMA and KELLEHER (1961a) examined genetic models which accounted for the breakdowns of such favorable gene complexes following intercrosses of two isolated populations. They demonstrated that the mean of intercrossed populations could decrease, offsetting the effect of selection, for several successive generations through the recombination of previously adapted genotypes. Experimental evidences of such cases may be found in the work by VETUKIEV (e.g. 1953 and others). Under these conditions, crossbred selection may be employed to utilize the divergence between the populations for further improvement of the character without destroying favorable complexes in purebreds drastically. In this sense, reciprocal recurrent selection may be a means to achieve high performance on the balance of genetic variances within and between populations.

As pointed out by ROBINSON, MOLL and KOJIMA (1961), RRS can be a powerful method to provide base populations from which to extract inbred lines that will be used in a conventional hybrid breeding program. The comparison of RRS mean performance with single cross performances strongly suggests such a possibility.

This proposal assumes that sufficient genotypic variability remains in purebred populations of RRS after many cycles of selection. In the present RRS program the crossbred performance has plateaued, and the genetic variance in crossbreds has become extremely reduced. This, however, does not mean an exhaustion of genotypic variability in the two purebred populations. The examination of the purebreds indicated that there was considerable genotypic variation within each of them, and that the plateauing of crossbred performance was probably the result of balance among more than one superior genotype rather than the result of selection for a single genotype of high egg production.

SUMMARY

A comparative study of purebred selection and crossbred selection was made by the use of the same base populations. The purebred selection employed was full-sib family selection (FFS), and the crossbred selection was reciprocal recurrent selection (RRS). The base populations were two long-term cage populations of *D. pseudoobscura*, and the character used was daily egg count. A FFS line was carried out for 13 cycles of selection from each of the base populations, while RRS utilized the two populations reciprocally as the tester and the tested for 16 cycles. Selection intensity, family size, and effective size of population were all kept equivalent in all cases.

The patterns of response in the two FFS lines were very similar. The total improvement in egg production for 13 cycles (total accumulated selection differential of 117.7 and 121.8 eggs for the two lines) was 3.53 eggs for one and 4.87 eggs for the other, after the adjustment was made for inevitable inbreeding. The estimates of additive genetic variance were obtained at each cycle of selection in each line. The magnitude of the pooled estimates was in agreement with that expected from the actual response to selection.

The pattern in the RRS study was quite different from that in FFS. A fairly substantial response took place till the tenth or 11th cycle of selection. This amounted to 14.72 eggs of total gain for 92.0 eggs of accumulated selection differential. Thereafter the positive response ceased rather suddenly and the performance has been plateauing up until the present time. The estimates of genetic variance in crossbred populations were estimated at each cycle. The pooled values for the first ten cycles and the last six cycles were in agreement with the values expected from the actual responses for the respective periods.

A large number of F_1 hybrids between random inbreds obtained from one base population and those from the other were made, and their performance was compared with the mean performance of the RRS material. The comparison indicated that the improved RRS material attained a level equivalent to the performance of the top four percent of all possible F_1 hybrids between the base populations.

Thus, it is concluded that RRS can be effective in improving a quantitative trait on hybrid basis, even when individual populations do not respond to purebred selection because of the lack of additive genetic variance within populations.

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