SELECTION FOR HIGH ADULT BODY WEIGHT IN DROSOPHILA POPULATIONS WITH DIFFERENT STRUCTURES[1]

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ABSTRACT

Selection for high adult body weight in *Drosophila melanogaster* was practiced for 18 generations in three selection lines. These lines were genetically similar and of equal size but different in population structure. One line represented a large mass-selected, random-mating population, while the other two lines simulated large populations that had been *subdivided* into partial isolates or demes. Mass selection and random mating occurred within each deme. These two subdivided lines were different only in the rate of effective migration among the demes (5% and 10%). Selection intensities of approximately 20% were applied to these populations. A fourth line served as a random mating control. Heritability of adult body weight in the base population was estimated to be 0.58± 0.22. The results indicate that significantly greater responses were achieved in the subdivided lines than in the large mass-selected line, in spite of the fact that larger selection differentials were applied to the latter. No significant differences in response were observed between the two subdivided lines. WRIGHT (1930, 1931) postulated that selection would be most efficient in subdivided populations with limited interdeme migration. The present findings appear to support this theory.

ONE area of the study of population genetics concerns the population structure which lends itself to the most efficient and fastest rate of evolution. FISHER (1930) proved in his Theorem of Natural Selection that the increase in average fitness of a population at any time is equal to its additive genetic variance of fitness at that time. This may be why the relative importance of epistasis in evolution was never stressed by FISHER. In discussing the implications of the Fundamental Theorem to evolution, FISHER (1930) implied that evolution would be fastest in a very large, random-mating population.

On the other hand, an alternative view of the evolutionary process was put forth by WRIGHT (1930, 1931) and was later termed the "three-phase shifting balance theory" (see WRIGHT 1970 for a more recent discussion). The three phases are, in order of occurrence, random drift, intrademe and interdeme selection. In this theory the importance of newly created epistatic systems within subdivisions of a large population is stressed.

Data collected from natural populations suggest that both epistatic systems and partial isolation have been of importance in the evolutionary history of

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many species (for example, see DOBZHANSKY 1970 and MAYR 1970). However, such evidence cannot be used to determine the kind of population structure that lends itself to the most efficient response to selection. What is required is to compare the responses to selection of populations with essentially equal sizes and genetic variability but that differ in structure. In addition, it is essential to have a knowledge of the selection pressures within each population at each generation. Biological data of this type can only be obtained from controlled laboratory experiments.

The present paper reports the results of selection for adult body weight in several populations of *Drosophila melanogaster* of equal size and genetic variability that differ only in their population structure.

MATERIALS AND METHODS

Genetic stock:

The strain of *Drosophila melanogaster* used in this study was a wild-type stock synthesized approximately 25 generations prior to the start of the present study by a four-way cross of four laboratory cultures (Seto, Swedish, B, Lauoanne S, and Wageningen). The population was maintained by randomly mating 40 pairs of parents each generation. This stock will be referred to as Crossbred.

Populations:

Each of 30 pairs of flies, randomly collected from the Crossbred stock, was placed in an individual vial. Although the females were most likely already inseminated, a male was included to assure fertility. The progeny that emerged from these vials comprised the base population.

Four pairs of flies were collected from each of the 30 families in the base population and used to establish four experimental lines, each consisting of 60 individuals. Each family was equally represented in each of the four lines by two sibs, a male and a female, so that the initial gene pools of the four lines were similar. The experimental lines were designated A, B1, B2, and C. Within each line, the 30 pairs of flies were randomly allotted to one of six bottles, five pairs per bottle. The resultant progeny that emerged within each line represented experimental generation 0.

Selection methods:

Lines A, B1, and B2 underwent selection for high adult body weight for a period of 18 generations. Line C served as a random-mating control population. All flies were reared on standard cornmeal media at 25° and approximately 65% relative humidity. All weighings were done on a Schultz Model 30 electronic microbalance and recorded to the nearest one-hundredth milligram. All flies were separated according to sex and aged from 36 to 48 hours after emergence prior to being weighed to reduce the phenotypic error variance since fluctuations in weight occur immediately following emergence.

In control line C, approximately 40 males and 40 females from each bottle were usually weighed separately *en masse*. However, individual weighings were performed at generations 0, 11, 15, and 18 so that variances of adult body weight could be estimated. Five males and five females were chosen at random from each bottle and assigned at random to each of six fresh bottles to become the parents of the next generation.

Mass selection and random mating were practiced in line A. In each generation approximately 25 males and 25 virgin females were collected from each of the six bottles and individually weighed. The thirty individuals of each sex with the highest adult body weight were selected to be parents and were randomly allotted to six fresh bottles.

Lines B1 and B2, however, simulated subdivided populations. Mass selection and random mating were, therefore, performed *within* each of the six bottles comprising each line. Thus,

the five heaviest of each sex within the sample from each bottle were selected as parents. In addition, the six bottles within both lines B1 and B2 exchanged a single selected female in a cyclic design. Such "migration" of females occurred every generation in line B1 but only every other generation in line B2. Hence the effective migration rates in lines B1 and B2 were ten percent and five percent, respectively.

After selection of parents in lines A, B1, and B2 was completed, an additional 20 females and males were collected and weighed *en masse*, sexes separately, from each bottle to obtain a more precise estimate of the mean weight for each line.

Under these selection schemes, line A represented a relatively large, mass-selected, panmictic population, while lines B1 and B2 simulated populations subdivided into six partial isolates. In particular, the three selection lines and the control line all were of equal size (but differed somewhat in *effective* size) and of similar genetic composition. Hence any differences that resulted among the responses of the selection lines might be attributed to population structure.

Relaxation of selection:

At generation 14, subcultures of lines A, B1, and B2 were used to establish relaxed selection lines designated RA, RB1, and RB2, respectively. In lines RB1 and RB2, the subdivided structure remained intact, and migration proceeded exactly as in lines B1 and B2. These relaxed selection lines were maintained until generation 18.

Estimation of heritability:

Heritability of body weight was initially estimated within the base population and again at generation 18 within each of the selection lines and the control line. The method of estimation was that of a nested analysis using full-sib data (TURNER and YOUNG 1969) in which only the sire components were used to estimate the additive genetic variances. Approximate standard errors of the heritability values were calculated according to DICKERSON (1959).

RESULTS

Estimates of the parameters of adult body weight in the base population are presented in Table 1. The disparity between the variances of males and females is well established in Drosophila and may be attributed to scaling effects (FALCONER 1960). Heritability of adult body weight in the base population was estimated to be 0.58 ± 0.22, suggesting that selection should lead to substantial genetic progress.

The statistics of the individuals collected from the base population and used as progenitors of the experimental lines are presented in Table 2. The mean weights within sexes among lines are nearly identical, as expected, since the gene pools of the four lines are similar.

Linear regression analyses of the means of the control line on generation number were performed. The regression coefficients and associated standard errors of the female, male, and pooled progeny body weight analyses were

TABLE 1

Adult body weight statistics of the base population

Sex	Number (N)	Mean (mg)	Variance	Coefficient of variation in percents
Females	120	1.56 ± 0.009	0.0104	6.54
Males	120	0.99 ± 0.004	0.0021	4.67

TABLE 2

Adult body weight statistics of progenitors of experimental lines

Line	Females			Males		
	N	$\bar{X}$ (mg)	C.V.	N	$\bar{X}$ (mg)	C.V.
C	30	1.57 ± 0.03	9.87	30	0.98 ± 0.01	6.43
A	30	1.57 ± 0.03	11.53	30	0.99 ± 0.01	7.98
B1	30	1.55 ± 0.03	10.00	30	0.99 ± 0.02	9.49
B2	30	1.55 ± 0.03	8.97	30	0.99 ± 0.01	7.88

-0.001 ± 0.003, 0.001 ± 0.001, and 0.000 ± 0.002, respectively. In all three instances, the regressions were nonsignificant statistically.

The mean weights of females, males and pooled progeny of the three selection lines (expressed as deviations from the control) are plotted against generation number in Figures 1, 2 and 3, respectively. In general, mass selection line A was superior to both subdivided lines B1 and B2 in mean weights until generation 5. From generation 5 onwards, both lines B1- and B2 tended to be superior over line A.

A nested factorial analysis of variance of body weight among generations, lines, and sexes was performed on the data. Because of unequal subclass numbers, the analysis was performed on the unweighted within-bottle sex means. An unbiased pooled error term was then obtained from available data over all generations by dividing the pooled estimate of individual variance by the harmonic mean of the various subclass numbers (SNEDECOR and COCHRAN 1967). Unbiased estimates of individual variances for each sex had previously been found to be homogeneous over both lines and generations by means of a

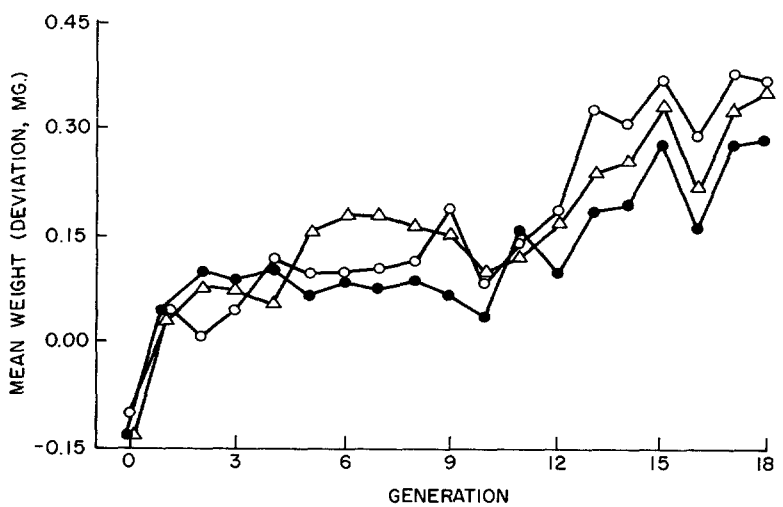

FIGURE 1.—Mean female weights of the three selection lines (expressed as deviations from the control). ●—● mass-selected line A; ○—○ subdivided line B1; △—△ subdivided line B2.

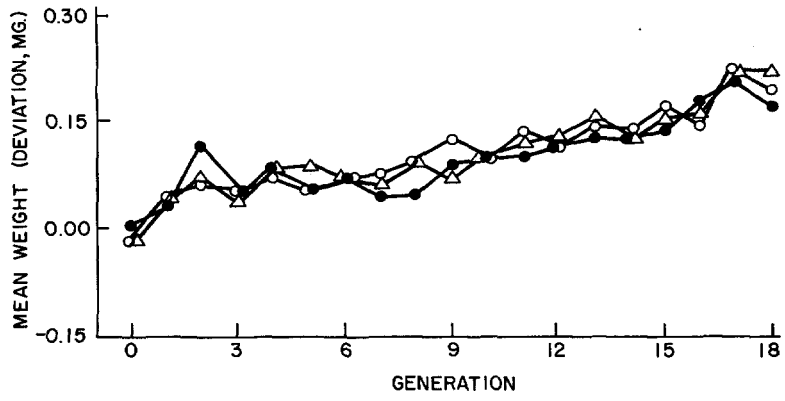

FIGURE 2.—Mean male weights of the three selection lines (expressed as deviations from the control).

Bartlett's test (SNEDECOR and COCHRAN 1967). In this analysis the within-bottle means of each sex were first transformed to logarithms, in an attempt to reduce the heterogeneity between female and male variances. Accordingly, the pooled estimate of individual variance utilized in the error mean square was also calculated from logarithmic units. A summary of the analysis is presented in Table 3. All main effects and interaction terms are highly significant. The estimated line effects (in untransformed units) are of particular interest and are presented in Table 4 together with orthogonal comparisons partitioned from the lines sum of squares.

The cumulated unweighted selection differentials of each line are presented

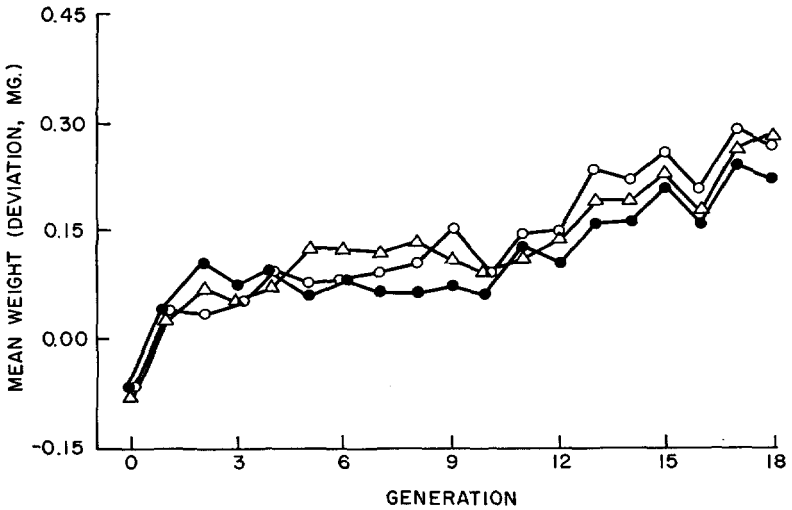

FIGURE 3.—Mean pooled weights of the three selection lines (expressed as deviations from the control).

TABLE 3

Analysis of variance of body weight between generations, lines, and sexes

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Between generations	18	0.380243	0.021125	105.63***
Between lines	3	0.372379	0.124126	620.63***
Between sexes	1	9.711919	9.711919	198202.43***
Generations × lines	54	0.136245	0.002523	12.62***
Generations × sexes	18	0. 11478	0.000638	13.02***
Lines × sexes	3	0.004016	0.001339	27.33***
Generations × lines × sexes	54	0.54542	0.001010	20.61***
Bottles within generations and lines	380	0.075978	0.000200	11.77***
Residual sexes × bottles	378	0.018504	0.000049	2.88***
Pooled error	>38000	----------	0.000017	

*** $P<.001$

in Table 5. The total cumulated selection differential of line A at generation 18 is 13% and 10% larger than those of lines B1 and B2, respectively.

It is interesting to note that while no significant difference is found between the effects of lines B1 and B2 (Table 4), both are significantly greater than that of line A ($P < 0.001$), in spite of the fact that *greater* selection differentials were consistently applied to line A over the 18 generations.

Estimates of realized heritabilities of female, male, and pooled progeny weights are presented in Table 6 for all three selection lines. The top estimates were obtained by regression of genetic gain (expressed as deviations from the control) on cumulated midparent selection differential. Pooled progeny realized heritabilities were also estimated by the ratio of total response (expressed as deviation from the control) to total cumulated selection differential (HILL 1972)

TABLE 4

Orthogonal comparisons between lines

Line effect $\hat{\beta}_C = -0.10$
$\hat{\beta}_A = 0.02$
$\hat{\beta}_{B1} = 0.04$
$\hat{\beta}_{B2} = 0.04$

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
β_C *vs.* β_A, β_{B1}, β_{B2}	1	0.364571	0.364571	1822.86***
β_A *vs.* β_{B1}, β_{B2}	1	0.007788	0.007788	38.94***
β_{B1} *vs.* β_{B2}	1	0.000020	0.000020	0.10^{ns}
Bottles within generations and lines	380	0.075978	0.000200	

*** $P<.001$

TABLE 5

Cumulated midparent selection differentials in body weight (mg) of the three selection lines

Generation	Line		
	A	B1	B2
0	0.00	0.00	0.00
1	0.14	0.14	0.12
2	0.27	0.23	0.21
3	0.39	0.34	0.36
4	0.50	0.46	0.44
5	0.61	0.57	0.54
6	0.75	0.69	0.69
7	0.88	0.80	0.85
8	1.02	0.94	1.01
9	1.16	1.08	1.14
10	1.32	1.21	1.28
11	1.50	1.35	1.42
12	1.68	1.48	1.52
13	1.84	1.61	1.66
14	2.01	1.75	1.82
15	2.18	1.89	2.00
16	2.34	2.02	2.14
17	2.46	2.19	2.29
18	2.69	2.38	2.45

and are also presented in Table 6 (bottom). The standard errors of all estimates of realized heritability in this study were calculated following the methods developed by HILL (1971, 1972) that corrected for the correlation of generations means due to random drift in finite populations.

It can be seen that in every case, greater realized heritabilities are obtained in subdivided lines B1 and B2 than in mass selection line A. No consistent relationship is found among the estimates of lines B1 and B2. Although female and pooled progeny heritabilities estimated by regression techniques are greater

TABLE 6

Estimates of realized heritability of female, male, and pooled weights for the three selection lines

	Line	Females (S.E.)	Males (S.E.)	Pooled progeny (S.E.)
I†	A	0.10 (0.02)	0.05 (0.01)	0.08 (0.01)
	B1	0.17 (0.02)	0.07 (0.01)	0.12 (0.01)
	B2	0.13 (0.02)	0.07 (0.01)	0.10 (0.01)
II††	A	....	....	0.11 (0.01)
	B1	....	....	0.14 (0.02)
	B2	....	....	0.15 (0.01)

† Realized heritability estimated using regression technique.
†† Realized heritability estimated using ratio technique.

in line B1, the realized heritabilities of males are the same. Furthermore, realized heritability of pooled progeny weight estimated by the ratio method is greater in line B2.

It is also interesting to note from Table 6 that realized heritability of female weight is about twice that of male weight in each line. This might suggest the presence of some sex-linked loci affecting adult body weight and/or a genotype-sex interaction (EISEN and LEGATES 1966).

For ease of inspection, the pooled progeny mean weights of each line (expressed as deviations from the control) are plotted against cumulated selection differential in Figure 4. The responses of each line appear to go through three phases. Rapid progress is achieved during the first two generations, followed by little gain from generations 2 to 10. Finally, from generations 10 to 18, each line again appears to achieve significant progress. Consequently, realized heritabilities were calculated for each line for each of these three phases. The results are summarized in Table 7. Estimates for phases 2 and 3 were calculated by means of regression, while those of phase 1 were calculated using the ratio method (HILL 1972).

As expected, very large realized heritabilities were obtained during the initial phase, ranging from 0.43 to 0.71. Since only two generations had elapsed in phase 1, it might be argued that the responses of the three lines during this period were replicates of each other. Hence a mean of the three realized heritabilities of this first phase, weighted by the reciprocal of the variances, was calculated. A value of 0.58 $\pm$ 0.05 was obtained, virtually identical to the estimate of heritability in the base population.

During the second phase of response (generations 2 to 10), lines B1 and B2 responded to selection at much smaller rates, while line A actually regressed.

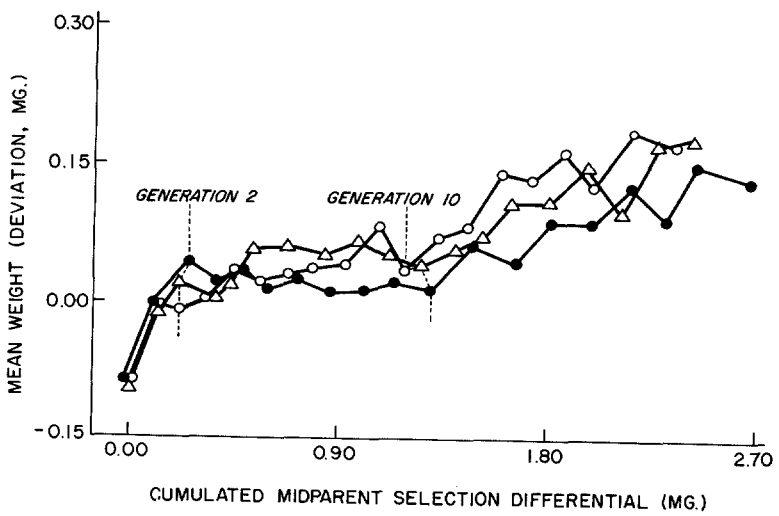

FIGURE 4.—Mean pooled weights of the selection lines (expressed as deviations from the control) plotted against cumulated midparent selection differential.

TABLE 7

Estimates of realized heritability of pooled weight during each of the three phases of selection response

Line	Phase 1	Phase 2	Phase 3
A	0.63 (0.08)	−0.03 (0.01)	0.11 (0.02)
B1	0.43 (0.09)	0.08 (0.01)	0.15 (0.02)
B2	0.71 (0.11)	0.04 (0.01)	0.15 (0.02)

From generations 10 to 18, all lines responded in a positive direction, although both subdivided lines again exhibited greater genetic gains per unit of selection differential than did line A.

Heritabilities of body weight were again estimated after 18 generations of selection by the nested full-sib analyses and are presented in Table 8. Heritability in the control line was estimated to be 0.68, in good agreement with that estimated in the base population (0.58). Heritabilities in lines A and B2 were quite similar and considerably less than that of the control line. However, heritability in line B1 was unexpectedly large (0.82). The standard errors for these estimates are large and are, no doubt, due to relatively small sample sizes used in the estimations. Therefore, these values of heritability can only be interpreted as being very approximate.

Mean weights (expressed as deviations from the control) of females, males, and pooled progeny of the relaxed selection lines are plotted against generation number in Figures 5, 6, and 7, respectively. The fitted regression lines are also included. The regression coefficients of the lines are presented in Table 9. Although all nine regressions were negative, none were significant statistically at the 5% significance level.

DISCUSSION

The primary aim of this investigation was to compare hypotheses, advanced respectively by FISHER (1930) and WRIGHT (1930, 1931), regarding the relationships between population structure and response to selection.

It is clear from the results that from generation 5 until the last generation, both subdivided lines B1 and B2 were consistently superior in weight to line A, in spite of the greater selection pressure applied to line A during this same

TABLE 8

Heritability of body weight obtained by full-sib analysis in lines C, A, B1, and B2 at generation 18

Line	h^2	Standard error	Number of observations
C	0.68	0.36	272
A	0.38	0.27	262
B1	0.82	0.38	247
B2	0.42	0.35	205

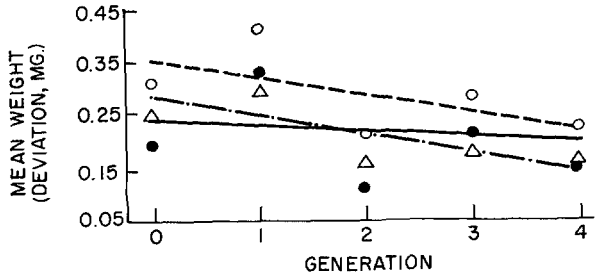

FIGURE 5.—Regression of mean female weights of the relaxed selection lines (expressed as deviations from the control). ●—● relaxed line RA; ○—○ relaxed line RB1; △—△ relaxed line RB2.

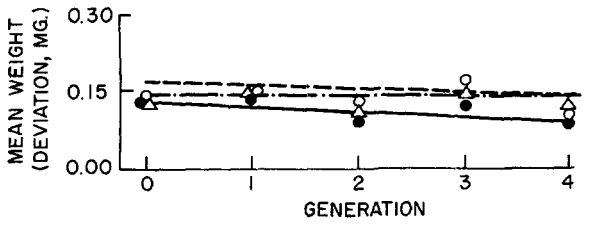

FIGURE 6.—Regression of mean male weights of the relaxed selection lines (expressed as deviations from the control).

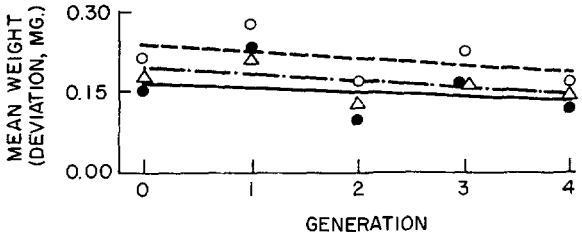

FIGURE 7.—Regression of mean pooled weights of the relaxed selection lines (expressed as deviations from the control).

period. Over the 18 generations of selection, both lines B1 and B2 had significantly greater mean weights than line A (Tables 4 and 5). Furthermore, various realized heritabilities of body weight calculated throughout this experiment showed that greater gains in body weight per unit of selection differential were obtained in the subdivided lines. It is reasonable to conclude, therefore, that under the present circumstances, selection was significantly more efficient in subdivided lines with limited migration than in a mass-selected panmictic line.

In general, no significant differences in selection response were observed between lines B1 and B2. Hence the difference in migration rates of these two lines (10% versus 5%) had apparently no significant effect upon the rate of gain in these lines.

TABLE 9

Summary of the regression analyses of the relaxed selection lines

Line	Female weight	Male weight	Pooled progeny weight
RA	−0.022 (0.028)	−0.008 (0.007)	−0.014 (0.016)
RB1	−0.031 (0.023)	−0.004 (0.008)	−0.015 (0.014)
RB2	−0.032 (0.014)	−0.002 (0.005)	−0.015 (0.009)

If the conclusions of the present study are correct, then it is pertinent to inquire as to why selection is more efficient in a subdivided population with limited migration. Since equal numbers of males and females were selected each generation, the effective size of the mass-selection line may be taken as slightly less than 60 individuals. The effective number is less than 60 because selected populations tend to become slightly more inbred than unselected populations (MORLEY 1954; ROBERTSON 1961). Within an individual isolate of the subdivided lines, the effective number is close to 10 individuals. In this instance the effects of migration among isolates would tend to offset any inbreeding due to selection. Obviously, a greater likelihood of random fixation (or extinction) of genes giving rise to adaptive epistatic systems (WRIGHT 1930, 1931) exists within the isolates of the subdivided lines than in the panmictic population.

GRIFFING (1960) has shown that, upon relaxation of selection, the population mean is expected to regress due to the random recombination of genes that leads to the loss or decay of the gain due to epistasis. In the present study, regressions of relaxed selection lines have been slight and nonsignificant statistically. Both relaxed subdivided lines RB1 and RB2 still maintained their superiority over line RA. The absence of any large and significant regression indicates either that epistatic effects were negligible in each of the selected lines, or that epistatic effects had been made permanent due to fixation in small populations. The superiority of the subdivided lines over line A could, therefore, be due to the chance occurrence of unique interactions within isolates followed by fixation of the genes involved.

An alternative explanation of the results is also possible. Assuming a completely additive model, WRIGHT (1951, 1952) has shown that the total genetic variance of a character in a population subdivided into partial isolates equals

$$\sigma^2 = (1+F)\sigma_0^2$$

where F is the inbreeding coefficient of the individual isolates, and σ_0^2 is the total genetic variance expected in a panmictic population with the same mean gene frequencies. Although selection in lines B1 and B2 was done entirely within isolates, the periodic migration among the isolates enabled selection to act, at least in part, on the total genetic variability within each subdivided line. Hence an alternative explanation of the superiority of subdivided lines B1 and B2 over line A could be due to the presence of the greater genetic variance in these lines.

KOJIMA (1961) investigated the effects of dominance on response to mass selection in finite populations. The conclusion is that changes in mean due to selection in small populations can be greater than, equal to, or smaller than

changes in larger populations, depending on the degree of dominance involved. In particular, gains in small populations are expected to be greater when dominance effects of the alleles involved are negative. In view of the high heritability of body weight estimated from the current population, the genetic variance due to dominance would be expected to be relatively small. Hence the superiority of the subdivided population, in terms of gain by selection, is unlikely to be due to the negative dominance of genes affecting body weight.

The experimental evidence presented in this study shows that the differences between the mass-selected line and the subdivided lines are large and highly significant statistically. The results, therefore, support WRIGHT's (1930, 1931) model of population structure in relation to rapid rate of selection response. The present study represents only an initial attempt to relate population structure to genetic gain.

In view of the possible implications of the importance of population structures on the rate of evolution and on the rate of genetic gain in breeding populations, further studies in this area appear to be of interest in both theoretical and applied genetics.

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