# SELECTION FOR PUPA WEIGHT IN *TRIBOLIUM CASTANEUM*. I. PARAMETERS IN BASE POPULATIONS[1]

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SELECTION is a useful tool in elucidating the genetic mechanisms involved in the inheritance of a quantitative character. Genetic changes in populations in response to different methods of selection depend on and therefore provide evidence concerning the underlying modes of inheritance of traits involved. (BELL *et al.* 1955; FALCONER 1955; FRASER and KINDRED 1960; KOJIMA and KELLEHER 1963; RICHARDSON and KOJIMA 1965; PROUT 1962; DAWSON 1965). The two main objectives of the selection experiment reported here are (1) to extend our understanding of the role linkage can play in the inheritance of a quantitative character and (2) to determine whether there is an appreciable contribution from overdominant loci to the genetic variation for the character. The scope of this paper is to describe the experimental approach in a long term selection study to attain these objectives and to characterize the base populations with respect to the genetic variance of pupa weight in the initial generations of the experiment. This study has much in common with work on postweaning growth in mice described by RAHNEFELD *et al.* (1963). It was initiated to complement the mouse study in ways possible with Tribolium but not mice.

## *Description of Experiment*

Two highly inbred lines of *Tribolium castaneum* were obtained from DR. A. SOKOLOFF at the University of California, Berkeley in 1963. These lines (CSI-5 and CSI-10) originated from the same synthetic stock and had been brother-sister mated for 38 generations at the time this experiment was initiated (see LERNER and HO [1961] for description of foundation stock). They were crossed to produce a segregating population to serve as a base for the selection experiment. The $F_3$ generation was subdivided into four populations of which two (the S-populations) were to be selected for heavier pupa weight and the other two (the C-populations) served as control lines.

Thirty-six males and 72 females are selected each generation in each population to serve as parents for the next generation. Each male is mated to two females. Matings are made at random with the one restriction being that full-sib matings are avoided. After the mating period, females are transferred to individual bottles for a three-day egg laying period. Pupa weighing is done on the 21st day counting from the middle day of egg laying. In each full-sib family five male and five female pupa are selected at random and weighed. If both female parents are fertile and leave sufficient progeny (at least five pupa of each sex), the data collected from a half-sib family will then consist of ten male and ten female pupa that had been sampled from the total number of pupa. Selection of individuals for use as parents is all on an intra-half-sib family basis. The heaviest male and two heaviest females are selected from each half-sib family in the S-popula-

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tions. The individuals (one male and two females) closest to the family mean for the appropriate sex are selected from each half-sib family in the C-populations. The four populations are divided into two-time replicates with one C-population and one S-population following the other two populations by a time lag of two weeks.

Individual selection will be continued within the S-population until it appears a plateau has definitely been reached. At that time the plateaued population will be subdivided into two populations. In one of the subpopulations, individual selection will be continued as a continuing check on the plateau. Selection for combining ability with one of the initial inbred lines will be initiated in the other subpopulation. The details of the experimental logic and approach for this stage of the experiment will be discussed in a later paper.

COMSTOCK and ROBINSON (1952) described an experiment (experiment 3 in their paper, but now commonly referred to as Design-III) for estimating "average dominance" of genes affecting a quantitative trait. Two homozygous lines and the segregating population derived from their cross are employed. Random individuals from the segregating population are backcrossed to each of the foundation lines and the progenies obtained are grown as the source of data for two genetic variance estimates. These in turn comprise the base for the estimate of "average dominance." In our use of this design, males from the segregating population are mated to females of both inbred lines to produce the backcross progenies. Data have been obtained using $F_2$ males. Later estimates are being obtained using males from both C and S-populations.

The experimental results that will be presented in this paper include (1) initial measures of heterosis to determine average directional dominance for pupa weight (2) a Design-III analysis to establish average levels of dominance for genes affecting pupa weight at the start of the experiment and (3) an analysis of the effects of the first 12 generations of selection for pupa weight as it relates to parameters in the populations.

## ANALYSIS AND RESULTS

*Heterosis for pupa weight:* During the establishment of the segregating populations that were to be used in the selection experiment a comparison was made between the reciprocal $F_1$ crosses and the original parent inbreds to check on heterotic effects for pupa weight. The mean pupa weights for the parent lines and reciprocal crosses for the two sexes are given in Table 1. The percent heterosis was measured as the difference between the averages of the $F_1$ means and the parental line means and expressed as a percentage above the parental line means. The heterosis exhibited for pupa weight indicates more dominance of genes for heavier pupa weight than for lighter weight. The amount of heterosis observed

TABLE 1

*Mean pupa weight by line and reciprocal crosses*

| Line | Pupa weight (micrograms) | |
|---|---|---|
| | Males | Females |
| CSI-5 | 1900 ± 43* | 2071 ± 31 |
| CSI-10 | 2377 ± 53 | 2514 ± 82 |
| CSI-5 male × CSI-10 females | 2504 ± 27 | 2558 ± 59 |
| CSI-10 male × CSI-5 females | 2333 ± 53 | 2471 ± 33 |
| Percent Heterosis | 13.0 | 9.7 |

* Standard errors calculated from full-sib family means with an average of four progeny per family.

TABLE 2

*Variance analysis for Design-III*

| Source of variations* | Degrees of freedom | Expected mean square† |
|---|---|---|
| Inbred lines | 1 | .... |
| Among $F_2$ males | $(n-1)$ | $\sigma_e^2 + 2b\sigma_m^2$ |
| $F_2$ males × inbred lines | $(n-1)$ | $\sigma_e^2 + b\sigma_{ml}^2$ |
| Bottles within lines and $F_2$ males | $2n(b-1)$ | $\sigma_e^2$ |

* Bottle means (progeny of a single inbred female) served as statistical unit.
† $\sigma_m^2$ is the progeny variance arising from genetic differences among $F_2$ male parents. $\sigma_{ml}^2$ is the progeny variance arising from interaction of genotypes of $F_2$ males and inbred parent females. $\sigma_e^2 = (1/n)\ \sigma_w^2 + \sigma_b^2$, where $\sigma_w^2$ is the variance among individuals within a bottle (progeny of a single $F_2$ male and one inbred female), and $\sigma_b^2$ is the variance due to progeny from different females of the same line being reared in separate bottles (this also includes any variance due to difference among females within an inbred line).

in this experiment was slightly larger than that reported by ENGLERT and BELL (1963) and BOYLAND and WONG (1965).

In addition to significant heterosis, an analysis of variance also revealed a highly significant difference ($P<.01$) between the two inbred lines in both sexes. The differences in the reciprocals was significant ($P<.05$) for the male data but was not significant in the female data. This is consistent with the work of BOYLAN and WONG (1955) where they interpret similar results as evidence that the sex chromosome contributes to the determination of pupa weight. In their results and also the results reported here, the male pupa were heavier when they had received the X chromosome from the heavier parent line.

*Design-III analysis to estimate levels of dominance:* The analysis of variance and mean square expectations for Design III are given in Table 2. The analysis was run separately for the two sexes with a bottle mean (five progeny from a particular $F_2$ male and a single female from one of the inbred lines) serving as the statistical unit. Average level of dominance ($\bar{a}$) was estimated from the square root of the ratio $\sigma^2_{ml}/2\sigma^2_m$. Table 3 gives the results of the Design-III analysis for the two sexes. The estimates of $\bar{a}$ of .75 and .57 for male and female progeny respectively are nearly the same as the results reported for $F_2$ males by ENFIELD *et al.* (1965). The results reported here are based on a larger body of

TABLE 3

*Results from the Design-III analysis*

| Source | df | Male progeny Mean squares | Female progeny Mean squares |
|---|---|---|---|
| Among $F_2$ ♂'s | 152 | 27,546 | 30,774 |
| $F_2$ ♂'s × Inbreds | 152 | 20,343 | 18,474 |
| Bottles within $F_2$ ♂'s × Inbreds | 362 | 10,902 | 12,470 |
| | $\sigma_m^2$ | 4161 ± 816 | 4576 ± 912 |
| | $\sigma_{ml}^2$ | 4720 ± 1235 | 3002 ± 1156 |
| | $\bar{a}^2$ | .57 | .33 |
| | $\bar{a}$ | .75 | .57 |

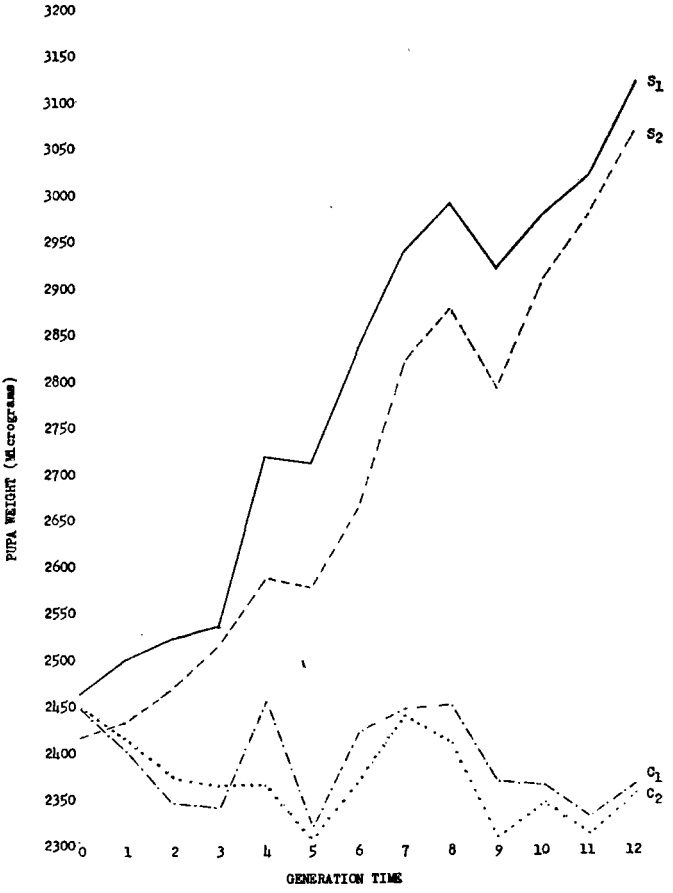


FIGURE 1.—Response to selection for heavier pupa weight.

data than the earlier report. The differences between sexes in the estimates of $\sigma^2_m$ and $\sigma^2_{ml}$ were not significant for either component.

*Response to selection:* Figure 1 shows the change in mean pupa weight for the four populations for the first 12 generations of selection. The regressions of the difference in mean pupa weight between the S-population and the corresponding C-population on generation time for the two replicates are 60.3 ± 4.8 and 61.8 ± 4.9 for the first and second replicates respectively.

The realized heritability was obtained from the ratio of the accumulated response to the adjusted accumulated selection differential. The selection differential was calculated each generation as the average selection differential for all half-sib families. This was then adjusted by weighting the parental pupa weights by the number of progeny contributing to the mean of the offspring generation. Realized heritabilities for the two replicates were .31 ± .025 and .28 ± .022. It should be pointed out that with the kind of selection employed only ¾ of the additive genetic variance is utilized since selection is on a within-half-sib family

basis. Likewise the phenotypic variance is the average variance within half-sib families rather than the total population phenotypic variance.

All measures of response to selection were determined as deviations from the mean of the C-populations. This assumed that either (1) the C-populations remain genetically constant over the period of selection or (2) forces changing the mean genotypic value of the C-populations would have the same effect on the S-populations. The regression of mean pupa weight on generation time is negative but nonsignificant in both C-populations ($-3.2 \pm 3.8$ in $C_1$ and $-6.1 \pm 3.2$ in $C_2$). These negative regressions increase the realized heritability by 1 and 2% in the two replicates compared with corresponding results that would be obtained using the absolute change in the S-populations each generation.

*Estimates of heritability for pupa weight:* Heritability estimates were obtained from the data collected in the first 13 generations of the selection experiment by four methods: realized heritability based on response to selection, sire-offspring regression, dam-offspring regression, and the intraclass correlation using the sire component of variance as an estimate of ¼ of the additive genetic variance. These results are summarized in Table 4.

The realized heritabilities given in the previous section were adjusted to a whole population basis to give a valid comparison between realized heritability and estimates obtained by other procedures. Assuming realized heritability with selection on a within-half-sib family basis to be $R/D$ where $R$ is response to selection and $D$ the average selection differential within each half-sib family, we can then write the expected realized heritability for mass selection within the whole population as $4R/(3D+R)$. The values given in Table 4 have been adjusted by this procedure.

All parent-offspring regressions were first calculated on an intrapopulation intrageneration basis and were then pooled over generations and populations by weighting the individual estimates inversely to their variances. The analysis of

TABLE 4

*Estimates of heritability for pupa weight*

| Method of analysis | Population | Male data | Female data |
|---|---|---|---|
| Realized heritability | $S_1$ | .37 ± .027 | |
| | $S_2$ | .34 ± .025 | |
| Components of variance | $S_1$ | .50 ± .10 | .23 ± .10 |
| ($4S/[S+D+W]$) | $C_1$ | .28 ± .09 | .31 ± .10 |
| | $S_2$ | .31 ± .08 | .28 ± .09 |
| | $C_2$ | .37 ± .09 | .26 ± .09 |
| | Pooled* | .36 ± .04 | .27 ± .05 |
| Sire-male offspring regression | Pooled | .34 ± .05 | |
| Sire-female offspring regression | | .36 ± .05 | |
| Dam-male offspring regression | | .57 ± .05 | |
| Dam-female offspring regression | | .53 ± .05 | |

* Pooled estimate was obtained by weighting the four population's estimates by the inverse of the variance.

variance for a nested classification with unequal class numbers used in this study for estimating sire, dam and within full-sib family components of variance was the same as described by KING and HENDERSON (1954). Adjustments were made in the sire component estimates taking into account that the sires had been selected by the procedure outlined by RAHNEFELD *et al.* (1963). All analyses of variance were done separately for the two sexes and the four populations.

The results of the analysis reported for a given population involved pooling corrected sum of squares and degrees of freedom from all generations and calculating the mean squares from the pooled data. Separate estimates were first obtained on an intrageneration basis where the results were subject to considerable sampling error. The justification for pooling all data over generations both in the parent-offspring regression analysis and the analyses of variance was based on the assumption that changes in the genetic variances and covariances were trivial over this period. The validity of this assumption was examined in two ways: (1) the regression of realized heritabilities on generations of selection and (2) the regression of within generation heritability estimates obtained from the sire component analysis on time. These regression estimates were as follows:

| | | Replicate 1 | Replicate 2 |
|---|---|---|---|
| Regression of realized heritability on generation time: | | —.01 ± .015 | —.0015 ± .011 |
| Regression of heritability from sire component analysis on time: | | | |
| S-populations | Male | —.021 ± .029 | —.045 ± 0.26 |
| | Female | —.003 ± .027 | .033 ± .029 |
| C-populations | Male | .039 ± .027 | .012 ± .020 |
| | Female | —.025 ± .023 | —.005 ± .025 |

No significant effects of time trend were indicated in either test.

A check on the effects of selection in changing the phenotypic variance of the populations was made by calculating the regression of the difference in the phenotypic variance in the S and C-populations on generations of selection. These estimates were 582 ± 340 and 1570 ± 216 in the two replicates. The second-replicate estimate was significantly different from zero while the first was not. The larger regression value in the second replicate was almost entirely due to an unusually large amount of variation in the S-population in the 12th generation. Considering the evidence from both replicates it would appear that total variation has increased slightly as the mean pupa weight has increased.

The statistical analyses of the data have been handled separately for males and females to determine whether gene effects are dependent on the sex of the organism. A measure of the correspondence of gene effects in the two sexes was obtained from the genetic correlation between male and female pupa weight using the sire components of variance and covariance to estimate the genetic correlation. If a sex-genotype interaction is an important source of variation then a correlation of less than 1.0 would be expected. The pooled estimate of .97 ± .13 gave no evidence of a sex-genotype interaction. Further evidence on this point is provided by the response to selection in the two sexes. With a much larger selection differential in males than females each generation, the difference between the performance of the two sexes would be expected to decrease with less than a

TABLE 5

*Pupa weight as related to reproduction*

| Regression coefficients | Pooled select populations | Pooled control populations |
|---|---|---|
| Progeny number on dam pupa weight | .0069 ± .0030 | .0055 ± .0032 |
| Progeny number on sire pupa weight | —.0079 ± .0028 | —.0009 ± .0030 |
| Average pupa weight on number of progeny per bottle | .38 ± .26 | .05 ± .27 |

perfect correlation (females are heavier than males for this species). No trend in the mean difference between the two sexes has been observed in the first 12 generations of selection.

*Pupa weight and its relationship to other characteristics of the population:* One of the possible causes for plateauing in a selection experiment can be a negative genetic correlation between the trait under selection and reproductive fitness. Two measures of reproduction are being followed in this experiment to evaluate their relationship with pupa weight. The first measure is the number of live progeny at 21 days resulting from a three-day egg laying period. The 21st day is counted from the middle day of egg laying and is the day on which the pupa are weighed. The second measure of reproduction is the percent of sterile matings per generation. No attempt has been made at this stage to break the sterility down into the male and female contributions.

The relationships between progeny number and pupa weight for the C and S-populations are given in Table 5. The first point of interest is the apparent increase in number of progeny produced by a female as the weight increases while there is a negative regression of number of progeny on sire weight. These results might be explained by a negative genetic correlation between reproductive rate and body weight combined with a positive maternal nongenetic correlation between weight in the female and her offspring. An examination of time trends over the first 12 generations does not indicate any significant effect of the selection for pupa weight on number of progeny produced when compared with the control population.

The percentage of sterile matings was determined each generation for both the C and S-populations to examine the effect of pupa weight selection on fertility *per se*. The regression of percent sterility on generations of selection was −.38 ± .20 and .14 ± .35 in the S and C-populations respectively. Even though neither of these values is significant it will be of interest to see if the observed trend continues as more data are collected. The number of sterile matings has been quite variable from one generation to the next but on the average has been higher in the control populations (19% as compared with 10%).

Another measure of the relationship of reproduction to pupa weight is the comparison of the original selection differentials with selection differentials adjusted for the differences in reproduction of the individuals selected as parents. When this adjustment was made by weighting the pupa weight of the parents by the number of pupa contributing to the mean of the offspring generation the following results were observed:

| Average selection differential | $S_1$-Population | $S_2$-Population |
|---|---|---|
| Unadjusted | 203 | 221 |
| Adjusted | 201 | 216 |

Although these results again indicate a slight negative relationship between pupa weight and reproduction, the effect on progress from selection appears to be trivial at this stage.

One of the questions posed by the operational procedure of the experiment was whether the number of progeny in a bottle (a full-sib family) would affect the average pupa weight. In other words, is it necessary to standardize the number of progeny per bottle to eliminate an effect of family size as it may be related to crowding or competiton? Analyses of the data on this point (Table 5) revealed no significant relationship between average pupa weight and the number of progeny per bottle.

## DISCUSSION

The estimates of heritability obtained from the components of variance analysis and the sire-offspring regression are in excellent agreement with the realized heritability estimates. In contrast with the discrepancy that is often observed where the realized heritability falls short of predicted results, these data lend support for the soundness of the quantitative genetic theory. It should be pointed out that the population sizes on which the comparison between predicted and actual response is made are larger in this experiment than has often been the case. This has permitted more refined estimates of heritability and at the same time reduced the effects of inbreeding on realized progress. Also, there is no evidence that a negative genetic correlation between reproduction and pupa weight is having much effect on realized progress at this stage.

The estimates of heritability obtained from the dam-offspring regression are significantly larger than estimates from the sire component analysis and sire-offspring regression. The most plausible explanation for this difference is an upward bias in the dam-offspring estimates from nongenetic maternal effects. Indirect evidence for the presence of maternal effects comes from the data involving reciprocal differences in the cross of the two inbred lines used to establish the segregating populations. The offspring were heavier when the heavier inbred line served as the maternal parent. DAWSON (1964) using reciprocal crosses of various strains of Tribolium concluded that maternal effects are an important source of variation for several quantitative characters. DEFRIES and TOUCHBERRY (1961) and MARTIN and BELL (1960) reported a negative nongenetic contribution to the correlation between maternal and offspring body weights in Drosophila. This was interpreted as being the result of more progeny having been produced by the heavier female with subsequent competition having a negative effect on weight of the offspring. The evidence on this point in our data based on the regression of average pupa weight on number of progeny per bottle indicates that this effect does not exist with the cultural practices being used in this experiment.

The estimates of heritability obtained from the sire-offspring regression and components of variance analysis agree with the results of BOYLAN and WONG (1965a) who had an estimate of .33 on a similar population which had been derived from the cross of two inbred lines. WILSON *et al.* (1963) obtained a realized heritability of .33 compared with his estimated heritability based on midparent-offspring regression in the zero generation of .46 ± .09. This estimate would contain a bias from maternal effects and in fact is very similar to the average of the sire-offspring and dam-offspring estimates in this study. BELL and MOORE (1958) had much higher estimates of heritability (.6 to .8) than others have reported.

The linearity of response to selection over twelve generations, the lack of evidence for appreciable change in additive genetic variance and the magnitude of the ratio of total response to additive genetic variance indicate that the genetic variation in pupa weight cannot be accounted for by a small number of genes. In view of this and since there are only ten pairs of chromosomes in Tribolium, a moderate amount of linkage disequilibrium among the genes affecting pupa weight must be considered probable in the early generations of populations derived, as ours were, from the cross of two inbred lines.

Some dominance of genes affecting pupa weight is indicated by both the initial heterosis and the Design-III data. The observed heterosis indicates that dominance in some degree is more prevalent among alleles for heavier weight than among those for lighter weight. The Design-III estimates of $\bar{a}$ (.75 and .57), obtained using $F_2$ males, are in the partial dominance range. If both linkage disequilibrium and a preponderance of dominance of alleles for heavier pupa weight were involved in our material, as appears probable, there is upward bias in the estimates. The rationale for linkage bias was presented by COMSTOCK and ROBINSON (1952) and evidence for such bias in data on grain yield in maize has been presented by GARDNER and LONNQUIST (1959) and MOLL *et al.* (1964). The obvious implication is that the correct value for $\bar{a}$ for genes affecting pupa weight is probably lower than estimates here reported. The further unanswered question concerns the distribution of individual values of $a$. In particular, does the range of $a$'s include a significant number greater than 1.0, i.e. is there a significant number of overdominance loci? As the experiment progresses we expect to obtain information on both issues. Design-III results using advanced generation C-population males will provide estimates having less linkage disequilibrium bias. Decisive information on the overdominance issue is hoped for from Design-III work using advanced generation S-population males. The rationale is as follows. Selection being practiced should in the long run increase gene frequencies more at non-overdominance loci than at the overdominance loci, if any, that actually exist. In fact, many of the non-overdominance loci should become homozygous or closely approach homozygosity. Then, because the Design-III estimate of $\bar{a}^2$ weights individual $a^2$'s in proportion to $\bar{q}\ (1-\bar{q})$ where $\bar{q}$ is gene frequency (see COMSTOCK and ROBINSON 1952), higher estimates of $\bar{a}$, quite possibly over 1.0, would be obtained if there really are a significant number of overdominance loci.

RAHNEFELD *et al.* (1963) discuss reasons for considering the heritability of a trait separately for the two sexes. If there is a lack of a perfect genetic correlation between the particular trait measured in the two sexes, the realized heritability would be expected to be smaller than the estimates from statistical analyses assuming other sources of bias have been removed. The evidence for a near perfect genetic correlation for pupa weight in the two sexes may be another reason for the closer agreement between the realized and estimated heritabilities. This high correlation may not exist for other traits in this or other species. Evidence on this point is generally lacking. ENFIELD (1960) estimated the genetic correlation between eight-week weight in male and female poultry to be .83 ± .05.

It would appear from the linearity of response to selection, the lack of any major interference from a negative genetic correlation between pupa weight and reproductive performance, and the estimates of heritability that selection will remain effective for a considerable number of generations.

## SUMMARY

Selection for heavier pupa weight was continued for 12 generations in two populations derived from the cross of two highly inbred lines. Response to selection was in close agreement with expected results based on estimates of heritability from the sire-offspring regressions and the components of variance analyses. Adjusted realized heritabilities were .37 and .34 in the two populations. Estimates of heritability from the components of variance were .36 ± .04 and .27 ± .05 for males and females. Heritability estimates obtained from the regression of male and female progeny weight on the sires weight were .34 ± .05 and .36 ± .05.—The genetic correlation between male and female pupa weight was .97 ± .13, giving evidence for the lack of interaction between gene effects and the sex of the organism.—Initial heterosis studies indicated some dominance for heavier pupa weight. Design-III estimates of average levels of dominance for genes affecting pupa weight in the base populations were in the partial dominance range .75 and .57 for males and females respectively.—No significant effects of selection in reducing additive genetic variance were observed.

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