

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

## II.\* EFFECT OF PREVIOUS SELECTION ON RATES OF INBREEDING

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### *Summary*

Three lines from the Canberra base population were selected for increased abdominal bristle number for up to 28 generations with 10 pairs of parents and 20% selection intensity. The effective population size as measured by either variance of family contributions to the next generation or by the rate of inbreeding was generally lowest when the lines were responding rapidly to selection. Consideration of the contributions of families in any generation to the lines five generations later showed that much of the genetic variation came from only few families in some generations.

In a second experiment, several lines which had been selected with mass mating for 15 or 38 generations were selected for five generations with single-pair mating of parents. On the whole, effective population size was lowest in lines giving appreciable response to selection. There was little reduction in effective population size in a few lines giving no response. However, there were considerable differences among replicates in both response and effective population size.

### I. INTRODUCTION

In the previous paper (Jones 1969), it was found that artificial selection reduced the effective population size appreciably during the early generations of selection. Although there was considerable variation among replicates in both response to selection and effective population size, lines giving most response generally had smaller effective population sizes.

After several generations of selection, the rate of progress should decline as useful genetic variation is fixed. Selection should then have less effect on the effective population size provided the environmental variance does not change.

Two experiments were done to investigate the effect of selection on effective population size in later stages of selection programmes. In experiment 1, three lines from the Canberra base population were selected for up to 28 generations. In experiment 2, several lines from the Canberra population, which had been selected with mass-mating of parents for a number of generations, were selected with single-pair mating for five generations.

The effect of selection on effective population size was studied using Wright's (1922) inbreeding coefficient and the "percentage of genes" technique of James and McBride (1958) in a similar manner to that used in the previous paper (Jones 1969).

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## II. EXPERIMENT 1

### (a) *Materials and Methods*

Three lines (VA, VB, and VC) were selected with 10 pairs of parents and 20% selection intensity for the number of bristles on one abdominal segment. The lines were initiated in a similar manner to the lines in the first paper. One pair of flies was taken from each of 10 full-sib families for each line. The parents were then single-pair mated at random, and selection was commenced the following generation (generation 0). Selection procedure and culture techniques were the same as in the first paper with two exceptions. Firstly, no spare matings were set up and so, in some generations, fewer than 10 families were scored. Secondly, the 10 families were divided into two groups of five for scoring and five pairs were scored from each family. The five highest pairs of flies were selected from each group and the 10 pairs were then single-pair mated at random, and allowed to lay eggs for 3 days in 3 by 1 in. vials containing fortified medium. This made the selection intensity comparable with that of the 10(20%) lines of Frankham, Jones, and Barker (1968), where 5 out of 25 pairs were selected from each of two cultures. This grouping did not greatly affect the choice of selected parents. When fewer than 10 families produced offspring, the families were split into two groups of equal size (as far as possible) and 25 pairs were scored from each group.

### (b) *Response to Selection*

The mean abdominal bristle numbers (averaged over sexes) every second generation are shown in Figure 1, together with the mean of the 10(20%) lines of Frankham, Jones, and Barker (1968). There was considerable variation in response among the lines, particularly after generation 10. In the early generations the three replicates were generally below the mean of the 10(20%) lines. After generation 12, VB passed 10(20%), while there was little difference between VA and 10(20%) after generation 16. Selection based on progeny from five cultures did not appear to be much less efficient than selection within cultures.

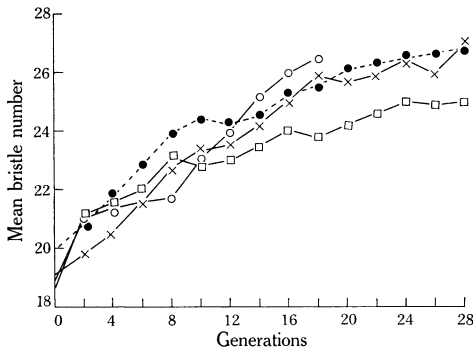


Fig. 1.—Response to selection of the individual lines in experiment 1 and mean of the mass-cultured lines [10(20%)]. ×VA; ○VB; □VC; ●10(20%).

After generation 12, the fitness of VB declined rapidly and the line became extinct after generation 18. Similarly, the fitness of VA declined after generation 16, and only about half the families in later generations produced five pairs of offspring. As with the lines in the first paper, VA, VB, and VC gave different patterns of response. VC gave greatest initial response, but it fell behind the other replicates after generation 10. VA responded steadily for about 18 generations and then its rate of progress declined. VB rose considerably in the first two generations. It then made only slight progress until generation 8 when its rate of progress increased considerably. The realized heritabilities calculated from the regression of response

on cumulative selection differential during the periods generations 0-9, 10-19, and 20-28 are given in the following tabulation:

Generations	Realized Heritability of Line		
	VA	VB	VC
0-9	$0.19 \pm 0.01$	$0.13 \pm 0.02$	$0.17 \pm 0.02$
10-19	$0.13 \pm 0.01$	$0.13 \pm 0.01^*$	$0.08 \pm 0.01$
20-28	$0.05 \pm 0.01$		$0.04 \pm 0.01$

\* For generations 10-18 only.

The heritabilities over the first nine generations were similar to those in the first paper and those of Frankham, Jones, and Barker (1968).

### (c) *Effective Population Size*

The effective population size ( $N_E$ ) can be estimated from the variance of the contributions of the families to the next generation ( $V_{n+1}$ ), since

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

where  $N$  is the number of parents (Jones 1969). The mean variances for five-generation periods and the harmonic mean of  $N_E$  are shown in Table 1 together with the harmonic means of the numbers of parents which produced offspring. The effective population size was generally less than the actual number but the reduction was not very great.

TABLE 1

VARIANCES OF THE PERCENTAGE CONTRIBUTIONS OF FAMILIES TO THE NEXT GENERATION, EFFECTIVE POPULATION SIZES ( $N_E$ ), AND NUMBERS OF PARENTS PRODUCING OFFSPRING ( $N$ ) (ALL AVERAGED OVER FIVE GENERATIONS)

Generations	Line VA			Line VB			Line VC		
	$V_{n+1}$	$N_E$	$N$	$V_{n+1}$	$N_E$	$N$	$V_{n+1}$	$N_E$	$N$
0-4	51.0	19.80	18.75	74.0	16.13	19.15	57.0	18.69	18.75
5-9	55.0	19.05	19.56	58.0	18.52	18.27	55.0	19.05	18.65
10-14	63.0	17.70	18.27	87.5*	14.55*	14.92*	51.0	19.80	19.15
15-19	101.0	13.24	13.43	312.5†	5.52†	6.96†	54.0	19.23	18.65
20-24	150.0	10.00	12.63				50.0	20.00	19.15
25-28	75.0	16.00	15.16				58.8	18.39	19.46

\* Generations 10-13 only.

† Generations 14-17 only.

Greatest reduction was in the early generations of VB. In VC there was no evidence of a change in the effective population size with time. The number of sterile matings in this line remained low throughout the selection programme. Natural selection reduced the effective population size drastically in VB after generation 12 when at least half the matings each generation were sterile until the line was lost at generation 18. Similarly, about half the matings in VA after generation 16 produced less than five pairs of offspring.

(d) *Variance of Contributions to Later Generations*

In the previous paper, the variance of contributions of individuals in any generation increased for a few generations. The mean for five-generation periods of the variance of the contributions in a particular generation to the line five generations later ( $V_{n+5}$ ) is shown in Table 2. Because of the low numbers of fertile families in VA and VB in later generations, variances for these generations are not shown. Table 2 also shows the ratio mean  $V_{n+5}$ /mean  $V_{n+1}$ . This ratio was generally about 2. The most notable exceptions were generations 0-4 of VB when  $V_{n+5}$  was no higher than  $V_{n+1}$ . In VB,  $V_{n+1}$  was considerably higher than in VA or VC at this stage but  $V_{n+5}$  was lower. After generation 5,  $V_{n+5}/V_{n+1}$  increased considerably in VB while in VA and VC there was not much change in this ratio throughout the programme.

TABLE 2  
AVERAGE FOR FIVE-GENERATION PERIODS OF THE VARIANCE OF THE PERCENTAGE CONTRIBUTIONS IN A PARTICULAR GENERATION TO THE LINE FIVE GENERATIONS LATER AND THE RATIO  $V_{n+5}/V_{n+1}$

Generations	Line VA		Line VB		Line VC	
	$V_{n+5}$	$V_{n+5}/V_{n+1}$	$V_{n+5}$	$V_{n+5}/V_{n+1}$	$V_{n+5}$	$V_{n+5}/V_{n+1}$
0-4	107.28	2.10	72.89	0.98	126.16	2.21
5-9	115.44	2.10	161.96	2.79	119.88	2.18
10-14	140.98	2.24	126.14*	1.44*	113.58	2.23
15-19	169.95†	1.68†			127.92	2.37
20-24					82.47	1.65

\* Generations 10-13 only.

† Generations 15-18 only.

The relationship between the lines can be calculated from the contributions of common ancestors. If  $P_{iA}$  and  $P_{iB}$  are the proportions of genes from the  $i$ th common ancestor in lines A and B, the genetic relationship is  $\Sigma P_{iA}P_{iB}$  (James 1962). As the initial parents came from 10 full-sib families the genetic relationship was initially 0.05. There was little overall change in the genetic relationship. After five generations, the relationship between VB and VC ( $r_{BC}$ ) increased to 0.076,  $r_{AC}$  declined to 0.036, whilst  $r_{AB}$  was unchanged at 0.050. This agreed with the results of Jones (1969), where the average genetic relationship between the lines did not change appreciably.

In the previous paper, individual families made very large contributions to some lines. This has occurred occasionally in the lines here with individual families in some generations making large contributions to the line five generations later. In VA, two families in generation 0 contributed 42.8 and 29.4% respectively of the genes in generation 5. This effect did not become very pronounced again in this line until generation 14, when three families contributed 96.2% of the genes. Similarly, 90.6% of the genes came from three families in generation 15, and 89.1% came from three in generation 16. In VB, 65.9% of the genes came from one family in generation 7, while 64.4% came from two families in generation 6. All the genes in VC at generation 5 came from only four families in generation 0, 79.7% coming from

two families. Again at generation 17, only four families contributed all of the genes still present in the line at generation 22, and in a few generations (9, 11, 16, and 18) only five families were still represented five generations later.

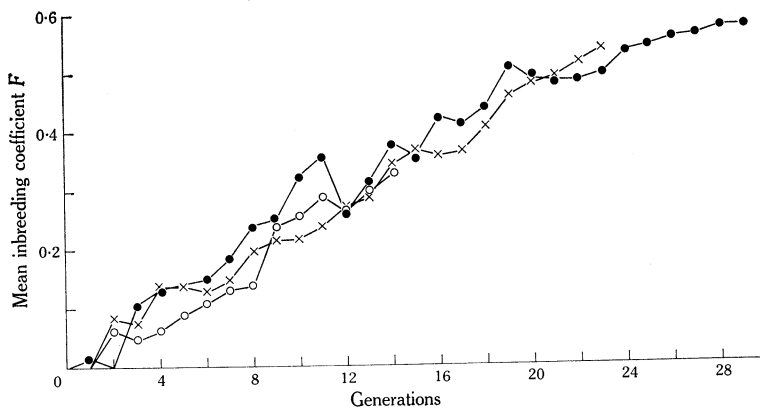


Fig. 2.—Mean inbreeding coefficients of the parents selected from each generation (experiment 1).  $\times$  VA;  $\circ$  VB;  $\bullet$  VC.

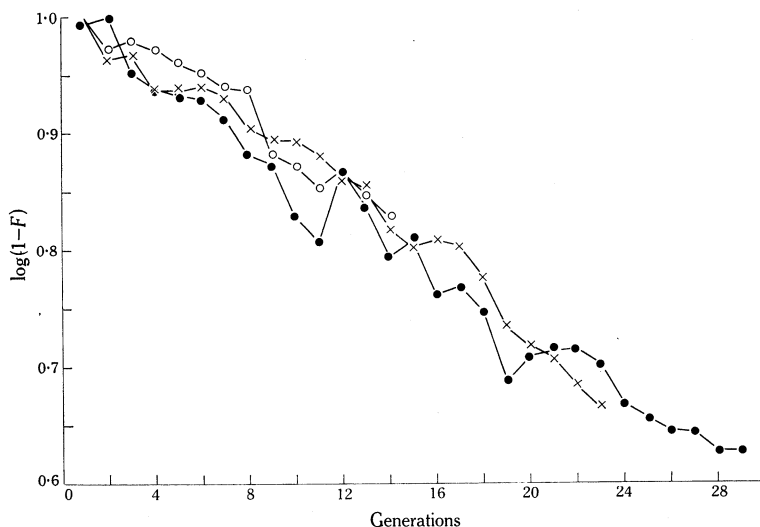


Fig. 3.—Change in  $\log(1-F)$  of the lines in experiment 1. Key as for Figure 2.

#### (e) Inbreeding Coefficients

The mean inbreeding coefficients ( $F$ ) of the parents selected each generation are shown in Figure 2. If the effective population size were constant,  $\log(1-F)$  would be expected to decline linearly with time. Figure 3 shows  $\log(1-F)$  for each generation. There were large generation to generation fluctuations, the most notable being considerable falls in  $F$  in VC at generations 11 and 19. As there was no restriction against full-sib mating, there was large variation in inbreeding coefficients among individuals within a line and generation. Also, McBride and James (1965) showed that highly inbred individuals were less likely to produce offspring. This accounted

for some of the generation to generation fluctuations of McBride and Robertson's (1963) lines. The rate of inbreeding was considerably higher in VC during the early generations, but from generation 11 onwards its inbreeding coefficient was similar to that of VA. The inbreeding coefficients of VB after generation 13 and VA after generation 22 are not given because of the low numbers of families producing sufficient progeny. The decrease in  $N_E$  due to natural selection would be sufficient to mask the effect of artificial selection and it is the latter in which we are chiefly interested.

The inbreeding effective population size ( $N_I$ ) can be estimated from the regression of  $\log(1-F)$  on generations. Estimates for different periods are shown in the following tabulation:

Generations	Inbreeding Effective Population Size in Line:		
	VA	VB	VC
0-9	20.58	17.18	13.02
10-19	13.02		13.48
20-28			17.48

$N_I$  was considerably less than  $N$  in VC during the first 20 generations but the reduction in  $N_I$  was less during the last few generations.  $N_I$  was quite high during the early generations of VA but it declined after generation 10.  $N_I$  in VB during generations 0-9 was intermediate between that of VA and VC.

### III. EXPERIMENT 2

#### (a) *Materials and Methods*

Lines were selected with 10 pairs of parents and a selection intensity of 20% for five generations. The lines were initiated from lines which had experienced several generations of individual selection with mass-mating of parents. There were two replicates of each treatment (designated *A* and *B*). As with the lines in the previous paper, the lines were initiated with one pair from each of 10 full-sib families. Thus, with reference to the mass selection line as base, the genetic relationship between replicates was 0.05. Selection and culture techniques were similar to those in the previous paper, with three spare matings set up each generation.

The selection lines used as base populations were:

- 100(50%): selected for 15 generations with 100 pairs of parents, 50% selection intensity
- 40(20%)*a*: selected for 38 generations with 40 pairs of parents, 20% selection intensity
- 10(20%)*a*: selected for 38 generations with 10 pairs of parents, 20% selection intensity
- 10(20%)*c*: same procedure as for 10(20%)*a*.

The responses for 40(20%)*a*, 10(20%)*a*, and 10(20%)*c* are described by Jones, Frankham, and Barker (1968). Treatment 100(50%) was provided by Miss B. Hollingdale. At the time these lines were initiated, 40(20%)*a*, 10(20%)*a*, and 100(50%) were still responding to selection. On the other hand, 10(20%)*c* was giving only small response in males and none in females.

#### (b) *Response to Selection*

The mean bristle numbers (averaged over sexes) each generation are shown in Figure 4. Table 3 shows the average of female and male heritabilities. Both replicates of 40(20%)*a* continued to respond at a similar rate while neither replicate of 10(20%)*c* gave any significant response. On the other hand, the two replicates of 100(50%)

diverged considerably even though both responded. One replicate (*B*) of 10(20%)*a* gave appreciable response while 10(20%)*aA* gave no response. Much of the difference in behaviour of these two lines may have been due to sampling in the first generation as 10(20%)*aB* started at a lower level than 10(20%)*aA*.

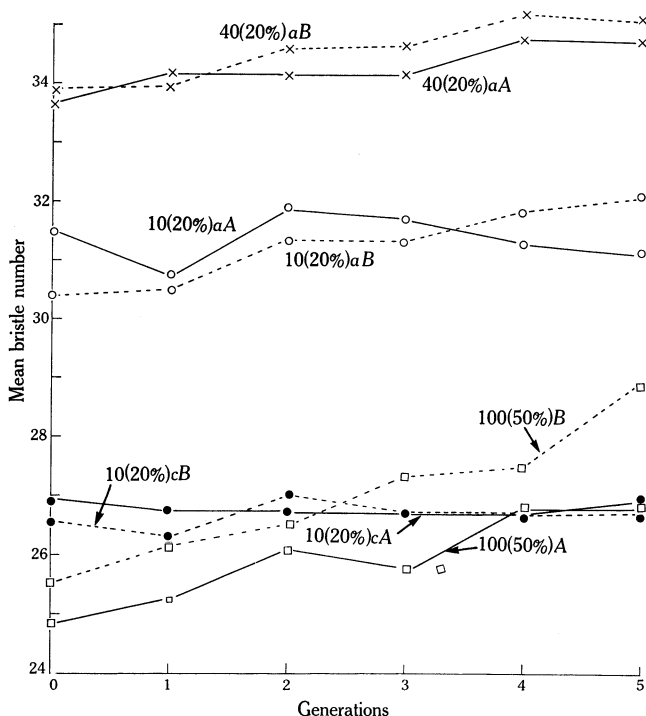


Fig. 4.—Response to selection of the individual lines in experiment 2.

TABLE 3  
AVERAGE OF MALE AND FEMALE REALIZED HERITABILITIES ( $h^2$ )  
IN EXPERIMENT 2

Line	$h^2$	Line	$h^2$
100(50%) <i>A</i>	$0.15 \pm 0.02$	10(20%) <i>aA</i>	$0.00 \pm 0.03$
100(50%) <i>B</i>	$0.21 \pm 0.02$	10(20%) <i>aB</i>	$0.12 \pm 0.02$
40(20%) <i>aA</i>	$0.07 \pm 0.02$	10(20%) <i>cA</i>	$-0.01 \pm 0.01$
40(20%) <i>aB</i>	$0.08 \pm 0.03$	10(20%) <i>cB</i>	$0.02 \pm 0.01$

(c) *Effective Population Size*

The variances of the contributions to the next generation are given in Table 4 together with the harmonic mean effective population size ( $N_E$ ) and the ratio of  $N_E$  to the effective population size expected with random sampling of parents from the same populations ( $N_R$ ).

A similar reduction in  $N_E$  occurred in 40(20%)*aA*, 40(20%)*aB*, 100(50%)*B*, and 10(20%)*aB* ( $N_E/N_R$  approximately 0.85), all of which responded to selection. The reduction in the remainder of the lines was less, and of these only 100(50%)*A* responded to selection.  $N_E$  was within the range of the 20% lines in the previous paper (Jones 1969). Sterility was quite low in the lines and the spare vials were needed only occasionally. Unfortunately, one family in each of 10(20%)*aB* and 100(50%)*B* in generation 0 were sterile. At this generation spare matings were not made so the expected effective population size was reduced slightly. This made only a small difference to the average over six generations.

TABLE 4  
VARIANCE OF THE PERCENTAGE CONTRIBUTIONS OF THE FAMILIES TO THE NEXT GENERATION, THE MEAN EFFECTIVE POPULATION SIZE, AND THE RATIO OF THIS TO THE EFFECTIVE POPULATION SIZE EXPECTED WITH RANDOM SAMPLING

Generation	100(50%)		40(20%) <i>a</i>		10(20%) <i>a</i>		10(20%) <i>c</i>	
	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>
0	40.0	70.0	40.0	70.0	55.0	40.0	30.0	20.0
1	70.0	25.0	45.0	45.0	35.0	40.0	35.0	60.0
2	55.0	35.0	35.0	55.0	45.0	40.0	65.0	20.0
3	35.0	50.0	60.0	70.0	55.0	70.0	40.0	50.0
4	35.0	65.0	35.0	75.0	25.0	90.0	35.0	35.0
5	35.0	85.0	105.0	40.0	35.0	50.0	50.0	70.0
Mean $V_{n+1}$	45.00	55.00	53.33	59.17	41.67	55.00	42.50	42.50
$N_E$	21.05	19.05	19.36	18.32	21.82	19.05	21.62	21.62
$N_E/N_R$	0.947	0.857	0.871	0.824	0.982	0.857	0.973	0.973

(d) Inbreeding Coefficients

The mean inbreeding coefficients of the parents selected each generation are given in Figure 5. Matings were set up for generation 6 but the progeny were not

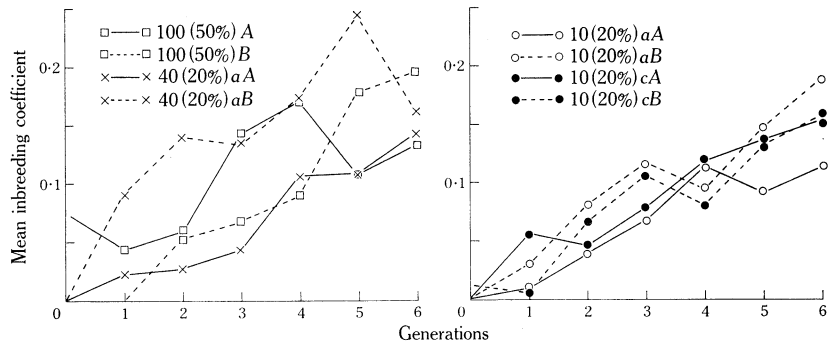


Fig. 5.—Mean inbreeding coefficients of the parents selected from generations 0 to 5 and of the progeny in generation 6.

scored, and values given for this generation were the mean coefficients of these progeny. There were large fluctuations between generations in a few of the lines. Over the short period here, it was not possible to get a reasonable estimate of effective



population size from the inbreeding coefficients. Highest levels of inbreeding at generation 6 were 40(20%)*aB*, 10(20%)*aB*, and 100(50%)*B*, which were also giving reasonable response to selection. However, the inbreeding coefficients of 10(20%)*cA* and 10(20%)*cB* were almost as high at generation 6. With the large fluctuations in some lines, it is difficult to discern any effect of the parent lines on inbreeding coefficients.

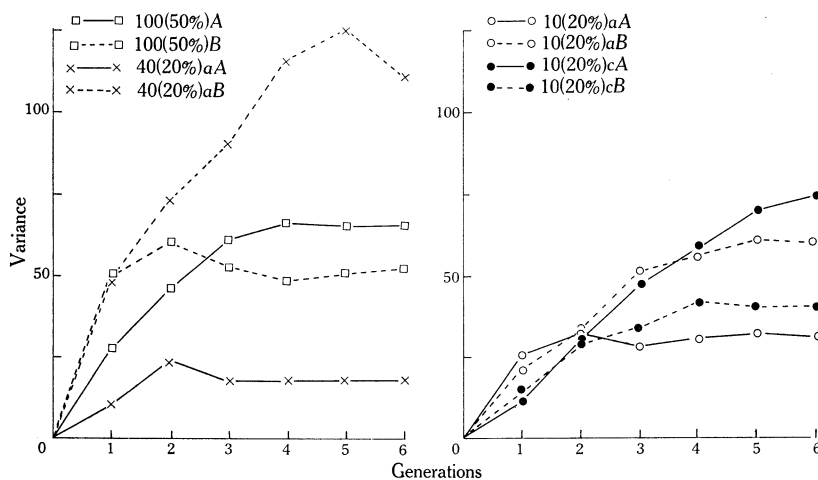


Fig. 6.—Variances of the contributions of the initial families to each generation.

#### (e) Contributions of Initial Families

The variance of the contributions of the initial families to each generation are shown in Figure 6. The variance generally increased for two or three generations and then remained steady. In 10(20%)*cA*, it was still increasing at generation 6. A similar pattern was found in the lines from the base population (Jones 1969) where the variance increased for several generations in a few lines, while in other lines it did not change after two or three generations. Genetic relationships ( $r_G$ ) between pairs of replicates at generation 6 are given in the following tabulation:

Treatment	100(50%)	40(20%) <i>a</i>	10(20%) <i>a</i>	10(20%) <i>c</i>
$r_G$	0.062	0.043	0.054	0.047

There were only small changes in the relationship from the initial values of 0.05 in any of the treatments.

#### (f) Contributions of Families in Later Generations

The variances of the contributions of families in early generations to generation 6 ( $V_6$ ) are given in Table 5, with the ratios of mean  $V_6$ /mean  $V_{n+1}$ . The only line in which the variance did not increase appreciably was 10(20%)*aA*. The numbers of families from each generation still represented at generation 6 are given in Table 6. Rarely were all families still represented at this generation. The lowest numbers still represented were in 40(20%)*aB* where only five families from generation 3 and six from generations 2 and 4 were still represented.

A large percentage of the genes at generation 6 in some lines came from only a few families. One family in each of generations 0 and 1 of 100(50%)*A* contributed 30.2 and 37.8% of the genes respectively. With 100(50%)*B*, 33.1 and 37.5% of the genes were contributed by one family in each of generations 0 and 3 respectively.

TABLE 5  
VARIANCES OF THE CONTRIBUTIONS OF FAMILIES IN EARLY GENERATIONS TO GENERATION 6, AND  
RATIO OF MEAN  $V_6$ /MEAN  $V_{n+1}$

Generation	$V_6$ of Line 100(50%)		$V_6$ of Line 40(20%) <i>a</i>		$V_6$ of Line 10(20%) <i>a</i>		$V_6$ of Line 10(20%) <i>c</i>	
	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>
0	119.4	125.9	81.9	146.5	74.5	149.9	100.0	60.9
1	122.1	43.9	72.5	151.0	61.7	103.1	69.6	97.3
2	95.8	74.4	82.0	108.6	33.2	164.8	68.3	81.5
3	51.9	129.4	130.9	161.6	70.9	181.2	59.7	154.4
4	53.8	92.5	105.0	118.8	27.5	88.8	55.0	98.8
Mean $V_6$	88.6	93.2	94.5	137.3	53.6	137.5	70.5	98.6
$V_6/V_{n+1}$	1.88	1.90	2.20	2.18	1.25	2.46	1.72	2.66

Two families in each of generations 3 and 4 of 40(20%)*aA* contributed 62.5 and 57.5% of the genes respectively. One family in each of generations 0 and 1 of 40(20%)*aB* contributed 34.4 and 34.1% respectively, while 71.9% of the genes came from three families in generation 2, 66.2% from two families in generation 3, and 74.5% from three families in generation 4. In 10(20%)*aA*, no families contributed more than 30% of the genes, but in 10(20%)*aB*, 30.2, 40.0, and 41.2% were contributed by one family in each of generations 1, 2, and 3 respectively. One family in generation 0 of 10(20%)*cA* contributed 32.0% of the genes, while one family in each of generations 3 and 4 of 10(20%)*cB* contributed 37.5 and 30.0% of the genes respectively.

TABLE 6  
NUMBER OF FAMILIES FROM EACH GENERATION STILL  
REPRESENTED AT GENERATION 6

Genera- tion	100(50%)		40(20%) <i>a</i>		10(20%) <i>a</i>		10(20%) <i>c</i>	
	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>	<i>A</i>	<i>B</i>
0	8	7	8	8	8	7	7	9
1	8	9	8	7	8	7	7	8
2	7	8	8	6	9	6	8	9
3	8	7	8	5	9	7	8	7
4	8	6	8	6	10	7	9	9
5	8	7	8	8	9	9	9	9

#### IV. DISCUSSION

An interesting feature of the response of the lines in experiment 1 was that the line (VC) giving most response in the early generations was the lowest after generation 10. This rapid initial response caused an appreciable reduction in the effective population size in the early generations of VC. Thus, only four of the families in

generation 0 of this line were still represented five generations later, with most of the genes coming from only two families. The poor response in later generations could have been due to this early restriction in population size. Robertson (1966) found that restricting the initial sample to one full-sib family reduced the level of the plateau to about two-thirds of that of a line starting from 25 pairs. Changes in the ranking of replicates occurred in later generations of a few of the treatments of Jones, Frankham, and Barker (1968) and have been found by other workers (Clayton and Robertson 1957). These changes were probably due to the more rapid inbreeding in lines giving most response in early generations. This inbreeding would reduce the response in later generations, as much of the genetic variation would be fixed.

In VB, a period of rapid response coincided with a drastic reduction in effective population size. Thus 65.9% of the genes at generation 12 came from one family in generation 7. This period of rapid response led to a marked decline in fitness, which reduced the effective population size even further. It is likely that the rapid response was due to the increase in frequency of a gene with a deleterious effect on fertility but which either increased bristle number or was linked to a gene affecting bristle number. Alternatively, fitness may have declined as a result of the rapid inbreeding during this period of response. The decline in fitness of VA was less sudden and did not correspond with any change in the rate of response, so was probably a consequence of inbreeding depression.

An interesting feature of the response in experiment 2 was the difference between the replicates of 10(20%)*a* and of 100(50%). Only one replicate of 10(20%)*a* responded to selection, while the 100(50%) lines diverged considerably. According to Robertson's (1960) limits model, the effect of sampling in later generations should be less as all genes reach appreciable frequencies. Jones, Frankham, and Barker (1968) found that 10-pair lines taken off 40-pair lines at generation 16 fell behind after a few generations. This indicated that some genes were lost by sampling even at this stage. Latter (1966) showed that linkage of a few genes of similar effect would delay response to selection and would cause appreciable differences in the response patterns of replicates even after the genes were at intermediate frequencies.

In the previous paper (Jones 1969), lines giving most response to selection generally had smaller effective population sizes. On the whole, the lines here fitted the same pattern. The periods of rapid response causing reductions in the effective population sizes of VB and VC have already been mentioned. In experiment 1, the line giving the least response (VA) had the largest effective population size as measured from either the variance of contributions to the next generation (i.e.  $N_E$ ) or from the rate of inbreeding (i.e.  $N_I$ ). On the other hand, VB gave little response to selection between generations 2 and 8 but had a low  $N_E$ . The variance of the contributions of families in the early generations of VB did not increase after the first generation, whereas in both experiment 1 and 2 it generally increased for several generations as expected from Robertson (1961). The large variance of contributions to the next generation in the early generations of VB could have been due to an increase in the between-culture environmental variance. This would increase the variance of contributions to the next generation but would have little effect on subsequent changes in the variance. Further,  $N_I$  in these generations was considerably higher in VB than in VC, which was responding faster. Thus, apart from the low

value of  $N_E$  in VB, the relationship between response to selection and effective population size was similar in early generations of experiment 1 to that found by Jones (1969).

In experiment 1, there was little evidence of any consistent trend with time, in the effect of artificial selection on effective population size. The effects of artificial and natural selection on effective population size were confounded in later generations of VA and VB, while the change in effective population size of VC after its rate of progress declined was small. The variance of the contributions to the next generation was as high after generation 20, but the variance did not increase to the same level as in earlier generations. The rate of inbreeding was also lower after generation 20.

In experiment 2, lines giving response to selection had lower effective population sizes than those that did not. Thus, there was little reduction in the effective population size of 10(20%)*aA*, 10(20%)*cA*, and 10(20%)*cB*. The variance only increased by a factor of 1.25 in 10(20%)*aA* and 1.72 in 10(20%)*cA* after the first generation, but increased by a factor of 2.66 in 10(20%)*cB*. The variance of contributions to generation 6 in 10(20%)*cB* was as high as some of the lines giving appreciable response to selection. This was rather surprising as this line did not respond. The main selection line of 10(20%)*c* gave a small response in males over this period but none in the females (Jones, Frankham, and Barker 1968). In the two replicates here there was apparently no response in either sex. A change in the environmental variance would alter the variance of contributions to the next generation but would not account for the increase in variance over several generations. Selection may have been favouring a few genes at low frequency but with effects too small to produce much response over the short period studied.

With this one exception, the lines in experiment 2 fit the general conclusion that the effective population size will be reduced most in the lines giving greatest response to selection.

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