# EFFECTS OF ARTIFICIAL SELECTION ON RATES OF INBREEDING IN POPULATIONS OF *DROSOPHILA MELANOGASTER*

## I. EFFECT IN EARLY GENERATIONS

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*Summary*

The rate of inbreeding was studied using the conventional $F$ value, as well as the "percentage of genes" technique of James and McBride (1958), in lines of *D. melanogaster* selected for increased abdominal bristle number for seven generations at intensities of 10, 20, and 50% with 10 pairs of parents.

There was large variation between replicates in both rate of response and rate of inbreeding, but generally the rate of inbreeding was highest in lines giving greatest response. The effective population size was reduced below that expected under random mating in some lines but not in others.

In a few lines particular individuals made large contributions to the line at later generations.

## I. INTRODUCTION

In artificial selection for a quantitative character, the importance of effective population size as one factor determining total response was demonstrated theoretically by Robertson (1960), and has since been confirmed in simulation studies (Gill 1965; Latter 1965*b*), and experimentally (Jones, Frankham, and Barker 1968). But selection itself should reduce the effective population size ($N_E$) as compared with the actual population size ($N$). From considerations of the effect of selection on the variance of family size, Robertson (1961) predicted that the relationship would be:

$$N_E = (N+C^2)/(1+C^2), \tag{1}$$

where $C^2$ is the variance of the selective advantage of families. In terms of the next generation,

$$C^2 = \tfrac{1}{2}h^2\bar{\imath}^2[1-h^2\bar{\imath}(\bar{\imath}-x)]$$

if there is no non-genetic variance between families, where $h^2$ is the heritability, $\bar{\imath}$ is the standardized selection differential, and $x$ is the abscissa of the unit normal curve at the point of truncation.

But contributions of genetically superior families should increase for a few generations, and this cumulative effect on the selective advantage of some families

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will further reduce effective population size. Robertson (1961) showed that, where several generations of selection are considered, the effective population size ($N_E'$) can be predicted by replacing $C^2$ by $4C^2$ in equation (1) above.

In selection experiments, effective population size is often calculated from the increase in Wright's (1922) inbreeding coefficient. The formulae of Robertson (1961) were derived from considerations of variance of gene frequency. The relationship between the variance effective population size and inbreeding effective population size were discussed by Kimura and Crow (1963). In certain breeding systems, the two population sizes may be very different, but in a dioecious population of constant size the differences are small.

James and McBride (1958) showed that the "percentage of genes" technique could add additional information in the study of inbreeding. This is essentially the analysis of changes in contributions of genes from particular ancestors. From the number of times a particular individual appears as an ancestor to individuals in a later generation, its contribution can be readily determined. As the authors point out, this assumes that the individual's genes, present in descendants several generations later, are a random sample of its genotype and so the method does not detect within-family selection. A similar assumption is made in the use of Wright's inbreeding coefficient. James (1962*a*) showed a simple relationship between genetic drift and the variation in the percentage of genes. The effective population size ($N_E$) of a population of $M$ males and $F$ females used as parents each generation is given by:

$$1/N_E = 1/8M + 1/8F + MV(P_S) + FV(P_D), \tag{2}$$

where $V(P_S)$ and $V(P_D)$ are the variances of the proportions of the genes in the next generation from sires and dams respectively.

The technique also allows us to study the effect of selection on the relationship between replicate lines. If lines A and B are drawn from the same base population, and $P_{iA}$ and $P_{iB}$ are the proportions of genes from the $i$th common ancestor, the relationship between the lines is $\Sigma P_{iA}P_{iB}$ (James 1962*b*).

In the experiments described here, the effect of selection on the rate of inbreeding and on the spread of genes was investigated. Lines of *Drosophila melanogaster* were selected at intensities of 10, 20, and 50% with 10 pairs of parents per generation for seven generations. Contributions of individuals to subsequent generations were estimated to measure the spread of genes. The effective population size was calculated from the variance of family contributions and from the change in Wright's inbreeding coefficient. The initial relationship between the lines was known and the effect of selection on this relationship was observed.

## II. Materials and Methods

The same strain (Canberra) and character (the bristle number of one abdominal segment) were used as in Frankham, Jones, and Barker (1968*a*), where this character had a realized heritability of about 0·16. The same dead-yeast fortified medium was used, and conditions of temperature (25·0±0·5°C) and humidity (65–70%) were identical to those of Frankham, Jones, and Barker (1968*a*). Parents were single-pair mated and allowed to lay eggs for 3 days in 3 by 1 in. vials. Pedigrees were kept for all matings.

To initiate the lines, 10 pairs of virgins were collected from an egg sample taken from a population cage containing about 4000–5000 adults and single-pair mated at random, each

individual being mated only once. Virgin progeny were collected and one pair of flies from each full-sib family was assigned to each line. The flies were then mated at random within each line to produce the next generation (generation 0). Equal numbers of flies were scored from each family in generation 0 and subsequent generations. The 10 highest flies of each sex were selected and mated at random. Three spare cultures were set up from the next highest flies and these were used if any of the other cultures failed. Three replicates of each treatment were carried out. The lines were designated thus:

$1a,b,c,$: 10/100 in each sex, 10 pairs scored per family

$2a,b,c,$: 10/50 in each sex, 5 pairs scored per family

$5a,b,c,$: 10/20 in each sex, 2 pairs scored per family

As the initial contribution of each of the 10 initial families was 0·1, the genetic relationship between any pair of lines was initially 0·05. For the system of mating used, $M=F=10$ and $V(P_S)=V(P_D)=\frac{1}{4}V_{n+1}$ in equation (2), and so

$$1/N_E=1/2N+\tfrac{1}{4}N(V_{n+1}), \tag{3}$$

where $N$ is the number of parents used each generation and $V_{n+1}$ is the variance of the contributions of the families to the next generation. In terms of family size this becomes

$$1/N_E=[2+V(k)]/4N,$$

where $V(k)$ is the variance of family size. This differs slightly from the formula of Kimura and Crow (1963), but James (1962*a*) showed that the effective population size was about one higher without replacement than with replacement.

In a large random-mating population, the distribution of family size is Poissonian with a mean and variance of 2. If $n$ individuals are measured in all families, the variance of family size is reduced by a factor of $1/n$. In terms of the next generation, the expected effective population size ($N_E^*$) is approximately given by

$$1/N_E^*=1/N[(1-1/2n)+(1-1/n)\,C^2], \tag{4}$$

and the expected effective population size with several generations of selection ($N_E^{**}$) is given by (Robertson 1961):

$$1/N_E^{**}=1/N[(1-1/2n)+(1-1/n)4C^2]. \tag{5}$$

If parents for the next generation were sampled at random from populations with ten, five, and two pairs per family, the variances would be 1·8, 1·6, and 1·0 respectively. In the selection lines here, the mean contribution per family was 10%, so the variances of percentage contributions expected with random sampling from populations of the same size would be 45, 40, and 25 respectively. As the mean family contribution was fixed by the size and structure of the selection programme, no degrees of freedom were used for its estimation. All the degrees of freedom (i.e. 10) were available to estimate the variance of the contributions (James 1962*a*).

## III. Results

### (*a*) *Response to Selection*

The mean female and male bristle numbers each generation are shown in Figure 1. There were large differences in response between replicates in all treatments. To compare treatments, realized heritabilities were calculated from the regression of response on cumulative selection differential. The averages of female and male heritabilities are shown in Table 1. There was large variation among the lines with no consistent effect of selection intensity on heritability. The highest heritabilities

were 0·26 for 5*c*, 0·21 for 2*b*, and 0·20 for 1*c*, while 1*a* and 2*a* had heritabilities of only 0·11 and 0·12. The average over all lines (0·17) was similar to that (0·16) of Frankham, Jones, and Barker (1968*a*), who also found large variation among lines. Losses of families because of insufficient numbers of progeny were not common and had little effect on the selection differentials.

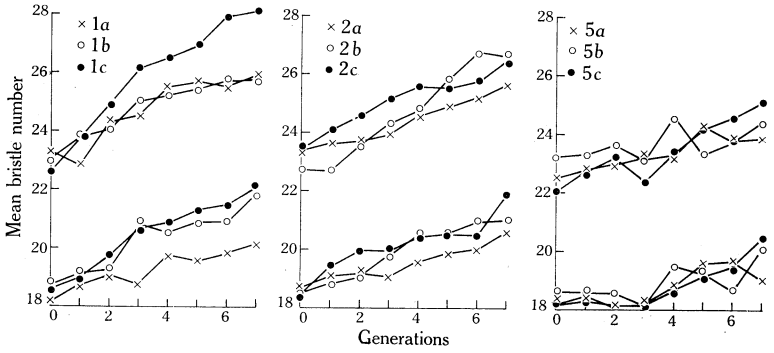


Fig. 1.—Response to selection of the individual lines. Upper sets of curves represent response in females, whilst lower ones represent that in males.

TABLE 1

REALIZED HERITABILITIES CALCULATED FROM THE REGRESSION OF RESPONSE ON CUMULATIVE SELECTION DIFFERENTIAL

| Replicate | Selection Intensity | | |
|---|---|---|---|
| | 10% | 20% | 50% |
| *a* | 0·11±0·02 | 0·12±0·01 | 0·19±0·02 |
| *b* | 0·13±0·01 | 0·21±0·01 | 0·13±0·04 |
| *c* | 0·20±0·01 | 0·16±0·01 | 0·26±0·03 |
| Mean | 0·15 | 0·16 | 0·19 |

### (*b*) *Effective Population Size*

The variances of the percentages of genes from families in each generation to the next generation are given in Table 2. There was considerable variation among lines and generations. The harmonic mean effective population size can be obtained by substituting the mean variance of the contributions in equation (3) above. The mean variances and effective population sizes are also given in Table 2. The greatest reduction in $N_E$ was in 1*c*, the mean being 14·68 compared to the actual size of 20. This was most pronounced at generation 2 where $N_E$ was only 8·5. There was also considerable reduction in 2*b*, the average $N_E$ being 16·84.

The effect of selection on effective population size can be best obtained by comparing the observed $N_E$ with that expected with random sampling from populations with the same number scored ($N_R$). From equation (4), with $C^2=0$, $N_R$ for

TABLE 2

VARIANCES OF THE PERCENTAGES OF GENES FROM FAMILIES IN EACH GENERATION TO THE NEXT GENERATION AND MEAN EFFECTIVE POPULATION SIZES

| Generation | Line | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1*a* | 1*b* | 1*c* | 2*a* | 2*b* | 2*c* | 5*a* | 5*b* | 5*c* |
| 0 | 65·0 | 80·0 | 75·0 | 60·0 | 45·0 | 55·0 | 25·0 | 15·0 | 30·0 |
| 1 | 25·0 | 95·0 | 60·0 | 20·0 | 50·0 | 80·0 | 30·0 | 40·0 | 45·0 |
| 2 | 55·0 | 60·0 | 185·0 | 25·0 | 80·0 | 50·0 | 30·0 | 40·0 | 25·0 |
| 3 | 45·0 | 50·0 | 20·0 | 50·0 | 90·0 | 50·0 | 25·0 | 30·0 | 20·0 |
| 4 | 35·0 | 50·0 | 145·0 | 40·0 | 85·0 | 65·0 | 50·0 | 20·0 | 30·0 |
| 5 | 60·0 | 35·0 | 120·0 | 30·0 | 55·0 | 40·0 | 25·0 | 35·0 | 50·0 |
| 6 | 50·0 | 50·0 | 40·0 | 50·0 | 95·0 | 30·0 | 15·0 | 15·0 | 30·0 |
| 7 | 45·0 | 25·0 | 45·0 | 40·0 | 50·0 | 30·0 | 40·0 | 20·0 | 25·0 |
| Mean | 47·50 | 55·62 | 86·25 | 39·38 | 68·75 | 50·00 | 30·00 | 26·88 | 31·88 |
| Mean $N_E$ | 20·51 | 18·93 | 14·68 | 22·38 | 16·84 | 20·00 | 25·00 | 26·02 | 24·43 |

the 10%, 20%, and 50% lines was 21·05, 22·22, and 26·67 respectively. The ratios of observed $N_E/N_R$ are shown in Table 3. The expected effective population size ($N_E^*$) was computed (equation 4) for each line, using its realized heritability, and expected values of $\bar{\imath}$ and $x$. The ratios $N_E^*/N_R$ are also given in Table 3.

TABLE 3

RATIOS OF OBSERVED ($N_E$) AND EXPECTED ($N_E^*$) EFFECTIVE POPULATIONS SIZES TO THAT EXPECTED WITH RANDOM SAMPLING FROM POPULATIONS WITH THE SAME NUMBER SCORED ($N_R$)

| Line | $N_E/N_R$ | $N_E^*/N_R$ | Line | $N_E/N_R$ | $N_E^*/N_R$ | Line | $N_E/N_R$ | $N_E^*/N_R$ |
|---|---|---|---|---|---|---|---|---|
| 1*a* | 0·974 | 0·873 | 2*a* | 1·007 | 0·917 | 5*a* | 0·938 | 0·967 |
| 1*b* | 0·899 | 0·858 | 2*b* | 0·758 | 0·871 | 5*b* | 0·976 | 0·977 |
| 1*c* | 0·697 | 0·808 | 2*c* | 0·900 | 0·895 | 5*c* | 0·916 | 0·958 |
| Mean | 0·857 | 0·846 | Mean | 0·888 | 0·894 | Mean | 0·943 | 0·967 |

The reduction in $N_E/N_R$ increased slightly with increased selection intensity. However, agreement between replicates was poor, 1*c* and 2*b* having much lower ratios than the rest. These two lines also gave greater response and had higher heritabilities than their replicates. Similarly 5*c* had a higher heritability and lower $N_E/N_R$ than 5*a* or 5*b*. In a few lines (1*b*, 2*c*, 5*a*, 5*b*, 5*c*), the observed ($N_E$) and expected ($N_E^*$) effective population sizes were in close agreement. In 1*a* and 2*a* the

reduction in $N_E$ was much less than expected, while in 1*c* and 2*b*, $N_E$ was reduced considerably more than expected.

### (*c*) *Inbreeding Coefficients*

The mean inbreeding coefficients of the parents selected each generation are given in Figure 2. The lines were set up for generation 8 but were not scored. The coefficients for this generation represent the average inbreeding coefficients of the offspring. There was considerable variation between lines in the rate of inbreeding. The fastest rates of inbreeding were in 1*c* and 2*b* which had mean coefficients of 32·7 and 28·5% respectively at generation 8. The mean effective population size can be calculated from the regression of $\log(1-F_t)$ on generations since

$$1-F_t=(1-1/2N)^t(1-F_0),$$

where $F_0$ and $F_t$ are the inbreeding coefficients at generations 0 and $t$ respectively (Falconer 1960).

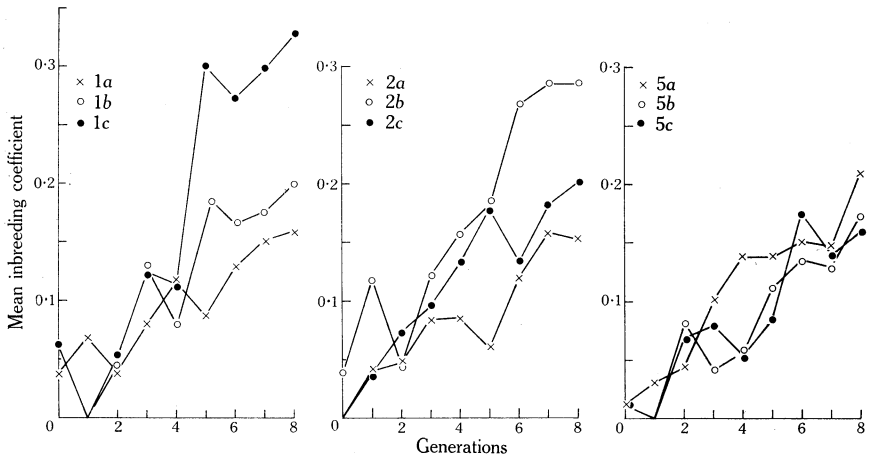


Fig. 2.—Mean inbreeding coefficients of the parents selected each generation from 0 to 7 and of the offspring in generation 8.

As the inbreeding effect of a generation should continue to increase for a few generations, the expected inbreeding effective population size ($N_I^*$) is given by $N_E^{**}$ in equation (5). This equation would overestimate the reduction in $N_I$ as the contributions in later generations would still be changing at the end of the experiment. Further, as there was large variation among the inbreeding coefficients of individuals within a generation in some lines, and as the mean inbreeding coefficient fluctuated considerably, $N_I$ could not be measured accurately. Again, the ratio $N_I/N_R$ would allow an easier comparison among selection intensities than $N_I$. The observed ($N_I/N_R$) and expected ($N_I^*/N_R$) ratios are given in Table 4. The reduction in $N_I$ in a few lines (1*c*, 2*b*, and 5*c*) was of the order expected, but in 1*a* and 2*a* there was virtually no reduction. The reduction was also less than expected in 1*b* and 2*c* but was greater than expected in 5*a* and 5*b*.

### (*d*) *Contributions of the Initial Families*

Table 5 shows the contributions of the initial families to each generation of line 1*a*. In this line there was little change in the contributions of the initial families after generation 2. The change in contributions can best be compared by observing the variance of the percentages from the initial families. These are given in Figure 3. In most lines the variance increased until generation 2, after which there was little change in some lines (1*a*, 1*b*, 2*a*, 2*c*, 5*b*, 5*c*) whilst in 1*c*, 2*b*, and 5*a* it increased for five or more generations. The variance was far larger in 1*c* and 2*b* than in the other lines.

TABLE 4

RATIOS OF OBSERVED ($N_I$) AND EXPECTED ($N_I^*$) INBREEDING EFFECTIVE POPULATION SIZES TO THAT EXPECTED IF PARENTS WERE SELECTED AT RANDOM FROM POPULATIONS OF THE SAME SIZE ($N_R$)

| Line | $N_I/N_R$ | $N_I^*/N_R$ | Line | $N_I/N_R$ | $N_I^*/N_R$ | Line | $N_I/N_R$ | $N_I^*/N_R$ |
|---|---|---|---|---|---|---|---|---|
| 1*a* | 1·181 | 0·633 | 2*a* | 1·152 | 0·733 | 5*a* | 0·736 | 0·881 |
| 1*b* | 0·786 | 0·602 | 2*b* | 0·569 | 0·629 | 5*b* | 0·826 | 0·915 |
| 1*c* | 0·466 | 0·512 | 2*c* | 0·842 | 0·681 | 5*c* | 0·836 | 0·852 |
| Mean | 0·811 | 0·582 | Mean | 0·854 | 0·681 | Mean | 0·799 | 0·883 |

TABLE 5

PERCENTAGE CONTRIBUTIONS OF ORIGINAL FAMILIES TO LINE 1*a* DURING THE FIRST EIGHT GENERATIONS

| Generation | Family | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1 | 17·50 | 0·00 | 15·00 | 2·50 | 2·50 | 10·00 | 12·50 | 15·00 | 10·00 | 15·00 |
| 2 | 16·25 | 0·00 | 22·50 | 1·25 | 5·00 | 8·75 | 8·75 | 17·50 | 8·75 | 11·25 |
| 3 | 15·62 | 0·00 | 25·00 | 1·25 | 5·00 | 8·13 | 8·75 | 15·00 | 8·13 | 13·12 |
| 4 | 17·19 | 0·00 | 25·00 | 0·94 | 4·38 | 7·19 | 8·75 | 15·31 | 7·19 | 14·06 |
| 5 | 18·59 | 0·00 | 23·12 | 0·78 | 3·44 | 7·81 | 9·06 | 15·47 | 7·81 | 13·91 |
| 6 | 17·35 | 0·00 | 23·59 | 0·70 | 4·38 | 8·75 | 7·73 | 15·23 | 8·75 | 13·52 |
| 7 | 16·72 | 0·00 | 23·52 | 0·55 | 4·61 | 9·45 | 7·46 | 15·04 | 9·45 | 13·20 |
| 8 | 16·70 | 0·00 | 23·63 | 0·62 | 3·40 | 10·41 | 7·68 | 15·06 | 9·24 | 13·26 |

The contributions of the initial families to each line at generation 6 are shown in Table 6. There was considerable variation in the contributions of the initial families. Largest contributions were 47·3% from family 8 to 2*b* and 44·4% from family 7 to 1*c*. Of the initial families, only 4, 9, and 10 were represented in every line and even these were at low frequencies in 1*a*, 2*b*, and 5*c* (0·7, 1·0, and 3·5% respectively). The highest average contributions were 12·99 and 13·04% from families 7 and 8 and the lowest were 6·60 and 5·68% from families 2 and 4 respectively.

The genetic relationships among the lines can be determined from the contributions of the initial families as given earlier. Genetic relationships between pairs of lines are given in Table 7. There was no consistent change in the genetic relationship

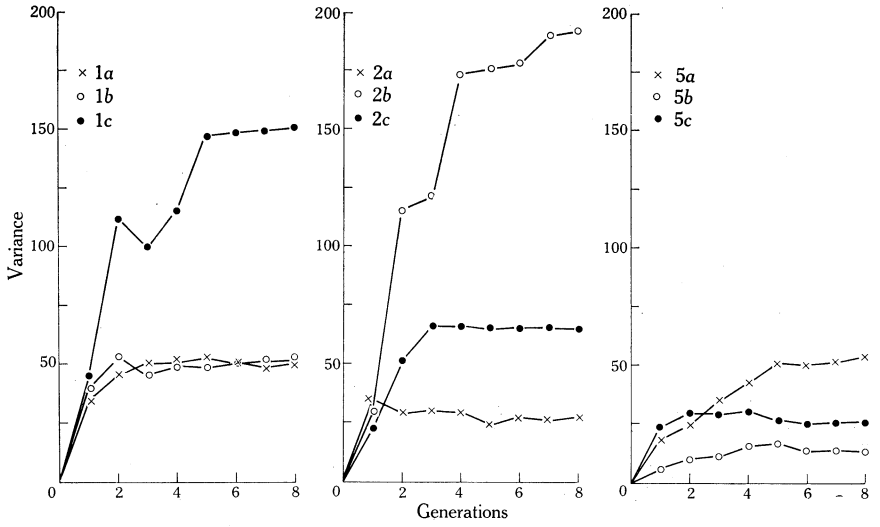


Fig. 3.—Variances of the percentage contributions of the initial families to the individual lines.

TABLE 6

PERCENTAGE CONTRIBUTIONS OF THE INITIAL FAMILIES TO EACH LINE AT GENERATION 6

| Line | Initial Family | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1*a* | 17·35 | 0·00 | 23·59 | 0·70 | 4·38 | 8·75 | 7·73 | 15·23 | 8·75 | 13·52 |
| 1*b* | 11·88 | 12·50 | 0·00 | 1·48 | 9·22 | 21·33 | 0·00 | 15·31 | 10·31 | 17·97 |
| 1*c* | 15·23 | 3·83 | 0·00 | 5·86 | 5·94 | 2·81 | 44·37 | 2·81 | 9·77 | 9·38 |
| 2*a* | 8·36 | 6·41 | 17·11 | 5·47 | 12·66 | 5·47 | 19·92 | 3·20 | 13·67 | 7·73 |
| 2*b* | 0·00 | 11·02 | 12·27 | 1·01 | 2·42 | 2·42 | 10·47 | 47·34 | 1·02 | 12·03 |
| 2*c* | 10·15 | 0·00 | 10·15 | 8·44 | 0·00 | 0·00 | 13·44 | 26·41 | 17·97 | 13·44 |
| 5*a* | 18·11 | 0·86 | 15·47 | 6·44 | 9·69 | 21·95 | 1·72 | 0·86 | 16·66 | 8·24 |
| 5*b* | 12·19 | 13·83 | 10·39 | 12·81 | 7·66 | 11·09 | 15·62 | 6·17 | 6·72 | 3·52 |
| 5*c* | 16·87 | 10·94 | 6·72 | 8·91 | 15·70 | 12·03 | 3·59 | 0·00 | 13·36 | 11·88 |
| Mean | 12·24 | 6·60 | 10·63 | 5·68 | 7·52 | 9·54 | 12·99 | 13·04 | 10·94 | 10·86 |

among the lines but the relationship between a few lines changed considerably from the initial value of 5·0%. The highest relationship was 8·5% between 2*b* and 2*c*. This was largely due to family 8 contributing 47·3 and 26·4% of the genes to 2*b* and 2*c* respectively. The lowest relationships were 2·3% between 2*b* and 5*a* and 2·4% between 2*b* and 5*c*.

### (e) *Contributions of Families in Later Generations*

So far, we have only considered the contributions of the initial families. A look at the contributions of families in later generations will throw further light on the inbreeding expected in selection experiments.

TABLE 7

GENETIC RELATIONSHIPS AMONG THE LINES AT GENERATION 6

| Line | Line | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1*b* | 1*c* | 2*a* | 2*b* | 2*c* | 5*a* | 5*b* | 5*c* |
| 1*a* | 0·050 | 0·046 | 0·054 | 0·065 | 0·063 | 0·060 | 0·046 | 0·047 |
| 1*b* | | 0·033 | 0·037 | 0·056 | 0·048 | 0·056 | 0·044 | 0·055 |
| 1*c* | | | 0·069 | 0·039 | 0·059 | 0·038 | 0·060 | 0·044 |
| 2*a* | | | | 0·040 | 0·050 | 0·051 | 0·052 | 0·049 |
| 2*b* | | | | | 0·085 | 0·023 | 0·042 | 0·024 |
| 2*c* | | | | | | 0·043 | 0·044 | 0·038 |
| 5*a* | | | | | | | 0·048 | 0·061 |
| 5*b* | | | | | | | | 0·049 |

The variances of the percentages of genes in generation 8 from families in earlier generations are shown in Table 8. 1*c* and 2*b* had much higher variances than the other lines, the highest being 529 at generation 4 in 1*c*. Only four of the families in 1*c* at this generation were still represented at generation 8 and the contributions

TABLE 8

VARIANCES OF THE PERCENTAGES OF GENES FROM FAMILIES IN EACH GENERATION TO GENERATION 8

| Generation | Line | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1*a* | 1*b* | 1*c* | 2*a* | 2*b* | 2*c* | 5*a* | 5*b* | 5*c* |
| 0 | 77·82 | 127·46 | 170·94 | 72·46 | 225·77 | 172·21 | 67·23 | 40·82 | 37·21 |
| 1 | 40·47 | 133·35 | 139·18 | 53·70 | 113·91 | 107·57 | 97·96 | 54·43 | 40·10 |
| 2 | 86·34 | 195·59 | 120·99 | 45·18 | 150·34 | 66·38 | 127·06 | 67·32 | 61·78 |
| 3 | 61·72 | 156·31 | 281·49 | 71·77 | 147·44 | 66·11 | 98·78 | 54·88 | 44·60 |
| 4 | 75·94 | 92·11 | 529·30 | 64·93 | 137·11 | 53·08 | 66·72 | 30·71 | 42·60 |
| 5 | 99·38 | 45·00 | 106·56 | 53·13 | 209·06 | 53·44 | 54·38 | 59·37 | 51·88 |
| Mean | 73·61 | 124·97 | 224·74 | 60·20 | 163·94 | 86·46 | 85·36 | 51·26 | 46·36 |

of the families were far from equal. The numbers of families from each generation represented at generation 8 are shown in Table 9. In only a few cases were all families from a generation represented. 1*b*, 1*c*, 2*b*, and 2*c* had the lowest numbers of families represented.

The families were often far from equally represented. There were a number of cases where a large proportion of the genes came from one or two families. In 1*b*, 47·8% came from one family in generation 2, and 38·4% from one in generation 3. With 1*c*, 44·6% came from one family in generation 0, 37·5% from one in generation 1, 85·6% from two in generation 3, and 77·5% from one in generation 4.

In 2*b*, 48·9% of the genes were from one family in generation 0, 60·0% from two in generation 2, 63·8% from two in generation 3, and 91·2% from three in generation 5. All of the genes in 2*c* came from only four families at generation 0. Of the 50% lines, 5*a* had a fairly high variance and some families had quite high contributions, e.g. individual families in generations 1, 2, and 3 contributed 30·2, 38·9, and 34·1% of the genes respectively. The other lines had low variances and had few families making high contributions.

TABLE 9

NUMBER OF FAMILIES FROM EACH GENERATION STILL REPRESENTED AT GENERATION 8

| Generation | Line | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1*a* | 1*b* | 1*c* | 2*a* | 2*b* | 2*c* | 5*a* | 5*b* | 5*c* |
| 0 | 7 | 6 | 6 | 9 | 8 | 4 | 9 | 9 | 8 |
| 1 | 9 | 7 | 6 | 9 | 8 | 6 | 9 | 7 | 8 |
| 2 | 7 | 6 | 7 | 9 | 6 | 7 | 9 | 7 | 7 |
| 3 | 8 | 6 | 5 | 7 | 7 | 8 | 9 | 8 | 8 |
| 4 | 8 | 7 | 4 | 8 | 6 | 7 | 7 | 10 | 8 |
| 5 | 7 | 8 | 7 | 8 | 6 | 9 | 9 | 10 | 8 |

## IV. DISCUSSION

A notable feature of the results was the large variation in the response of the lines. Poor agreement between replicates occurred in earlier selection experiments with the Canberra population (Frankham, Jones, and Barker 1968*a*), particularly in the smaller populations (10 pairs of parents). Realized heritabilities in their experiments were of a similar order to those in the lines here. In their experiments, five pairs of parents were mated per culture, and selection was within cultures. The similar heritabilities indicate that selection based on progeny from several cultures was as efficient as within-culture selection. This was expected as the between-culture environmental variance in this population was small (Sheridan *et al.* 1968). The selection lines of Frankham, Jones, and Barker (1968*a*) would have been less related at initiation than the lines here as their lines were initiated from a large sample, while here the lines were started with equal representation from 10 full-sib families. The relationship was still quite low (0·05) so the poor agreement between replicates could have been due to initial sampling.

There was also large variation among replicates for effective population size, which prevents us from making an accurate measure of the effect of selection on effective population size ($N_E$). However, the results indicate that a rapid rate of inbreeding will accompany fast response to selection. The lines showing the most progress (1*c* and 2*b*) also had the lowest effective population sizes. With the lowest selection intensity (50%) there was little reduction in $N_E$. 5*a* had the highest rate of inbreeding and fairly high heritability (0·19). 5*c* had the highest heritability (0·26) and highest variance of percentage contributions to the next generation (31·88), but the rate of inbreeding and the variance of contributions of families in early generations to generation 8 was similar to that of 5*b* and considerably less than

that of 5*a*. The response expected in the 50% lines was fairly small so that the realized heritabilities have high standard errors (about 0·03).

The effective population sizes estimated from the rate of inbreeding were generally lower than those estimated from the variance of family size. This was especially true for lines 1*c*, 2*b*, 5*a*, and 5*b*. In 1*c*, 2*b*, and 5*a* the variance of the contributions of the initial families increased for several generations. Robertson (1961) predicted that the contributions of particular families would increase for a few generations so that the inbreeding due to a particular generation would also increase. This cumulative effect of selection on effective population size can best be seen from a comparison of the variance of the percentages of genes contributed to the next generation (Table 2) with that of the contributions to generation 8 (Table 8). Generally, the variance increased after the next generation. This was quite pronounced with 5*a*, which had similar variances to 5*b* and 5*c* for contributions to next generation but had much higher variances for contributions to generation 8. Similar increases were pronounced with 1*b*, 1*c*, and 2*b*, but changes were only small in 1*a*, 2*a*, and 2*c*.

McBride and Robertson (1963) found that individual selection for the sum of the bristle numbers of two abdominal segments at an intensity of 10% reduced the effective population size to about three-quarters of the actual. The reduction was greatest in the early generations when the lines were still responding rapidly to selection. However, Robertson (1961) showed that the reduction in effective population size of these lines was similar to that expected.

McBride and Robertson (1963) found a drastic elimination of some families and only half the original families made permanent contributions to the lines. The genetic relationships between replicates increased from 0·050 to 0·065 for one pair and to 0·13 for another by the fourth generation. The increase in genetic relationship was greater than in the lines here where there was little overall change. This difference was probably due largely to the higher heritability in their lines (0·50 as against 0·17). Differences between methods of initiating the lines would also account for the higher genetic relationship between replicates with their lines. They selected the highest individuals over the 10 initial families as parents for the lines. The selected parents were then split into two groups, care being taken to ensure that the contributions of any particular family to both lines were equal. In the lines here, one pair of flies from each of 10 families was assigned to each line and these were mated at random, selection being commenced the following generation. Although the initial contributions of the 10 families from the base population were the same in each case, the delay in selection would lower the chance of particular families being concentrated. Further, selection in the first generation of McBride and Robertson's (1963) lines would have tended to concentrate the same families in both replicate lines and to eliminate the same ones.

A surprising feature in the lines here was the very large contribution of some of the initial families to one or two lines and their loss from others. Thus family 7 contributed 44·4 and 19·9% of the genes of 1*c* and 2*a* respectively, while it made little or no contribution to 1*a*, 5*a*, and 5*c*. Similarly, family 8 made large contributions to 2*b* and 2*c* and hardly any to 1*c*, 2*a*, 5*a*, and 5*c*. This would be likely to occur if one of the parents of family 8 was heterozygous for a gene which had a fairly large effect on bristle number and was at a low frequency in the base population. The gene would be expected to be present in a few lines and absent from others. In lines which received

the gene, it would soon be favoured and give rapid response to selection. At the same time it would increase the rate of inbreeding in the line. Thus, initial sampling would increase the variance between lines for both response to selection and the rate of inbreeding. Latter (1965*a*) showed that a gene of large effect at low initial frequency would give more rapid response to selection than that expected from its contribution to additive genetic variance.

Linkage of genes affecting the selected trait would increase the variance between lines for response to selection (Fraser and Hansche 1965). There is no critical evidence of the effect of linkage on the variance among lines of the rate of inbreeding. Gill and Clemmer (1966) suggested that linkage increased this variance. However, Bogyo and Ting (1968) showed that this increase was due to their method of measuring inbreeding. Suitable interactions would also account for the large variance between lines. Without actually measuring the effects of individual genes, it is difficult to determine the relative importance of single genes with large effects, linkage, and interactions. Their effects on selection response, regression on relaxation, and heritability are similar, if the genes concerned have a deleterious effect on fitness (Frankham, Jones, and Barker 1968*b*).

Reduced effective population size as compared with actual population size has been found in other studies. James and McBride (1958) found a rapid and continuing elimination of some ancestors in a poultry flock under selection for egg production. Analyses of pedigree breeds of cattle by McPhee and Wright (1925), Lush (1946), Davey and Barker (1963), and others, and of pigs (McPhee 1965) and sheep (Carter 1965) showed that the effective population size of breeds of livestock may be much less than the actual number. Particular individuals have contributed large proportions of the genes in most breeds, due largely to the existence of a breed structure with the genetic composition of a breed determined by the breeding practices of only a few breeders. As Robertson (1961) pointed out, the inbreeding due to a particular ancestor may be small until he appears four or five generations back in the pedigree. The delay may be partly due to the cumulative effect of selection on effective population size predicted by Robertson and which has occurred in some of the *Drosophila* lines. Selection of animals on their pedigrees and deliberate prevention of matings of closely related animals will further delay the inbreeding due to particular ancestors.

In the lines here, selection has been solely individual selection for a quantitative trait. As predicted by Robertson (1961), there was a severe reduction in effective population size in some lines. The failure of selection to reduce the effective population size of some lines and the variation of the response to selection indicated that initial sampling in setting up the lines was important.

The "percentage of genes" technique of James and McBride (1968) offered a useful variation in the study of inbreeding. It proved more informative than the inbreeding coefficient, particularly as there were large fluctuations in the latter. Further, it would enable detection of inbreeding bottlenecks produced by selection well before the effect of the bottleneck on the inbreeding coefficient was clear.

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