# RESPONSE TO SELECTION AND COMBINING ABILITY IN *TRIBOLIUM CASTANEUM*

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A Thesis

Presented to

the Faculty of Graduate Studies and Research

The University of Manitoba

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In Partial Fulfillment

of the Requirement for the Degree

Master of Science

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by

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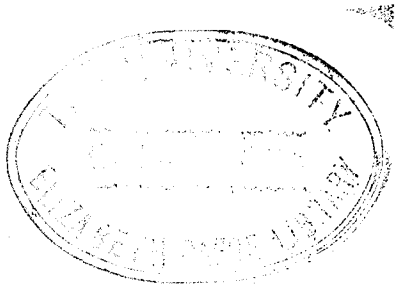
September 1965



ACKNOWLEDGMENT

The author wishes to express his sincere appreciation and gratitude to Dr. W. J. Boylan, Assistant Professor, Animal Science, for his encouragement, advice and guidance during the course of graduate study and preparation of this thesis.

Sincere thanks are also extended to Dr. Hans Meyer for his assistance and advice in preparing the data for analysis on the computer.

The investigation was financed by an assistantship from The University of Manitoba and a grant from the National Research Council of Canada.

ABSTRACT

A selection experiment using flour beetles, Tribolium castaneum, was initiated in January, 1963. Mass selection for a single trait, first day pupal weight, was practiced in a segregating population originated by crossing two inbred lines. Sires in the segregating population were mated at the same time to females from one of the parental inbred lines. Thus, every sire had contemporary purebred and crossbred progeny.

The primary objectives of this study were to evaluate: (1) response to selection in a segregating population, (2) the extent of genetic improvement by selection in a purebred population being reflected in the crossbred population and (3) agreement between predicted and observed response as a check on quantitative genetic theory.

The estimates of genetic parameters include: (1) phenotypic and genetic variances, (2) genetic covariance and correlation between purebred and crossbred progeny having a common sire and (3) genetic correlation between two sexes.

One of the parental lines (E) was maintained as a control population: (1) to measure temporal changes in environmental and (2) as the source of female for the crossbred population. The other progenitor line (C) was also maintained as a possible control population. Heritability estimates for

pupal weight were .029 ± .026 for the E line and .286 ± .024 for the C line. It was concluded that the latter was not suitable as a control.

The heritability estimate of pupal weight for the purebred population calculated from information from the sire component of variance and parent-offspring regression was .237 ± .015. The realized heritability was .32.

The sire components of variance for purebreds and crossbreds and the sire component of variance between the two populations were estimated to be 3699 ± 1170, 4807 ± 1037 and 2269 ± 767 ugm. (micrograms) respectively. Genetic correlation for pupal weight between purebreds and crossbreds was estimated to be .69 ± .20. The high genetic correlation indicated that selection based on purebred performance would be relatively effective in improving the crossbreds.

The agreement between predicted and observed response was not completely satisfactory for the purebred population, while the agreement between predicted and observed response was good in the crossbred population. The observed progress in crossbreds was only slightly less than one-half of that of the purebreds suggesting that gene action was predominantly additive.

The average genetic improvement was estimated to be 83.23 ± .30 ugm. per generation for purebreds and 32.10 ± 5.49 ugm. per generation for crossbreds. Total response for

nine generations of selection for pupal weight was approximately seven and three times the additive genetic standard deviation of purebreds and crossbreds respectively.

Analyses of data also indicated a high genetic correlation between the sexes, although it was not perfect.

The correlated response of egg count for a 48-hour period suggested that a negative genetic relationship existed between pupal weight and egg count. Evidence from various sources suggested that a continued response to selection will occur in the generations immediately ahead.

TABLE OF CONTENTS

Page

Page

LIST OF TABLES

# LIST OF FIGURES

# INTRODUCTION

Artificial selection had long been recognized as a powerful tool for the improvement of livestock performance and the increase in crop yield even before the development of modern genetic theory. However, the interpretation of various phenomena of selection with the concept of quantitative genetics began only during the last three or four decades. Since further and more effective improvement must be based on sound genetic theory, more investigations should be undertaken in order to thoroughly understand the role played by quantitative genetics in selection.

One question that has arisen among animal breeders is whether genetic improvement in a purebred population will be reflected in crossbred offspring, and the extent of any improvement. This question especially concerns swine breeders because of the extent of commercial cross-breeding in the swine industry. Experiments conducted in order to tackle the problem have been reported by a few workers. The results have been rather contradictory. Therefore, no definite conclusions have been reached so far. Some workers have pointed out that further investigation is required for a thorough understanding of the issue.

An experiment with Tribolium castaneum in selecting a single trait, first day pupal weight, was thus designed with

the dual purpose of obtaining information on response to selection in purebreds and combining ability in crossbreds. It would also provide knowledge concerning quantitative genetic theory in general. The response to selection in this study will be evaluated in terms of estimates of phenotypic and genetic parameters using various methods. The parameters estimated include: (1) phenotypic and genetic variances, (2) genetic covariance and correlation between offspring in purebreds and crossbreds having a common sire and (3) genetic covariance and correlation between the sexes. The pooled heritability estimates and certain genetic covariance estimates will be used for the prediction of purebred and crossbred performances respectively.

The main objectives of this experiment are as follows: (1) the study of response to mass selection in a segregating population originated from two inbred lines, (2) the degree of response to selection in purebred population being reflected in a crossbred population and (3) the comparisons of observed and expected progress as a check on quantitative genetic theory.

# LITERATURE REVIEW

The purposes of artificial selection for a metric trait, according to Lerner (1958) are: (a) to modify its mean (directional selection), (b) to reduce its variability (stabilizing selection) and (c) to extend its range in one direction (directional selection to produce a record performance). Most of the studies reported in the literature in both plants and animals were concerned with the first of these goals, because of its practical importance.

## A. Mass, Family and Index Selection

These three methods of selection were the earliest and most common of the techniques used by the breeders. All three methods of selection are aimed for the best utilization of the additive genetic variance, and hence the effectiveness of these techniques depends on the amount of additive genetic variance existing in the traits to be selected, although in the index selection, the genetic correlation between traits included in the index further complicates the situation.

### 1. Selection in Plants

A considerable number of experiments in selection have been done in corn, partly because it is a suitable and convenient material for this purpose and partly because it is an important economic crop.

A long term experiment selecting for high and low protein and high and low oil content of kernels in maize has been conducted by the Illinois Agricultural Experiment Station. Thus, four strains were developed, all initiated from a single open-pollinated variety. The original variety had a mean protein content of 10.9% and a mean oil content of 4.7%. In summarizing the results of ten generations of selection, East (1910) reported that a rapid initial response was followed by a decreasing rate of response. He concluded that phenotypic levels in all four strains would rapidly become stabilized. After 28 generations of selection, Winter (1929) observed that the high protein and the high oil strains increased to 15.61% and 9.86% respectively, while the low protein and low oil strains decreased to 8.38% and 1.51% respectively. He predicted that continued rapid response to selection was likely in the high protein and the high oil strains, and a physiological limit was probably reached in the low oil strain at that stage. Woodworth et al. (1952) again summarized the results after 50 generations of selection. Two of their observations were contradictory to Winter's (1929) prediction. After 60 generations of selection, Leng (1961) reported that the mean oil contents were 14.83% and .77% for the high oil and low oil strains, and the corresponding values for protein were 22.84% and 4.96% respectively. None of the four strains responded in the manner of Woodworth et al. (1952) prediction.

Leng (1961) then pointed out that simple extrapolations of regression trend lines for the phenotypic mean values, or computations involving heritability estimates and variance data, did not yield satisfactory predictions of response in these complex characters. However, the effectiveness of selection on these traits is considered satisfactory despite the fact that the responses were erratic.

Leng (1962) also reported the results of 13 generations of reversed selection on the above mentioned strains beginning at 48 generations of forward selection. Mean chemical composition showed significant and rapid response in each of the four strains. The regular and reverse populations were completely separated in phenotypic range in the low oil and high protein material. The result indicated that a large amount of genetic variance was still existing in these traits after 48 generations of selection.

Smith and Brunson (1925) conducted an experiment in selection for corn yield by the method of ear-to-row breeding. They found that the difference in productiveness between the high-yield and low-yield strain was brought about mainly through a decrease in low-yield strain. They also suggested that mass selection would be just as effective as the more complicated method of continuous ear-row breeding.

Another example of achievement of improved yield in plants was reported by Manning (1955). He stated that lint

yield in cotton was increased after six generations of selection employing a selection index based on number of seeds and lint yield.

Edwards and Cooper (1963) made selections for both extremes of individual leaf size and rate of leaf appearance at the seedling stage within some varieties of rye grasses. The responses to selection were in all cases large. The realized heritability estimates in general agreed fairly well with statistical estimates. They concluded that considerable additive genetic variation was present for these two seedling characters within the population sampled.

Graham et al. (1965) reported mass selection was very effective after three cycles of selection for resistance to common leaf spot in two varieties of alfalfa. The final cycle had a higher degree of resistance than the most resistant check variety.

2. Selection in Animals

Selection experiments with laboratory species contribute the largest amount of information about selection response in animals. Drosophila and mice are the most common species used in selection experiments. In domestic animals, selection experiments have been conducted mainly with swine and poultry. However, work done for both theoretical and practical purposes has contributed to an understanding of the

genetic basis of response to selection.

Goodale (1938) reported that selection for 60-day weight of mice was highly effective. He found that total increase of body weight was 40% and 37% of the average initial weight for males and females respectively after 16 generations of selection.

A similar experiment was reported by Lewis and Warwick (1953) in selection for small, medium and large 60-day weight in a mouse population for five generations. They observed that selection for large and small 60-day weight was effective in both inbred and outbred populations.

Another experiment with mice was conducted by Rahnefeld et al. (1963) selecting for post-weaning growth (weight from 21 - 42 days) for 17 consecutive generations. The selected population was derived from a cross of two highly inbred lines. They observed that the increase in body weight was about six times the additive genetic standard deviation and about 43% of the original mean growth. Over all heritability estimates were .243 $\pm$ .074 and .264 $\pm$ .078 for males and females respectively. They suggested that selection would remain effective in the generations immediately ahead since additive genetic variance appeared to be as great as in the early generations and there was no indication that artificial selection for growth would be counterbalanced by natural selection for fitness as the genetic correlation be-

tween growth and litter size was positive.

MacArthur (1949) reported that two way selection for 60-day body weight in mice was highly effective for 21 generations. The divergence between mice of large and small size was equivalent to 10.9 phenotypic standard deviations. Realized heritability measured by the divergence was 16.96%. The coefficient of variation continued throughout at about the same percentage. However, the heritability declined from about 25 to 10%.

In another two way selection for six-week body weight in mice, Falconer (1953) observed that response to selection was asymmetrical, being greater in the small line. Heritability was about 20% for upward and 50% for downward. The cause of the difference was attributed mainly to inbreeding. He also found that the variance increased in the large line and decreased in the small, but the coefficient of variation was equal in the two lines and did not change until the end.

A similar experiment was conducted by Legates et al. (1958). They reported that two way selection for six-week and 12-day body weight in mice was effective for nine generations.

An experiment designed to investigate the causes of a selection limit was described by Falconer and King (1953). Two strains of mice selected independently by Goodale

(1938) and MacArthur (1949) for large body size and which were both thought to have reached limits, were crossed. The renewed response to selection in the cross-bred strain was interpreted as showing that the limitation of response in the parent strains was due to the loss of genetic variance. Direct evidence was given that neither opposing natural selection nor a physiological limit were operative. The selection limits of the cross-bred populations were attributed primarily to the exhaustion of the initial variability as a result of the selection itself; only a part of the loss of genetic variance could have resulted from the previous inbreeding.

Combined family and individual selections were carried out by Tanaka and Takasaki (1958) in a European, a Chinese and several Japanese races of the domestic silkworm for increase of cocoon-shell weight and its percentage to the total cocoon weight. In the European race, the single cocoon-shell weight which was about 38 cg. in the initial stock advanced to 97 cg. after thirty generations of selection. They pointed out that the weight was the highest ever achieved, and there was no sign that selection would not continue to be effective. The percentage of cocoon-shell weight to the total cocoon weight also increased strikingly during the experiments. Similar results had been obtained with the Chinese race. They also reported that selection in Japanese

races proved, on the other hand, ineffective, partly owing to the fact that mortality in summer culture was usually much higher than in spring culture, thus eliminating elite homozygotes which survived the spring culture, and leaving only heterozygotes for reproduction.

Martin et al. (1953) studied the efficiency of selection for broiler growth in chickens at various ages. They reported that heritability of live weight at three, six, nine and 12 weeks was estimated as approximately .31, .29, .27 and .31 respectively. The best index from this study was secured on the basis of the six and twelve week weights. However, they pointed out that the slight gain in efficiency did not justify the expense of taking two weights.

Maloney et al. (1963) collected data from ten generations of selection for high and low 12-week body weight in chickens. Again response to selection was asymmetrical, being greater in the high line. This is contradictary to what Falconer (1953) observed in mice. The relaxation of selection at the fifth generation in the high line showed a non-significant increase in body weight, while the low line returned almost immediately toward the mean of the original population. This observation is just the reverse of that reported by Robertson (1955) in Drosophila. The contradictary results from different workers indicate that the response to selection in two way selection behaves differently in different

species.

Similar experiments were reported by Godfrey and Goodman (1955) and Siegel (1962b) separately in their high and low selection for body weight in chickens.

Dettmers (1962) reported the results of selection for small size in swine based on weight at 154 days of age. She estimated from pooled analyses the heritability to be .15 ± .06. Expected genetic decrease in weight on the basis of parameters obtained in that study was about two pounds per year. The total decrease in weight observed was 24 pounds in seven years, so that about 60% of the change was attributed to genetic cause. The author predicted that response to selection would continue since genetic variation was still present.

Results of selection experiments conducted for the purpose of examining the adequacy of existing genetic theory in predicting genetic progress were reported by Clayton and Robertson (1957). The experimental material was Drosophila melanogaster and the selection criterion was abdominal bristle number. In the short-term selection, it was reported that estimates of the heritability of the character by parent-offspring, full-sib and half-sib correlation were in good agreement, with the mean value being 0.52. The response to selection over seven generations, based either on individual or family score, was in fair agreement with predictions from

estimates.

In the long-term selection, they observed that the rate of response had decreased considerably in many lines after 20 generations of selection. In some lines, however, response continued until the 30th generation. In many of the lines, the cessation of response did not mean exhaustion of genetic variability. In three of the high lines, they found that the high variability was apparently due to continued selection of heterozygotes for a lethal gene. In the low lines, a sudden increase of variation in females was followed by a rapid response in that sex. Genetic variation was maintained in many of the low lines after response had ceased. They indicated that the situation was caused by the combination of lethal genes, infertility of extremely selected females and a heterozygosity for inversion. They concluded that in such situations, the conventional heritability approach appeared to break down completely.

In an earlier study of the effect of long-term selection, Mather and Harrison (1949) reported similar results in number of abdominal chaetae of Drosophila melanogaster. In the downward selection, chaeta number fell erratically for 35 generations, at which time sterility terminated the line. A mass culture, begun at generation 20, maintained its chaeta number with fair consistency. Further selection, whether for high or low chaeta number, from this mass culture became in-

creasingly difficult because sterility resulted in terminating the selected lines increasingly early. They suggested that a balanced system between chaeta number and sterility was building up in the low mass culture. The high selected line showed a progressive increase in chaeta number and decrease in fertility until generation 20, when the number of flies produced was so small that selection was abandoned and the line was maintained as a mass culture. The chaeta number of this mass culture fell back 80% of the way to the mean of the unselected population in five generations. Reselection was initiated again at generation 24 and resulted in recovery to the level of generation 20 in four generations, but without the extreme loss of fertility observed earlier. The line so selected was maintained over 100 generations and a mass culture made from it showed no fall in chaeta number over a similar length of time. They suggested that selection prior to generation 20 led to a fall in fertility by correlated response of sterility and between generations 20 and 24 natural selection for fertility led by a corresponding correlated response in chaeta number led to a fall in chaeta number.

In both of the above two long term selection experiments, infertility was encountered in later stages of selection because natural selection acted against extreme individuals.

Robertson (1955) reported another selection experiment with the same species but a different trait. He selected for large and small body size and observed that the response was immediate and sustained. The response tended to be asymmetrical since selection for small size produced a greater change than selection for large size. The actual levels of size at which corresponding strains stabilized were approximately the same. Parallel strains behaved in the same way when selection was reversed. At a comparatively early stage of the experiment, he found that reversal of selection brought size back to the original level in both large and small strains. At a later stage, after response to selection had ceased, selection downward from the large strains resulted in size being reduced rapidly to the original level, whereas in the small strains, reverse selection was ineffective behaving as if they were homozygous. Further improvement of the plateaued stocks was attained by selection among the crosses of lines selected for large body size.

It has become increasingly popular to use Tribolium for selection experiments in the last few years. The consequences of various combinations of selection (high and random) and levels of X-radiation (0, 100 and 1,000r per generation) on body weight at pupal stage were investigated by Bartlett and Bell (1964) over 11 generations in two strains of Tribolium castaneum. Reproductive fitness in terms of fer-

tility, number of offspring, and adult viability were measured each generation. They observed that high selection contributed to a significant response in body weight in all strains so treated; but the degree of response was negatively correlated with the amount of irradiation. Even though an increase in additive genetic variance was observed in some of the irradiated lines, a decline in reproductive fitness contributed to a smaller selection differential.

Using independent culling levels with the same species, Burris and Bell (1965) reported the effects of selection for four combinations of high or low larval weight with high or low pupal weight. A control line was also maintained. The total period of selection was seven generations. Observations that they made included total number of larva produced per family from a 24-hour egg production, while larval weight, pupation time, pupal weight, sex, adult emergence time and adult weight were determined on a sample of eight. They found that the selected populations ranged from 60% to 14% of the control for larval weight and from 80% to 120% of the control for pupal weight. Selection differentials and responses for both of the selected traits were greatest in populations selected high in both traits or low in both traits. Among traits, pupation time was increased about one day by low larval weight selection and decreased about half as much in the lines selected high. Adult emergence time was highly associated with

pupation time and changed inversely with larval weight. Adult weight changes closely approximated changes in pupal weight.

In addition to body weight, developmental rate in Tribolium has also been investigated. The selection for early and late pupation time in Tribolium castaneum was reported by Englert and Bell (1964). In a replicated experiment, the effects of selection for pupation time upon two other components of the growth complex (13-day larval weight and pupal weight) were examined for six generations. They obtained realized heritability estimates of .38 ± .03 for early pupation and .26 ± .03 for late pupation. A large difference between the selection differentials, which arose as a result of an increasing variance in the late lines and a decreasing variance for the early lines, was attributed as being responsible for the asymmetrical response observed. Realized genetic correlations were estimated to be -.76 in the early line and -.86 in the late lines between pupation time and larval weight. Pupal weight revealed no consistent relationship with pupation time.

Another similar experiment was reported by Dawson (1965). In his selection for fast and slow development in Tribolium castaneum and for fast development in T. confusum, he succeeded in producing strains which differed from the foundation stocks with respect to this character. He observed that selection for fast development in both species had been

opposed by natural selection to such an extent that in the later generations negative response to selection was observed. Since a control line was maintained only in T. confusum, the negative response he observed cannot be assessed with certainty. Asymmetrical response was also observed in later generations of selection. Finally, he concluded that developmental rate was maintained at an intermediate level in the foundation populations, possibly as a result of superiority of heterozygotes with respect to fitness.

Kirdle et al. (1946) presented the results of selection for rapid and slow growth in Hampshire swine for four generations. Selections were based on weight at 150 and 180 days. The estimates for heritability pooled over four generations were 16 and 19% for 150 and 180-day weight respectively.

A similar experiment selecting for high and low individual feed requirements per pound of gain in Duroc swine for five generations was reported by Dickerson and Grimes (1947). They observed a lower heritability for feed requirements relative to daily gain, and they explained that this was due to a much stronger negative correlation between a dam's genetic and environmental influences on the feed requirements than on the growth rates of her pigs.

Several general features for mass selection can be summarized as follows:

a) Selection has resulted in a marked change in the mean performance of many traits in numerous

species when additive genetic variance was present;

b) in short-term selection, the response to selection was always in good agreement with the prediction obtained from heritability estimates;

c) in long-term selection, the prediction from heritability estimates was not always reliable; in some cases the conventional usefulness of heritability breaks down completely;

d) as selection was continued in long-term experiments, infertility usually built up due to a correlated response of fitness with the selected character;

e) in two-way selection, response to selection was generally asymmetrical, and in most cases response to downward selection was faster because of combined forces of inbreeding and natural selection;

f) in long-term selection, a plateau was usually reached with undiminished phenotypic variability, while the heritability may have decreased abruptly at the end;

g) further improvement could be attained when two plateaued populations selected in the same direction were crossed and subjected to further se-

lection. Heterosis was observed in such cross-bred populations in many cases.

B. Genotype-environmental Interaction in Selection

In some selection experiments, selection for the same trait in different environments results in a different rate of response and total response. Renewed response to selection in the same trait is demonstrated when a plateaued population is subjected to further selection in a different environment or to certain treatments, either chemical or physical. These facts are of particular interest to animal breeders because of the consideration of practical problems; such as what will be the best environment for selection and whether the genetic improvement of a trait in one environment will be reflected in another environment. Some work has been done to investigate the problems and a tentative conclusion has been reached.

In the study of the effect of the plane of nutrition on the improvement in body weight in mice, Falconer and Latyszewski (1952) reported that average weight increase under selection was 1.5% per generation on the full diet and 1.3% on the restricted diet strain compared to unselected mice. Heritability was insignificantly higher in the restricted diet strain, being 29% on restricted diet and 20% on full diet. Exchange of nutritional levels were made after five, seven and eight generations of selection. When reared on a restricted

diet, the restricted diet strain was superior in six-week weight, while the full diet strain showed no improvement over the unselected level. When reared on a full diet, the full diet strain was superior but the restricted diet strain closely approached the performance of the full diet strain. They indicated that improvement of the genotype carried the restricted line toward a considerable improvement for growth on a higher plane.

The same experiment was done by Korkman (1961), except that his restricted diet was imposed at a different age of the mice. The general observations agreed with those of Falconer's et al. (1952), although in regard to weight gain, no significant response was observed in the low plane of nutrition, and the relationship between heritability of the high and low plane nutrition reversed the direction of that of Falconer's et al. (1952) although not the same magnitude. He concluded that in both experiments, the performance was most effective by selection on that plane of nutrition on which the performance was subsequently measured.

In an earlier separate study of the environmental influence on the growth rate of males and females, Korkman (1957) found that restricted feed retarded growth of the males more than the growth of the females.

Another experiment of the same nature was reported by Fowler and Ensminger (1960) in interaction between geno-

type and plane of nutrition in selection for rate of gain in swine. Again, the observation was in good agreement with the above workers, except that the realized heritability estimates were about the same for the two lines. When the environment was exchanged, the low plane pigs shifted to the high plane showed the highest rate of average daily gain, followed by the high plane pigs remaining on the high plane, low plane pigs remaining on low plane and high plane pigs shifted to low plane. He concluded that the results in general supported the contention that breeding animals should be selected in the environment under which their progeny are expected to perform.

Experiments conducted with Tribolium castaneum in obtaining genetic parameters needed for predicting direct and correlated response from selection for increased pupal weight in two environments (70% versus 40% relative humidity) was reported by Bell and McNary (1963). They found that heritabilities of pupal weight in the two environments were not significantly different (.58 in wet and .55 in dry) and the genetic correlation between the two traits was estimated to be .98. The predicted direct and correlated response in both environments were checked in a replicated selection experiments spanning nine generations.

Good agreement between predicted and observed direct response was obtained for each of the four selected populations. Also, the average observed correlated response including both

environments was accurately predicted. Yet the observed correlated response in each replication for the population selected in dry was approximately twice that predicted, while those observed in the population selected in wet were only half of the predicted values. Evidence from realized genetic correlations led them to conclude that the observed asymmetry of correlated response was due to the effective genetic correlations being different for the two environments.

Another more sophisticated selection experiment with the same species was designed by Yamada and Bell (1963). They selected for large and small 13-day larval weight for 16 generations to evaluate the effectiveness of geneotype environment interaction under two levels of nutrition. The principal difference between the levels consisted of 10% dried brewers yeast in the Good ration while the Poor ration contained no yeast. In addition to an unselected control, there were eight experimental populations as follows: GL = selected large on performance under the good level each generation, PL = selected large on performance under poor level each generation, GPL = selected large on average performance under both levels, gpl = selected large under good or poor levels in alternating generations, and similar four populations selected for small size. They found that the gain per generation in GL population under good and poor levels were 65 ugm. (direct response) and 60 ugm. (correlated re-

sponse) respectively, and corresponding values in PL were 55 ugm. (correlated response) and 98 ugm. (direct response). GPL and gpl were intermediate between GL and PL or a little more similar to those of PL. On the other hand, selection for small gave a completely different picture. The gain per generation for PS under the two environments were alike (87 ugm. vs 73 ugm.) but were greatly different in GS (106 ugm. vs 53 ugm.). They also found that asymmetrical selection responses observed depend entirely on the environment, i.e. larger response toward small size under good but reverse under poor. Realized heritability seemed to be higher for small direction than for large.

Sang (1962) reported that selection of lines of Drosophila melanogaster for fast and slow-growing larvae on a low-pyridoxine diet was effective up to eight generations. The selected larvae showed no pyridoxine requirements up to the tenth generation, but the lines developed at different rates under optimal conditions. In the same report, selection for fast and slow-development lines on a low-casein diet gave a different picture. Selection was reported to be effective throughout the 15 generations, but the realized heritability was one-half that of the previous experiment. The optimal requirements of the two lines were still the same, and there was little difference in their development rates when reared on an optimal diet.

In the study of modification of selection limits, Lawrence (1964) subjected a cross population of Drosophila melanogaster to selection for high and low sternopleural chaeta number in two environments, 18°C and 25°C. When selection had reached a plateau, a sub-line was established from each main line and transferred to a foreign environment, selection being continued. He found that only one sub-line, that of the low line from the 18°C environment, made some progress due to a major mutation. The sub-lineswere then transferred to the environment of their respective main lines, where one, that of the high line from the 25°C environment, made an intermediate response to selection. He suggested that the 18°C environment had increased the average frequency of recombination and hence increased the supply of genetic variance, but due to the unfavorable foreign environment, the availability of genetic variance had been restricted.

A similar experiment has been reported by Abplanalp (1962). He subjected a plateaued laying hen population to weekly periods of 24-hour feed deprivation, and selected for egg number under these conditions. He found that in two replicate populations genetic gains of about 20 eggs were made under shock treatments to 40 weeks of age over five and six generations of selection. Almost similar gains were achieved when the birds were placed under normal management.

C. The Recurrent and Reciprocal Recurrent Selection

As breeders realized that intra-population selection becomes ineffective for characters which have reached a selection limit and also characters which have been subjected to continued natural selection, they began to think of new methods for further improvement of crops and livestock. Jenkins (1940) postulated a method of selection for general combining ability for yield of grain in maize. His method of selection is based on the performance of crossbred offspring, but the selection is still acting on the additive genetic variance. Hull (1945) proposed recurrent selection for specific combining ability. The selection is also based on the performance of progeny obtained by crossing the selected population with an inbred tester. The method would be highly effective if overdominance was important. Comstock et al. (1949) proposed a modified scheme called reciprocal recurrent selection which would be effective for both specific and general combining ability. In this method, the selected populations served as testers for each other.

1. Selection in Plants

Sprague et al. (1959) reported that recurrent selection for specific combining ability following two cycles of selection resulted in an increase in corn yield of 6.5 bushels in the Lancaster x Hy (inbred tester) and 20 bushels

in Kolkmeier x Hy series. Because the hybrids between parents and offspring of successive generations of the two series exhibited increasing yield trends, they concluded that for the material used in their study partial and complete dominance provided the best explanation for gene action involved in yield heterosis. It is doubtful that this conclusion is completely justified for only two cycles of selection as carried out in their experiment.

Lonnquist and McGill (1956) reported that yields of four synthetic lines of corn after two cycles of recurrent selection averaged 96% of the control line compared with 82% for the first cycle populations. Moisture at harvest averaged 105% and 103% of the check for the second and first cycle synthetics. It must be pointed out here that selection for combining ability seems to be effective for an increase in yield, but the average yield is still lower than the control.

Working with corn, Douglas et al. (1961) reported that three cycles of reciprocal recurrent selection had been effective for increasing yield. In terms of standard deviations (s), the second and third cycle means were equal but higher than the first cycle selection in Ferguson's Yellow Dent as compared to the check variety. In Yellow Surcropper, the differences between the selected variety and check variety were 1.36s, 1.65s and 2.86s respectively for the three cycles.

They suggested that the favorable dominant hypothesis was in operation rather than the overdominance theory.

Dudley et al. (1963), employing recurrent selection for specific combining ability in alfalfa, found significant increases in rust resistance and leafhopper yellowing tolerance in two strains of alfalfa. They also observed that genetic variance for rust reaction was reduced whereas genetic variance for leafhopper reaction increased with cycles of selection. The changes in genetic variances were considered to be due to changes in gene frequency.

2. Selection in Animals

The few experiments reported on recurrent and reciprocal recurrent selection to date in animals are mainly in laboratory species. The effectiveness of these selection methods is rather controversial, both promising and discouraging results have been obtained by different workers.

A detailed experiment in this respect was reported by Bell et al. (1955). In two separate experiments with Drosophila melanogaster, three methods of selection to maximise heterosis were compared with conventional closed population selection based on individual and family merit. The three methods were: (a) recurrent selection to an inbred tester for specific combining ability, (b) reciprocal recurrent selection for specific combining ability and general combining ability and (c) inbreeding and hybridization. In the first

experiment of 16 generations, selection in each of these systems was based on a performance index composed of two traits, fecundity and egg size. In the second experiment of 39 generations, selection was based mainly on fecundity. The results of the two experiments led to similar conclusions. For characters of medium to high heritability (and also for characters of low heritability in the early stages of selection), the closed population led to the highest rate of improvement. However, for all characters the recurrent selection method led to a higher final performance because of the higher initial level due to the inherent high general combining ability in the inbred tester. Reciprocal recurrent selection did not lead to as high performance for highly heritable traits as either of the previous techniques. For characters of low heritability it was as efficient as recurrent selection because the rate of improvement was constant whereas closed population selection ceased to respond after several generations. The performance of single crosses of inbred lines derived from the same foundation stock was higher than the cross populations of the recurrent and reciprocal recurrent selections. This led Bell et al. (1955) to suggest that in order to achieve the necessary level of homozygosity to maximise heterosis, some inbreeding of the recurrent and reciprocal recurrent population would be required.

Comstock and Robinson (1956) pointed out that there was

no indication in the experiment of Bell et al. (1955) that the reciprocal recurrent selection had reached a selection limit, while the progress by any non-recurrent system such as inbreeding and hybridization was expected to be asymptotic.

Bell and Moore (1958) repeated their earlier experiment using Tribolium castaneum instead of Drosophila. The trait selected was a highly heritable trait, body weight (they did not define the stage of the body weight). In two replicated experiments, they found that the performance of individual and family selection ranked at the top, followed by the reciprocal recurrent selection, the control and finally, the inbred hybrids. These results were obtained after 16 generations of selection. They pointed out that much of the superiority shown by the closed population was due to a larger selection differential which was inherent in the design. These results are different from those of the previous experiment in that the inbred hybrids showed the poorest improvement. This is probably due to differences in the species and trait.

In comparing the effectiveness of mass selection and reciprocal recurrent selection in a crossbred population from two plateaued populations of Drosophila melanogaster, Brown and Bell (1960) reported that both methods were equally effective.

Three experiments of reciprocal recurrent selection

with Drosophila melanogaster were reported by Rasmuson (1956). In the first experiment, selection for egg production for 20 generations resulted in a 6% increase over the control population. In the second experiment, selection for 13 generations for hatchability of eggs resulted in a 2% increase. In the third experiment, selection for body weight for six generations resulted in a 2% increase. The lack of clear-cut and lasting effects of selection were interpreted as due to scarcity of loci showing overdominance with major effects and the presence of epistatic interaction.

A similar study had been carried out by Kojima and Kelleher (1963) in Drosophila. During 13 generations of mass selection for egg number, a total improvement of 3.53 eggs and 4.87 eggs was obtained for two different lines, while a total gain of 14.72 eggs obtained in reciprocal recurrent selection. In comparisions with hybrids of inbred lines developed from the base populations, they found that the improved reciprocal recurrent selection material attained a level equivalent to the performance of the top four per cent of all possible $F_1$ hybrids between base populations. They concluded that reciprocal recurrent selection could be effective in improving a quantitative trait on a hybrid basis, even when individual populations do not respond to purebred selection because of the lack of additive genetic variance within a population.

Two separate experiments of recurrent selection, one with mice and another with Drosophila, were reported by Bowman (1962). In the selection for large litter size in mice, a net increase of .90 young per litter was attained after four generations of selection. In selection for low bristle number in Drosophila, a decrease of 6.3 bristles was achieved over 14 generations of selection. He indicated that response to selection in each experiment was close to or less than the expected response calculated on the assumption that all the variance between sires in crossing performance was additive genetic variance. Hence, he suggested that the apparent ineffectiveness of recurrent selection in both experiments was due to the lack of overdominance.

Experiments conducted to investigate the combining ability between purebred and crossbred populations have been reported by several workers in different species and different traits. Working with chickens, Enfield (1960) found that the sire component of variance was much larger in crossbreds than in purebreds for egg production and the genetic correlation between purebred and crossbred half-sib families from the same sire were high for all traits. He suggested that selection based on purebred performance would be relatively effective in improving the crossbreds.

In an experiment of reciprocal recurrent selection with chickens, Krause et al. (1965) estimated the genetic co-

variance and correlation for the comparison of a sire's pure and crossbred progenies in age of sexual maturity and survivor's per cent of production. Positive covariances were generally observed except for a negative relationship for the production trait. Genetic correlations estimated were low for both traits. As a matter of fact, three positive and one negative (production trait) values of genetic correlation were not significantly different from zero. This means that the genetic improvement in the purebreds will not be reflected to a great extent in the crossbreds.

Working with mice in post-weaning growth, Rahnefeld (1961) reported similar results as Enfield (1960). His estimate of genetic covariance between pure-line parent and crossbred offspring was .25 $\pm$ .05 g. He also found that the expected progress for the crossbred performance was .20 g. per generation when the parameter estimates were based on purebred performance, while the expected progress was only .13 g. per generation when the parameter estimates were based on crossbred performance. He arrived at the same conclusions as Enfield (1960). However, Boylan (1962) continued the experiment reported by Rahnefeld (1961), and found that later results were not so promising. He reported that the sire component of variance in crossbreds and the genetic covariance between purebreds and crossbreds were .11 and .10 respectively, while the genetic correlation was .71. It is necessary to point out here that the genetic covariances

estimated by the two workers should be comparable. He indicated that although the theory for predicting response in crossbred performance based on purebred performance was still valid, the deviation that was found between observed and predicted response was large enough to emphasize that the issue deserved continued investigation.

Other promising results came from Seale (1965) working with sheep. He reported that the average genetic improvement in rate of gain per generation through mass selection was .029 lb. for purebreds and .045 lb. for single crosses. He indicated that improvements in two pure breeds through mass selection could be effective in increasing the performance of crossbreds resulting from crosses of the two breeds. He further suggested that if improvement in rate of growth of crossbred lambs was the objective of a breeding program, selection techniques other than mass selection within the pure breeds concerned did not seem to be necessary.

Comstock and Robinson (1956) raised the question of whether a cross might be improved more rapidly by conventional intra-population selection in the parent populations rather than from the reciprocal recurrent selection. They used the genetic correlation as an indication of the effectiveness of such selection. Analysis of data in eight-week weight of chickens showed that the correlations were relatively high in four instances but low in the other two. They

suggested that as revealed from the results, intra-population selection might be effective for improvement of a population cross in some cases, not in others.

Kojima and Kelleher (1963), after their comparisons of effectiveness of closed population selection and reciprocal recurrent selection, proposed two conditions in which reciprocal recurrent selection would be superior to closed population selection. The first was the condition of low heritability in purebred populations. Such a condition might be a result of either previous artificial or natural selection due to a close relationship of the character to a fitness scale. The second condition was the situation where the genetic structures of individual populations were so integrated that crossing them destroyed the existing epistatic gene complexes favorable to desirable performance in purebreds.

Due to the scarcity of work done in this respect, a definite conclusion whether the recurrent and reciprocal recurrent selection are effective techniques in the improvement of livestock cannot be arrived at. But, from the results obtained so far, it is more promising than discouraging.

## SOURCE OF DATA

A selection experiment using the flour beetle, Tribolium castaneum as the experimental organism was initiated in January, 1963. This manuscript reports analysis of the data from cycle (or generation) 1 to 15. The initiation of a synthetic population to provide the experimental material for this study and the amount of heterosis involved was reported for the first three generations by Boylan and Wong (1965).

The basic design of the experiment consisted of mass selection for a single trait in a genetically segregating population of beetles. The population in which selection was eventually employed was formed by crossing two inbred lines. Matings in each generation were made randomly among selected individuals in the segregating population. At the same time, this segregating population was also crossed with one of the parental inbred lines. Occasionally, the reciprocal crosses were made between the parental inbred line and the segregating population. Both of the parental inbred lines were maintained during the course of the experiment by the mating within each line of individuals picked at random.

A. Genetic Stocks

The inbred lines of beetles were obtained from two sources: (a) the $CSI_{10}$ line was obtained from Dr. Alexander Sokoloff, University of California and (b) the $E_2$ line was received from Dr. George Clayton, Institute of Animal Genetics, Edinburgh. The origin and description of the inbred lines used in this experiment are as follows:

1. $CSI_{10}$ - this line was produced by 37 generations of continuous full-sib matings. Five males and seven females were received for this line. It is called the C line in the experiment.

2. $E_2$ - this line was produced by 39 generations of continuous full-sib matings. Six males and six females were received for this line. It is called the E line in the experiment.

The two inbred lines described above are assumed to be of diverse genetic origin and non-related. No artificial selection of any kind has been practiced in the two lines.

B. Construction of S Population

The C and E lines were crossed reciprocally to produce the population in which selection was eventually practiced. This synthetic population was designated as the S population or line and will sometimes be referred to hereafter as the purebred population. After the formation of the

$F_1$, it was followed by five generations of random mating to $F_6$. Cycles and generations of the S line are completely parallel. No matings were made in cycle four for C and E lines, therefore, the generation number of these lines is one less than the cycle number from that cycle on. All the parents of any cycle in each of the lines were raised in the immediate preceeding cycle. Selection in the S line was first employed among the $F_6$ individuals which became the parents of cycle seven of the experiment. The construction of the S line is shown in Figure 1.

Figure 1

Genetic Structures of S Population Initiated by Crossing Two Inbred Lines (C and E)

| | | | Matings |
|---|---|---|---|
| $F_1$ | Random selection of parents | Cycle 1 | E males x C females<br>C males x E females |
| $F_2$ | Random selection of parents | Cycle 2 | EC x EC, EC x CE,<br>CE x EC, CE x CE |
| $F_3$ | Random selection of parents | Cycle 3 | S x S |
| $F_4$ | Random selection of parents | Cycle 4 | S x S |
| $F_5$ | Random selection of parents | Cycle 5 | S x S |
| $F_6$ | Random selection of parents | Cycle 6 | S x S |
| $F_7$ | Selected parents | Cycle 7 | S x S |

C. Selection Criterion

The single trait on which mass selection was employed in the S was pupal weight at one day of age. Those pupae were selected as parents of the next generation which had the highest pupal weight at one day of age. Performance of the S x E crossbred (males will be written first in all crosses mentioned henceforward) individuals was not considered in any way for the selection of parents for S x S matings.

No selection was practiced in C and E lines, except perhaps indirectly in the E line, females which pupated first being used to continue the line. C and E females used for the S x C and S x E matings were picked at random.

D. Management of the Populations

During the mating period the males were kept with the females for four days. Then the males and females were separated and transferred to new containers with fresh media. The number of eggs laid by each female was counted approximately 48 hours later. The eggs were discarded after counting. The females were then put into new containers with fresh media. Except in the E x E line, they were transferred after five days, and the eggs in the container were left for hatching. Because of the smaller number of eggs laid by E females, they were transferred from the containers just before the larvae began to pupate. The larvae pupated at about 17

days after egg count. The weighing of the pupae lasted for 10 to 14 days. Each container was checked daily for pupae during the pupation time.

Pupae selected or saved to be the parents of the next generation were put in separate containers and numbers were assigned to identify them according to their line and generation. During mating, individuals coming from separate containers were painted with different colors to identify them. The containers used were three-quarter ounce glass creamers. For ease in handling, creamers were placed in steel-mesh baskets which would hold about 28 creamers. All eggs, larvae, pupae and adults were kept in an incubator at 29°C. The relative humidity was recorded in the incubator in which the experiment was carried out. This was 70% and, in general, it varied within ±10%.

A No. 60 mesh-sieve was used to separate eggs from the media for egg count and a No. 40 mesh-sieve was used to separate the pupae. The sex of the pupae was determined under a binocular-stero-microscope before weighing. Pupae were weighed to the nearest microgram on a Cahn electrogram balance. Whole wheat flour with the addition of five per cent brewers yeast was used as media. The media was sieved and dry sterilized at a temperature of 80°C for approximately two hours. The beetles were raised in the creamers filled with approximately five grams of media. The media was freshly made

as required.

E. Mating Scheme

In each cycle 20 to 24 selected S line males were randomly mated with 40 to 48 selected S line females, i.e. each S line male was mated with two S line females. At the same time each S line male was mated with two E line females. This meant that each S line male was mated with two S line females and two E line females. Generally, data from five male and five female offspring were collected from each pair mating. In E line female offspring and very rarely in S line male and female offspring more than five were weighed in order to obtain sufficient individuals to be the parents of the next generation. One restriction that was imposed on the selection of S line males was that not more than three males would be selected from any one sire. This restriction was made to minimize an increase in inbreeding of the S line. Concurrently with the S line matings about 10 to 12 C line males and 10 to 14 E line males were each mated to two females of their respective lines. In cycle five, the purebred and the crossbred crosses were made simultaneously in the same container. It was found that whenever the paint used to identify them broke off more than two individuals, they could not be identified. In order to minimize the loss, the purebred and crossbred crosses were made separately in the subsequent cycles. From cycle six to ten, the crossbreds were made preceeding the

purebred crosses. It was then found that there was considerable amount of time loss due to the slower development of the E line. In the subsequent cycles S x S, C x C and E x E matings were made on the same day and the E females were taken randomly from those which had attained their mature age. Sufficient males were obtained at the time of mating. S x E matings were made four days later and by that time most E line females had reached their mature age. Thus, unnecessary waiting for all individuals to attain their mature age was avoided, and about seven days were shortened from every cycle.

Due to the change in order of time of the mating scheme, the age at the time of mating was quite variable. Generally, the age ranged from ten to 30 days of age, but in rare cases some beetles reached 40 days. Despite the fact that the E line developed slower, cycle and generations were completely parallel, except that no matings were made at cycle four for both C and E lines.

In cycle 16, the parents of cycle 14 were remated again in order to serve as another way of measuring the environmental fluctuations. Because the mating was not successful due to the low fertility, only the generation means were listed in the result.

Unfortunately, in cycle 15, the thermostat of one of the incubators did not function properly and all the beetles in that incubator except some mass cultures were lost. The

incident killed both the parents and offspring of cycle 15. The experiment was continued from the parents of cycle 14 which were preserved in another incubator. Those matings were successful and sufficient offspring were left to continue the experiment. In the analysis of results, the data collected from the first series of cycle 14 and 15 were not used in any analysis.

F. High and Low S Group

Beginning with cycle seven and continuing through the rest of the cycles, in addition to the selection of the highest pupal weight males in the S population, three of the lightest males were also selected and each was mated at random with two high females. Each of the low S males were also mated with two E line females selected at random. The selection of low pupal weight was done to increase the precision of estimates of parent-offspring covariances and regressions (i.e., reduce the standard errors of the estimates). All offspring from the low males were discarded at the end of each cycle.

G. Collection of Data of the Populations

The following data were collected on each beetle: date of pupation, date of egg count, age at egg count, number of eggs and pupal weight at one day of age. Information on every beetle was punched on an IBM card, and the data were

processed with an IBM 1620 computer.

The populations throughout the course of the experiment have appeared in good health. No cases of disease among beetles were found at any time during the course of the experiment.

# METHODS OF ANALYSIS

The data were processed with an IBM 1620 computer to obtain all but the more simply computed parameters. Data on the two sexes were treated separately by cycle and line, except in the case of egg count where information was available for only one sex. Analyses were made by cycle (generation) for each line.

## A. Selection Differentials

Two selection differentials were calculated in each generation:

1. The expected selection differential was calculated as the difference between the simple unweighted mean of the selected individuals and the population mean;

2. the effective selection differential was calculated as the difference between the weighted mean (weighted by number of offspring produced) of the selected individuals and the population mean.

## B. General Procedures in Parameter Estimation

Standard statistical procedures were employed to obtain the various intermediate quantities from which the ultimate parameter estimates were computed.

1. Parent-Offspring Covariance and Regression

In the case of sire-offspring and dam-offspring

covariances and regression the variates used in computation were the sire and dam phenotypic values and the offspring phenotypic values. In the case of mid-parent-offspring regression the phenotypic values of the mid-parent and the offspring were used.

The "b" values obtained in each cycle were subjected to a covariance analysis to test for homogeneity in order to justify the pooling of data. The averaged "b" value was arrived at by weighting the individual "b" values inversely to their approximated variances.

The variance of covariance estimates were approximated, substituting estimates for corresponding parameters in the following general expression for the variance of a covariance estimate.

$$V(\text{Cov } xy) = \frac{V_x \cdot V_y + (\text{Cov } xy)^2}{f + 2}$$

where:

Cov xy = estimate of covariance between x and y

$V_x$ = variance of x

$V_y$ = variance of y

$f$ = degrees of freedom for the estimate

2. Other Simple Covariances

These include covariances between means (by sires) of S line males or females with SE line males or females. Variances of these quantities were approximated as described

above for parent-offspring covariances.

3. Analysis of Variance and Covariance

The form of variance analysis and expectations of mean squares are presented in Table I. Separate analyses were conducted by line and sex within cycle. The pooled analysis was done by pooling over all cycles by line and sex. In the pooled analysis, the form is analogous to that in Table I with the addition of another source of variation.

TABLE I

Analysis of Variance and Mean Square Expectation

| Source of Variance | d.f. | Mean Square | Mean Square Expectations |
|---|---|---|---|
| Sires | $s - 1$ | $M_1$ | $W + K_2D + K_3S$ |
| Dams within sires | $d - s$ | $M_2$ | $W + K_1D$ |
| Within full-sib families | $N - d$ | $M_3$ | $W$ |

where:

$s$ = total number of sires

$d$ = total number of dams

$N$ = total number of individuals

$$K_1 = \frac{1}{(d - s)}\left[ N - \sum_i \left( \frac{\sum_j n_{ij}^2}{n_i} \right) \right]$$

$$K_2 = \frac{1}{(s-1)}\left[\sum_i\left(\frac{\sum_j n_{ij}^2}{n_i}\right) - \frac{\sum_i\sum_j n_{ij}^2}{N}\right]$$

$$K_3 = \frac{1}{(s-1)}\left[N - \frac{\sum_i n_i^2}{N}\right]$$

$n_i$ = total number of offspring from the $i^{th}$ sire

$n_{ij}$ = total number of offspring from the $j^{th}$ dam mated to the $i^{th}$ sire

S = variance due to differences among sires

D = variance due to differences among dams

W = variance due to differences among full-sibs

The variances of variance component estimates were obtained as outlined by Comstock and Robinson (1951). All these estimates were taken to be linear functions of mean squares. For example, the estimate of variance of the sire component was as follows:

$$V(\hat{S}) = \frac{V(M_1)}{K_3^2} + \left[\frac{K_2}{K_1K_3}\right]^2 V(M_2) + \left[\frac{K_2 - K_1}{K_1K_3}\right]^2 V(M_3)$$

where:

$V(M_1)$ = variance of the mean square for between sires source of variance,

$V(M_2)$ = variance of the mean square for dams within sire source of variance,

$V(M_3)$ = variance of the mean square for within litters source of variance, and

$K_1$, $K_2$ and $K_3$ are defined in Table I

The variances of the mean squares were approximated by substitution of the observed mean square for its expectation in the general expression

$$V(M) = \frac{2\ E(M)^2}{f}$$

where:

M = any mean square

E(M) = expectation of M

f = degrees of freedom for M

The variance of heritability estimates is expressed as the following formula:

$$V(h^2) = \frac{V(4S)}{V(P)}$$

$$= \frac{16\ V(S)}{p^2}$$

(where P = S + D + W = total phenotypic variance)

and

$$\text{standard error of } h^2 = \sqrt{V(h^2)}$$

C. Population Change in Response to Selection

A linear regression of mean performance on time was used to measure changes in S and SE populations in response to selection. Population mean performance, expressed as a deviation from the control (E line), was the dependent variate and cycle number was the independent variate. Variation in

the control line was assumed to measure variation in environmental effect. Of course this requires that there is no genotypic-environment interaction in the lines.

Response as described above was used in calculating realized heritability ($Rh^2$). According to Falconer (1960) this is defined as the ratio of response (R) to the selection differential (S.D.).

Thus

$$Rh^2 = \frac{R}{S.D.}$$

# RESULTS AND DISCUSSION

## A. Control Population

The primary role of a control population is to provide some means to measure the environmental fluctuation in various periods of an experiment. The systems of measurements in a continuous selection study cover a wide range of time and space. Thus, considerable fluctuations are expected in the test environments at the successive cycles of selection. Genetic changes due to selection can be shown only after a proper adjustment of raw data is made for the environmental fluctuations represented by the performance of control included in each cycle. This was done by maintaining the long inbred E and C lines as control populations. Given genetic stability as a result of the prior inbreeding, variation in performance of the control provides a continuous measure of environmental effects.

### 1. Genetic Variance in the E Population

As a check on the assumed genetic stability, estimates of variance components and heritability were computed. Table II lists estimates of variance components and heritability obtained from analysis of variance. The additive genetic variances were expressed as four times the sire component of variance (4S) which were 6,608 ugm. and -152 ugm. for males and females respectively. Table III contains the

TABLE II

Parameter Estimates from Analysis of Variance

for Control Population (E)

| | W | D | S | 4S | $V_p$ | $\frac{4S}{V_p}$ |
|---|---|---|---|---|---|---|
| Males | 25097 | 2816 | 1652±1258 | 6608 | 29565 | .224±.045 |
| Females | 30624 | 1169 | -38± 960 | -152 | 31830 | -.005±.036 |

TABLE III

Parent-Offspring Regression Estimates of Heritability

for Control Population (E)

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | d.f. | b | $S.E._b$ | $h^2$ | d.f. | b | $S.E._b$ | $h^2$ |
| Sire-offspring | 942 | -.017 | .038 | -.034±.076 | 1093 | .005 | .039 | .010±.078 |
| Dam-offspring | 942 | .028 | .030 | .056±.060 | 1093 | .028 | .028 | .056±.056 |
| Midparent-offspring | 942 | .020 | .046 | .040±.092 | 1093 | .037 | .044 | .074±.088 |

estimates of heritability obtained from parent-offspring regression. When the separate estimates of heritability from analysis of variance and regression were pooled, the averaged values obtained were .118 ± .097 and .022 ± .027 for males and females respectively. The over all average, pooling over males and females, was .029 ± .026. The pooled heritability estimate is not statistically different from zero ($P > .05$) suggesting that the genetic variability is very low in the population.

Another source of information concerning the magnitude of the genetic variance in the control line is the regression of SE offspring on E line dams. Estimates are presented in Table IV. As expected, both estimates for males and females are small and not significantly different from zero ($P > .05$)

TABLE IV

Estimates of Regression of SE Offspring on E Dams

| | d.f. | b | $S.E._b$ |
|---|---|---|---|
| Males | 1397 | .024 | ±.030 |
| Females | 1404 | .001 | ±.035 |

2. Genetic Variance of C Population

It was decided at the beginning of the experiment to carry on the other parental line, the long inbred line C, as a possible additional control population. Data were also analyzed for genetic variance. Table V lists estimates of variance components and heritability of pupal weight obtained from analysis of variance. Table VI contains the estimates calculated from parent-offspring regression. The pooled values of heritability estimates from different sources were .286 ± .024 for males and .272 ± .025 for females. The overall average, pooled over the sexes, was .279 ± .017. Here, the pooled heritability estimate suggests that a large amount of additive genetic variance is still existing in the population, despite the fact that this is a long inbred line.

3. Population Means (E and C)

The population means of the E and C lines are presented in Table VII by sex and cycle of the experiment, and shown graphically in Figure 2. Figure 2 indicates that C line is more variable than E line and also the C line has shown some trend of declining.

4. Selection Differentials (E and C)

While no deliberate selection was practiced in the controls, selection differentials were calculated and are presented in Table VIII and Table IX for E and C lines re-

TABLE V

Parameter Estimates from Analysis of Variance

for Control Population (C)

| | W | D | S | 4S | $V_p$ | $\frac{4S}{V_p}$ |
|---|---|---|---|---|---|---|
| Males | 30844 | 8781 | 3145±2152 | 12980 | 42769 | .303±.042 |
| Females | 46315 | 9288 | 2455±2463 | 12275 | 58059 | .211±.039 |

TABLE VI

Parent-Offspring Regression Estimates of Heritability

for Control Population (C)

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | d.f. | b | $S.E._b$ | $h^2$ | d.f. | b | $S.E._b$ | $h^2$ |
| Sire-offspring | 976 | .146 | .033 | .292±.066 | 1018 | .142 | .038 | .284±.076 |
| Dam-offspring | 976 | .144 | .028 | .288±.056 | 1018 | .184 | .031 | .368±.062 |
| Midparent-offspring | 976 | .267 | .041 | .267±.041 | 1018 | .300 | .045 | .300±.045 |

TABLE VII

Mean Pupal Weight (Micrograms) of Control Population (C and E) by Cycle and Sex

| | C Line | | | | | E Line | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Males | | Females | | | Males | | Females | | |
| Cycle | N | Mean | N | Mean | Population* Mean | N | Mean | N | Mean | Population* Mean |
| 1 | 40 | 2608.03 | 40 | 2828.75 | 2718.39 | 20 | 1764.65 | 20 | 1961.55 | 1863.10 |
| 2 | 99 | 2518.74 | 105 | 2717.03 | 2617.89 | 36 | 1888.03 | 32 | 1981.47 | 1934.75 |
| 3 | 38 | 2461.00 | 90 | 2781.97 | 2621.48 | 62 | 1874.45 | 58 | 2007.05 | 1940.75 |
| 4 | - | - | - | - | - | - | - | - | - | - |
| 5 | 51 | 2487.92 | 53 | 2669.83 | 2578.88 | 76 | 1713.58 | 99 | 1824.07 | 1768.83 |
| 6 | 71 | 2348.65 | 73 | 2502.29 | 2425.47 | 75 | 1780.28 | 86 | 1893.76 | 1837.02 |
| 7 | 75 | 2304.63 | 80 | 2535.04 | 2419.84 | 80 | 1787.58 | 104 | 1918.92 | 1853.25 |
| 8 | 102 | 2298.91 | 102 | 2376.63 | 2337.77 | 69 | 1812.86 | 103 | 1917.19 | 1865.03 |
| 9 | 106 | 2323.75 | 103 | 2356.77 | 2340.26 | 73 | 1856.95 | 106 | 1985.98 | 1921.46 |
| 10 | 105 | 2356.88 | 108 | 2444.04 | 2400.46 | 88 | 1822.31 | 106 | 1963.26 | 1892.79 |
| 11 | 70 | 2251.51 | 74 | 2353.54 | 2302.25 | 93 | 1806.93 | 119 | 1986.50 | 1896.72 |
| 12 | 115 | 2306.42 | 115 | 2360.56 | 2333.49 | 99 | 1858.32 | 112 | 1963.30 | 1910.81 |
| 13 | 114 | 2334.33 | 112 | 2403.12 | 2368.73 | 92 | 1710.01 | 115 | 1846.95 | 1778.48 |
| 14 | 73 | 2376.78 | 102 | 2570.49 | 2473.41 | 60 | 1767.12 | 70 | 1905.29 | 1836.20 |
| 15 | 106 | 2314.10 | 108 | 2421.81 | 2367.96 | 63 | 1904.94 | 81 | 1988.54 | 1946.74 |
| $14^1$ | 91 | 2286.41 | 91 | 2417.91 | 2352.16 | 93 | 1759.73 | 117 | 1881.50 | 1820.62 |
| $15^2$ | 86 | 2351.57 | 83 | 2420.84 | 2386.20 | 29 | 1719.52 | 15 | 1808.87 | 1764.20 |
| $14^r$ | - | - | - | - | - | 6 | 1782.67 | 5 | 1850.00 | 1816.34 |

$^1$ and $^2$ are the previous cycle 14 and 15 before the incubator broke down.

$^r$ is the repeated mating of cycle 11 parents at cycle 14.

* is the unweighted average of males and females.

TABLE VIII

Selection Differentials (Micrograms) for Pupal Weight Gain for Control Population (E)

| | Males | | Females | | Mean | |
|---|---|---|---|---|---|---|
| Cycle | Expected | Effective | Expected | Effective | Expected | Effective |
| 1 | 32.41 | 63.84 | 35.76 | -50.19 | 29.09 | 6.83 |
| 2 | 46.32 | 33.02 | -26.76 | -46.14 | 9.78 | -6.56 |
| 3 | 24.15 | -47.73 | 36.75 | 26.93 | 6.30 | -10.40 |
| 4 | - | - | - | - | - | - |
| 5 | 24.25 | 69.79 | 103.26 | 24.62 | 63.76 | 47.21 |
| 6 | 72.89 | 73.10 | 20.74 | -42.39 | 46.82 | 15.36 |
| 7 | -19.66 | 142.52 | 2.79 | 77.09 | -8.44 | 109.67 |
| 8 | 22.20 | -25.20 | 23.20 | 40.52 | 22.70 | 7.66 |
| 9 | -100.16 | -111.35 | -91.55 | -98.77 | -95.86 | -105.06 |
| 10 | -50.02 | -52.39 | -90.87 | -86.23 | -70.45 | -68.31 |
| 11 | -136.14 | -39.66 | -33.11 | -28.78 | -84.63 | -34.27 |
| 12 | -135.68 | -164.36 | -65.09 | -49.24 | -100.39 | -106.80 |
| 13 | -77.94 | -69.73 | -109.59 | -84.95 | -93.77 | -77.34 |
| 14 | 102.80 | 118.40 | 18.38 | 29.70 | 60.59 | 74.05 |
| Total | -242.88 | -10.38 | -186.09 | -288.02 | -264.50 | -147.87 |

TABLE IX

Selection Differentials (Micrograms) for Pupal Weight Gain for Control Population (C)

| Cycle | Males | | Females | | Mean | |
|---|---|---|---|---|---|---|
| | Expected | Effective | Expected | Effective | Expected | Effective |
| 1 | 57.71 | 85.11 | 111.25 | 133.47 | 84.48 | 109.29 |
| 2 | 57.53 | 119.04 | -19.53 | -44.22 | 19.00 | 37.41 |
| 3 | 35.80 | 18.65 | 54.43 | 258.96 | 45.12 | 138.81 |
| 4 | - | - | - | - | - | - |
| 5 | 46.66 | 134.29 | 62.84 | -25.07 | 54.75 | 54.61 |
| 6 | 68.55 | 41.67 | 10.96 | -53.50 | 39.76 | -5.92 |
| 7 | -54.21 | -38.68 | -87.25 | -53.37 | -70.73 | -46.03 |
| 8 | -58.24 | -58.48 | -123.75 | -86.58 | -91.00 | -72.53 |
| 9 | 72.23 | 92.15 | -1.48 | 1.55 | 35.38 | 46.85 |
| 10 | 16.12 | -40.57 | 51.29 | 8.12 | 33.71 | -16.23 |
| 11 | -22.84 | -22.64 | 5.29 | 10.68 | -8.78 | -5.98 |
| 12 | -30.83 | -22.49 | -16.60 | 10.85 | -23.72 | -5.82 |
| 13 | 71.34 | 141.64 | -36.67 | 5.03 | 17.34 | 73.34 |
| 14 | 98.93 | 96.82 | 6.22 | 28.67 | 52.58 | 62.75 |
| Total | 358.75 | 546.51 | 17.00 | 194.59 | 187.89 | 370.55 |

spectively.

5. Conclusions About the E and C Lines as Control Populations

Results shown for the E line indicate that the additive genetic variance for body weight (pupal stage) is low in this line. All individual heritability estimates from different sources and the pooled estimates are not significantly different from zero ($P>.05$), except the one calculated from the sire component. The low values found for regression of SE offspring on E dams give additional support to the assumption that little genetic variance exists in E line.

As for the C line, the results suggest that the additive genetic variance is high. All individual and pooled heritability estimates are highly significant ($P<.01$). The situation is further revealed by the selection differentials. The total effective selection differentials, expressed in terms of standard deviations (s) is -.84s in the E line and 1.65s in the C line for 13 cycles. However, this is still not critical compared with the parallel figure of 11.05s in the S population for nine generations of selection.

From all available evidence it can be concluded that the E line is justified to serve the purposes of a control population for the experiment while the C line is not reliable as an ideal control.

B. Purebred (S) and Crossbred (SE) Populations

1. Population Means and Response Curves

Population mean performance for pupal weight is presented for S and SE lines by sex and cycle in Table X (the S and SE lines referred to from here on will be the high S, i.e. excluding the low-sire offspring). The same data are presented graphically in Figure 2 in addition to those of E and C lines. The means of reciprocal crosses between C and E lines for the first generation and the mean of the midparent (unweighted average of population means of C and E lines) for the first three generations are also shown on the same graph.

The mean performance of S and SE offspring are also summarized in terms of deviations from the mean of the control population (E). These data are calculated from cycle six to cycle 15 in Table XI. The same data are presented graphically in Figure 3.

Heterosis was reported by Boylan and Wong (1965) in the first generation of S line. Expressed as $F_1$ means exceeding the midparent mean, the percentages of heterosis were 5.0% for males and 3.7% for females in terms of their respective pupal weight. A maternal effect was found in pupal weight among males, comparing results of reciprocal crosses in the $F_1$. Males were heavier when their dams were from the heavier parental line.

TABLE X

Mean Pupal Weight (Micrograms) of S and SE Populations by Cycle and Sex

| | S Population | | | | | SE Population | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Males | | Females | | | Males | | Females | | |
| Cycle | N | Mean | N | Mean | Population* Mean | N | Mean | N | Mean | Population* Mean |
| 1 | 67 | 2295.51 | 57 | 2483.65 | 2389.55 | - | - | - | - | - |
| 2 | 170 | 2168.53 | 170 | 2279.84 | 2224.19 | - | - | - | - | - |
| 3 | 170 | 2207.91 | 165 | 2338.47 | 2273.19 | - | - | - | - | - |
| 4 | 161 | 2300.47 | 158 | 2427.22 | 2363.85 | - | - | - | - | - |
| 5 | 109 | 2088.03 | 109 | 2290.21 | 2189.21 | - | - | - | - | - |
| 6 | 143 | 2132.55 | 143 | 2217.90 | 2175.23 | 123 | 1982.48 | 129 | 2140.36 | 2061.42 |
| 7 | 209 | 2210.11 | 212 | 2294.21 | 2252.16 | 139 | 1962.92 | 128 | 2156.48 | 2059.70 |
| 8 | 183 | 2307.79 | 192 | 2437.64 | 2372.72 | 166 | 2025.21 | 158 | 2168.79 | 2097.00 |
| 9 | 187 | 2450.34 | 188 | 2555.12 | 2502.73 | 145 | 2097.82 | 151 | 2255.19 | 2176.51 |
| 10 | 206 | 2547.09 | 201 | 2650.17 | 2598.63 | 171 | 2141.02 | 159 | 2289.52 | 2215.27 |
| 11 | 142 | 2616.96 | 142 | 2724.52 | 2670.61 | 155 | 2099.79 | 153 | 2259.03 | 2179.94 |
| 12 | 168 | 2663.13 | 166 | 2758.77 | 2710.95 | 165 | 2249.87 | 167 | 2381.94 | 2315.91 |
| 13 | 153 | 2748.33 | 143 | 2854.39 | 2801.36 | 140 | 2196.51 | 143 | 2331.60 | 2264.06 |
| 14 | 193 | 2868.91 | 189 | 2972.50 | 2920.48 | 136 | 2122.61 | 148 | 2280.24 | 2201.43 |
| 15 | 145 | 2849.88 | 181 | 2971.53 | 2910.71 | 68 | 2353.35 | 79 | 2545.81 | 2249.58 |
| $14^1$ | 200 | 2830.53 | 197 | 2946.51 | 2888.52 | 174 | 2200.19 | 179 | 2345.39 | 2272.79 |
| $15^2$ | 169 | 2975.44 | 164 | 3072.55 | 3024.00 | - | - | - | - | - |
| $14^r$ | 13 | 2477.61 | 12 | 2708.17 | 2592.89 | 18 | 2230.94 | 16 | 2545.81 | 2388.38 |

$^1$ and $^2$ are the previous cycle 14 and 15 before the incubator broke down.

$^r$ is the repeated mating of cycle 11 parents at cycle 14.

* is the unweighted average of males and females.

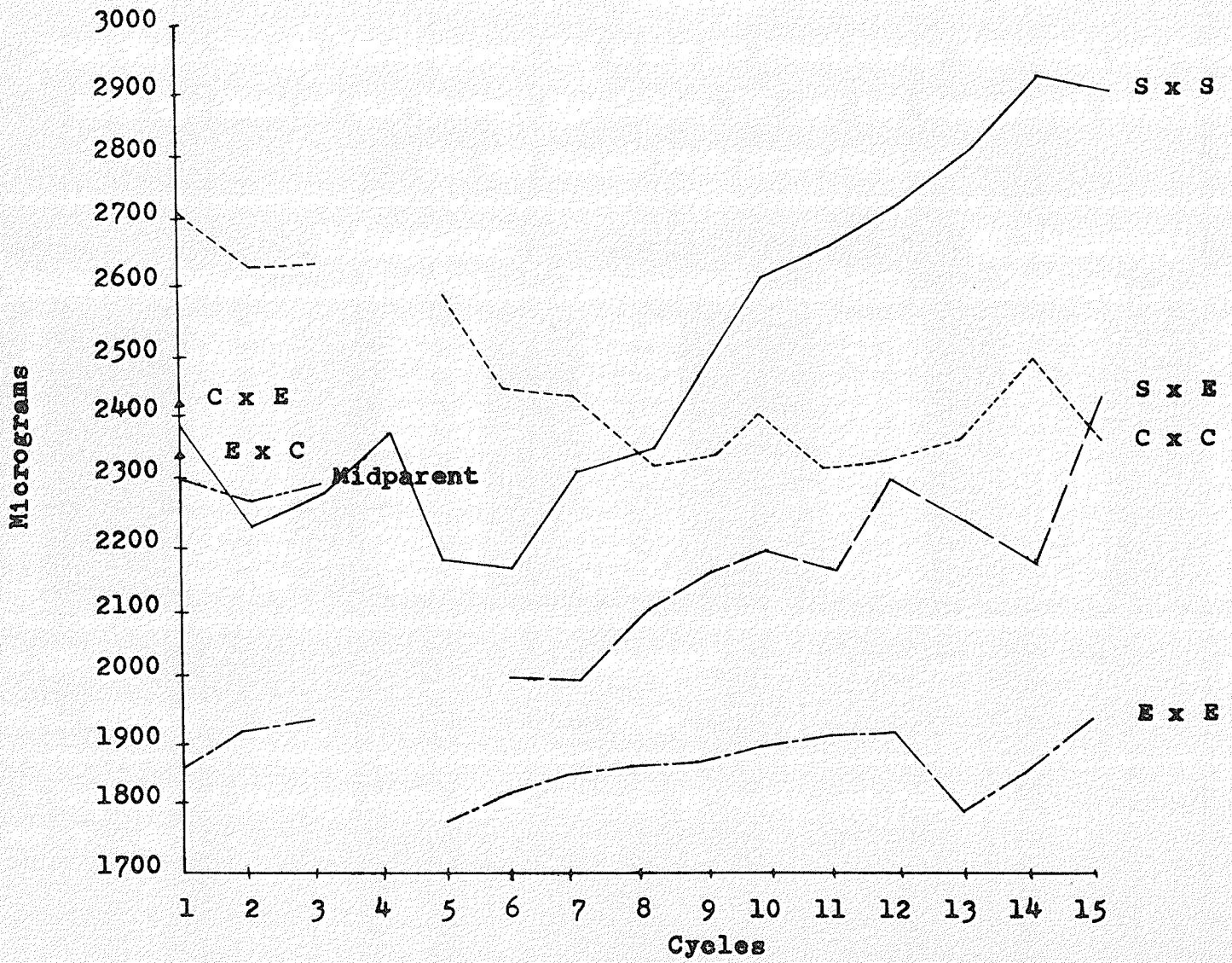



Figure 2. Population Means of Reciprocal Crosses (Between C and E Lines) in the First Generation, Midparent (Between C and E Lines) for the First Three Generations, S, SE, C, and E Lines.

TABLE XI

Mean Pupal Weight (Micrograms) for S and SE Populations Expressed as Deviations From the Mean of the Control Population (E) and the Regression Coefficients (b) for Change Over Time (Cycles)

| | S Population | | | SE Population | | |
|---|---|---|---|---|---|---|
| Cycle | Males | Females | Population* | Males | Females | Population* |
| 6 | 352.27 | 324.14 | 338.20 | 202.20 | 246.60 | 224.40 |
| 7 | 422.53 | 375.29 | 398.91 | 175.34 | 237.56 | 206.45 |
| 8 | 494.93 | 520.45 | 507.69 | 212.35 | 251.60 | 231.98 |
| 9 | 593.39 | 569.14 | 581.27 | 240.87 | 269.21 | 255.04 |
| 10 | 724.78 | 686.91 | 705.85 | 318.71 | 326.26 | 322.49 |
| 11 | 810.03 | 737.75 | 773.89 | 292.86 | 272.35 | 282.70 |
| 12 | 808.81 | 795.47 | 802.14 | 391.55 | 418.64 | 405.10 |
| 13 | 1038.32 | 1007.44 | 1022.88 | 486.50 | 484.65 | 485.58 |
| 14 | 1101.79 | 1067.21 | 1084.50 | 355.49 | 374.95 | 365.22 |
| 15 | 944.94 | 982.99 | 963.46 | 448.41 | 557.27 | 502.84 |
| b (6-15) | | | 83.23** | | | 32.10** |
| S.E. b(7-15) | | | 7.30 | | | 5.49 |

* Population mean is unweighted average of males and females.

** ($P < .01$).

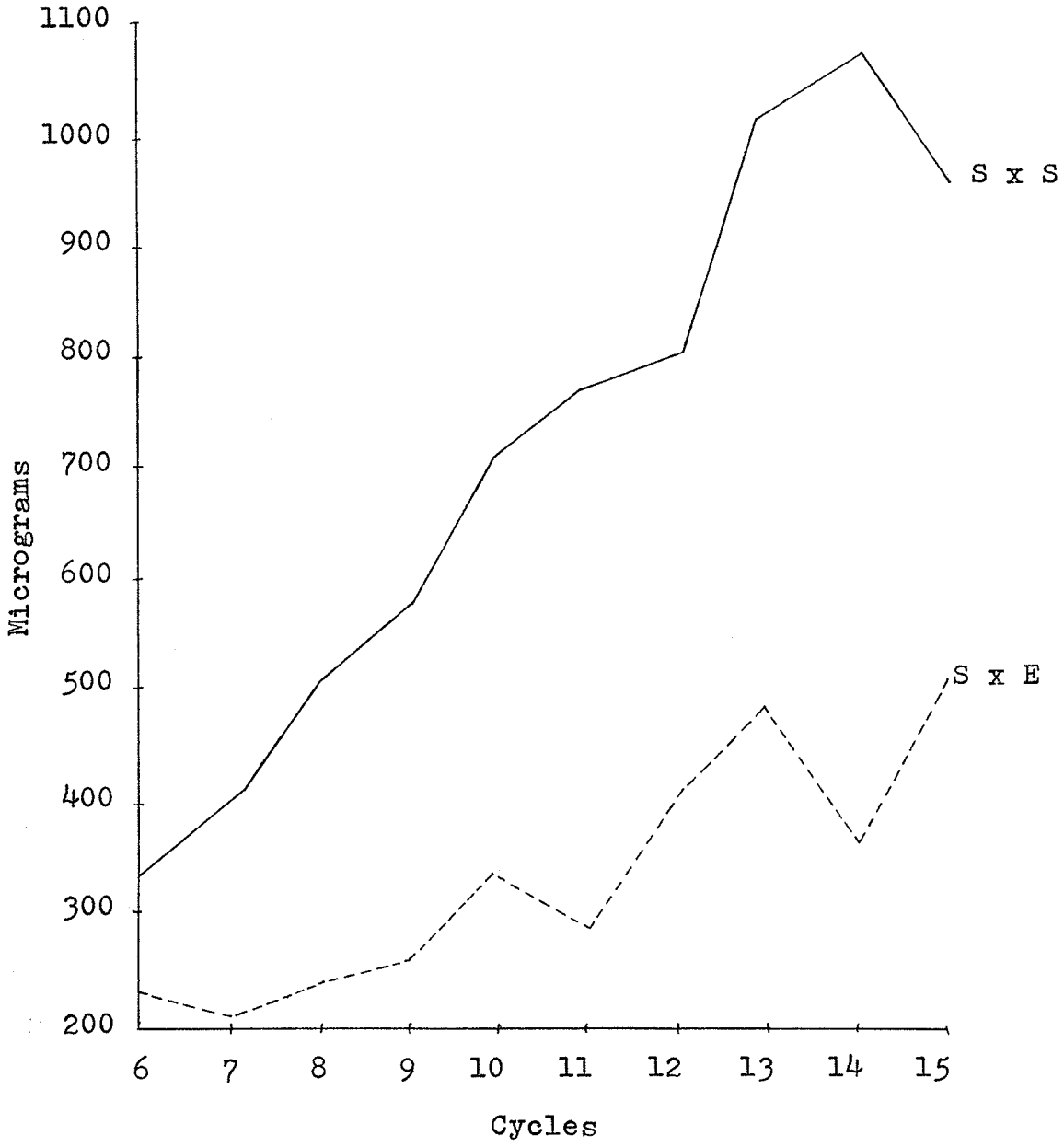



Figure 3. Response to Selection for Pupal Weight for S and SE Populations Expressed as Deviations from the Control (E)

An inspection of Figure 3 suggests that S line performance is great and consistent in the ascending manner, except in the last cycle. However, the linearity of response was tested using the method described by Anderson and Houseman (1942), again using performance expressed as deviations from the control (Table XI). The test indicated that deviation from linearity was not statistically different from zero ($P>.05$). It is concluded that response to selection was linear at the present stage.

2. Selection Differentials

Selection differentials for pupal weight in the S population are presented in Table XII from cycle 6 to 14. The effective selection differentials of males is slightly higher than the expected selection differentials, while the result for females is just the reverse, ending up in such a way that the unweighted means of the two sexes in selection differentials are practically identical for the population. This fact indicates that there is no natural selection, either in favor or against the population at the present stage.

3. Additive Genetic Variance and Heritability in the S Population

Estimates of components of variance, additive genetic variance, heritability and phenotypic variance are presented in Table XIII for S males and females from analyses of variance.

TABLE XII

Selection Differentials (Micrograms) for Pupal Weight of the S Population

| | Males | | Females | | Mean | |
|---|---|---|---|---|---|---|
| Cycle | Expected | Effective | Expected | Effective | Expected | Effective |
| 6 | 284.65 | 268.30 | 177.28 | 164.16 | 230.97 | 216.23 |
| 7 | 310.93 | 306.68 | 276.96 | 265.66 | 293.95 | 286.12 |
| 8 | 324.75 | 345.42 | 274.53 | 243.55 | 299.64 | 294.49 |
| 9 | 307.58 | 308.62 | 244.17 | 237.64 | 275.88 | 273.13 |
| 10 | 310.08 | 423.30 | 224.66 | 211.65 | 267.37 | 317.48 |
| 11 | 251.21 | 277.05 | 146.65 | 114.60 | 198.93 | 195.82 |
| 12 | 348.95 | 304.44 | 228.06 | 243.07 | 288.51 | 273.76 |
| 13 | 279.70 | 285.33 | 214.40 | 192.48 | 247.05 | 238.91 |
| 14 | 226.65 | 230.15 | 209.26 | 200.09 | 217.96 | 215.12 |
| Total | 2798.86 | 2864.99 | 1995.97 | 1872.79 | 2320.26 | 2311.06 |

TABLE XIII

Parameter Estimates from Analyses of Variance for the S Population

| | W | D | S | 4S | $V_p$ | $\frac{4S}{V_p}$ |
|---|---|---|---|---|---|---|
| Males | 29205 | 8210 | 3587±1617 | 14348 | 41001 | .350±.032 |
| Females | 35079 | 9133 | 2229±1699 | 8916 | 46441 | .192±.031 |

TABLE XIV

Parent-Offspring Regression Estimates of Heritability for the S Population

| | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | d.f. | b | $S.E._b$ | $h^2$ | d.f. | b | $S.E._b$ | $h^2$ |
| Sire-offspring (incl. L-male) | 1878 | .136 | .018 | .272±.036 | 1907 | .133 | .020 | .266±.040 |
| Dam-offspring | 1718 | .004 | .035 | .008±.070 | 1746 | .061 | .037 | .122±.074 |
| Midparent-offspring | 1718 | .131 | .052 | .131±.052 | 1746 | .178 | .055 | .178±.110 |

The additive genetic variances are represented by four times the sire component. The values are 14,384 ugm. for males and 8,916 ugm. for females.

Parent-offspring regression estimates are presented in Table XIV. In the case of sire-offspring regression, the heritability estimates were obtained by including the low-sire offspring (incl. L-sire). In case of dam-offspring, the heritability estimates were obtained by excluding the low sire offspring. The advantage of including a few low sires in each cycle can be demonstrated by comparing the variances of coefficients of regression of excluding and including the low-sire offspring. In the sire-offspring regression, the variances of b values, when excluding low-sire offspring, are 5.0 times for males and 4.2 times for females higher than those obtained when including low-sire offspring (the exact figures for variance are .0015 for excl. L-sire and .0003 for incl. L-sire in males and the corresponding values in females are .0017 and .0004). By use of this particular design, more reliable heritability estimates were obtained.

Individual heritability estimates from different sources with a single pooled estimate are presented in Table XV. The heritability estimates computed from dam-offspring regression are extremely low. The values for both males and females are not statistically different from zero. As has been pointed out by Boylan and Wong (1965), sex-linked in-

heritance is involved for this trait in the population. But any of such effect is expected to bias the estimate upward instead of downward. The lower estimate in males suggests that the effect is greater in males than females. This is in agreement with what has been observed before, except that the direction is just the opposite. Further investigation is required in this respect before a meaningful explanation can be given. The heritability estimate of females calculated from the sire component from analysis of variance is observed to be lower than the estimate for males. This difference is significant ($P<.05$). The same trend is also observed in the two control populations, although the difference is not significant.

The pooled estimates of heritability were .260 $\pm$ .021 for males and .209 $\pm$ .023 for females. A single estimate of $h^2$ for the S population, combining estimates of males and females, was .237 $\pm$ .015. This estimate is much lower than that estimated by Bell and McNary (1963) for the same trait. Their estimate was .58 in 70% relative humidity which was regarded as optimal environment. But as far as the trait (body weight) is concerned, this estimate agrees fairly well with estimates of other species, although it may still be somewhat biased downward by including some very low individual estimates in the pooling.

TABLE XV

Estimates of Heritability ($h^2$) for S Population

| Method | Males | Females |
|---|---|---|
| Sire component | .350±.032 | .192±.031 |
| Sire-offspring regression (incl. L-sire) | .272±.036 | .266±.040 |
| Dam-offspring regression | .008±.070 | .122±.074 |
| Midparent-offspring regression | .131±.052 | .178±.100 |
| Pooled | .260±.021 | .209±.023 |
| Pooled males and females | .237±.015 | |

TABLE XVI

Parameter Estimates From Analysis of Variance for SE Population

| | W | D | S | 4S | $V_p$ |
|---|---|---|---|---|---|
| Males | 27566 | 6040 | 3867±1593 | 15468 | 37473 |
| Females | 38069 | 5428 | 2803±1696 | 11212 | 46300 |

4. Genetic Variance in the SE Population

Estimates of components of variance in the SE population were obtained in the same manner as for S progeny and are presented in Table XVI.

5. Genetic Covariance Between Purebreds (S) and Crossbreds (SE)

The genetic covariance between S and SE offspring was estimated in two ways.

a. Half-sib Family Means

This measures the genetic covariance between purebreds and crossbreds having a common sire. The sire means by sex and line were used in estimating the covariance. The value is designated as $Scov_{S.E.}$. Results of these analysis are presented in Table XVII.

TABLE XVII

Estimates of Genetic Covariance ($Scov_{S.E.}$) Between Purebred Progeny (S) and Crossbred Progeny (SE)

| Estimates from Covariance of Half-sib Family Means | d.f. | $Scov_{S.E.}$ |
|---|---|---|
| S males - SE males | 182 | 2231 ± 1072 |
| S females - SE females | 179 | 2308 ± 1098 |
| Estimates from Sire-offspring Covariance | | |
| S sire - SE male offspring | 1508 | 3790 ± 1050 |

Table XVII (cont.)

| Estimates from Sire-offspring Covariance | d.f. | $Scov_{S.E.}$ |
|---|---|---|
| S sire - SE female offspring | 1850 | 3161 ± 996 |
| Estimate from pooled covariance | | 2873 ± 528 |

b. Sire-offspring Covariance

Covariance was computed by using the records of performance of S sires and SE offspring (including low sires and offspring). This value is called $2Scov_{S.E.}$. The covariances were divided by two to convert them to estimates of $Scov_{S.E.}$. Results of these analyses are also presented in Table XVII for comparison with those of paternal half-sibs. The estimate from sire-offspring covariance is higher than those of paternal half-sibs, although the difference is not significant. An average estimate of genetic covariance between S and SE progeny was computed by weighting the separate estimates inversely to their approximated variances. This average estimate was 2873 ± 528, and is shown in Table XVII.

A comparison of estimates of sire components of variance ($S_S$) and ($S_{SE}$) obtained for the S and SE populations respectively and the comparable genetic variance estimates ($Scov_{S.E.}$) is provided in the table below. Both ($S_S$) and

($S_{SE}$) values were calculated by including the low-sire offspring to make them equivalent to $Scov_{S.E.}$.

| | $S_S$ | $Scov_{S.E.}$ | $S_{SE}$ |
|---|---|---|---|
| Males | 4205 ± 1618 | 2232 ± 1072 | 4766 ± 1614 |
| Females | 3108 ± 1690 | 2308 ± 1098 | 4826 ± 1353 |
| Average | 3699 ± 1170 | 2269 ± 767 | 4807 ± 1037 |

Theoretically, if gene effects for pupal weight were completely additive, the magnitude of all three values should be the same. But the average estimates shown in the table for $S_S$ and $S_{SE}$ are considerably larger than $Scov_{S.E.}$, while $S_{SE}$ is slightly larger than the $S_S$. This suggests that the same sire may contribute a larger effect on crossbreds than purebreds. However, a definite conclusion cannot be made because of the large sampling error.

An estimate of the genetic correlation between S and SE progeny was calculated using the average estimates of the additive genetic variance and the sire components of variance. The general formula for the estimate is as follow:

$$R_g = \frac{Scov_{S.E.}}{\sqrt{(Svar_{S.S.})\ (Svar_{SE})}}$$

where:

$R_g$ = genetic correlation

$Scov_{S.E.}$ = sire component of additive genetic covariance obtained from the pooled covariance (paternal half-sibs and sire-offspring covariance)

$Svar_S$ = sire component of variance in the S progeny

$Svar_{SE}$ = sire component of variance on the SE progeny

The genetic correlation obtained was .686 $\pm$ .198. The standard error was calculated as described by Robertson (1959). This estimate agrees fairly well with estimates of other workers. The four high figures out of six reported by Comstock and Robinson (1956) for eight-week weight in poultry were .76, .87, .87 and .63. Boylan (1962) reported that the estimate of genetic correlation for post-weaning growth in mice was .71. The values given by Krause et al. (1965) were so low that they were not statistically different from zero. The estimate of genetic correlation in this study suggests that the genetic correlation between purebreds and crossbreds is moderately high, although it is not perfect. Genetic improvement in the crossbreds would be highly effective by conventional intra-population selection in the purebreds.

6. Genetic Correlation of Pupal Weight Gain Between Males and Females

It is assumed by many workers in the analyses of data that the genetic correlation between the sexes is high for the selection criterion. In order to justify that assumption in this experiment, two sources of information were used to evaluate the genetic correlation between the sexes. The first one was the relative magnitude of parent-offspring regressions (Table XIII). If the genetic correlation were high, it would be expected to find the regression estimates of comparable size in sire-daughter and sire-son and similarly in dam-daughter and dam-son analyses. On the contrary, if the genetic correlation between the sexes were low, it would be expected to find higher estimates of regression when parents and offspring are of the same sex. This seemed to be the case, i.e. sire-son was higher than sire-daughter and dam-daughter was higher than dam-son although the evidence is very weak. Another source of information is sire-offspring covariance between S sire and SE progeny (Table XVII). The result suggests a higher covariance between sire and male offspring than with female offspring. Again this cannot be stated with certainty because of the large standard error. These factors suggest that the genetic correlation may be less than perfect.

Genetic correlation between growth in the sexes was estimated for S and SE lines using the same method as mentioned

in the previous section. The estimate of genetic covariance was calculated between males and females of the same population (including low-sire offspring). Estimates of the additive genetic variance for each sex were obtained from the sire component estimates of the analysis of variance for the S and SE lines (low-sire-offspring included). The genetic correlation estimates are presented in Table XVIII. The estimates suggest a high genetic correlation between the sexes. It is suggested that sampling errors are the reason for the estimates exceeding unity.

TABLE XVIII

Genetic Correlation Between Male and Female Pupal Weights for S and SE Populations

| | d.f. (sires) | Genetic Correlation ($r_g$) |
|---|---|---|
| S males and females | 209 | 1.14 |
| SE males and females | 193 | 3.11 |

Although this result conflicts with those of regression estimate comparisons, it does give some evidence for the assumption that a high genetic correlation exists between pupal weight of males and females.

7. Predicted and Observed Response to Selection in S and SE Population

In the populations subjected to selection, the expected genetic progress can be obtained as the product of heritability estimate and the selection differential, thus

$$E.\ P._{(S)} = h^2\ (S.D.)$$

where:

$E.\ P._{(S)}$ = expected genetic progress in S line

$h^2$ = estimate of heritability

S.D. = selection differential

Expected genetic progress in SE performance, based on selection in the S line, can be predicted by using an estimate of genetic covariance and the selection differential and phenotypic variance of the S line. The general formula can be expressed as follow:

$$E.\ P._{(SE)} = \frac{2(Scov_{S.E.})\ S.\ D.}{V_p}$$

where:

$E.\ P._{(SE)}$ = expected genetic progress resulting from selection in the S line

S. D. = selection differential in S line

$Scov_{S.E.}$ = genetic covariance in sire effects between S and SE progeny

$V_p$ = phenotypic variance of S line

b. Observed progress (R) in S and SE population was measured in terms of linear regression on time of deviations of mean performances from the control (Table XI). This would eliminate the environmental factor intermingled in the real genetic improvement.

The realized heritability ($Rh^2$) according to Falconer (1960), can be obtained by dividing the observed response by the selection differential. The equivalent quantity, referred to as realized covariance, R(Scov), can be calculated by dividing the product of observed response and phenotypic variance of the S line with two times the selection differential of S line.

c. The respective above mentioned values are listed below in tabular form for nine generations of selection (cycle six to 15). Estimates of realized heritability (Est. $h^2$) and genetic covariance (Scov) are also shown for comparison. Selection differentials used in the predictions are the effective selection differentials. The units for selection differentials, expected progress and response, are micrograms.

| Population | S.D. | E.P. | R | $Rh^2$ | R(Scov) | Est.$h^2$ | Scov |
|---|---|---|---|---|---|---|---|
| S | 2311 | 555 | 749 | .32 | - | .24 | - |
| SE | 2311 | 299 | 289 | - | 3069 | - | 2873 |

By examining the observed and predicted response in the S population, it is found that the agreement between the two is not completely satisfactory. The expected progress is much lower than the observed response, although the difference is not statistically significant ($P>.05$). This result throws some doubt on Clayton and Robertson's (1957) finding, i.e. prediction based on heritability estimate in short term selection is in good agreement with observed response.

The situation is inspected in two ways: (a) the reliability of the control: because the observed response is measured in terms of S deviation from control E, it is suspected that the control may decline in successive cycles so that part of the deviation is environmental rather than genetical. This suspicion was investigated using regression of generation means on cycle number to see whether there is any time trend in the control. The lack of a significant change over time as indicated by the non-significant regression ($b = 1.82 \pm 4.67$) indicates that the control is effective. (b) the reliability of heritability estimates: as has been mentioned before, the individual heritability estimates from dam-offspring regression are extremely low, virtually zero for dam-son regression. This greatly lowers the single pooled estimate and as a consequence the estimate of heritability may be too low. Moreover, it should also be pointed out here that estimates of heritability based on estimates of additive

genetic variance from the sire component of variance, where parents are selected as was done in this experiment, tend to be biased downward. No correction for effects of selection were made and hence the estimates from the method may be under estimates.

On the other hand, agreement between the observed and predicted response in the SE population is very good. The expected response is slightly higher than the observed, and the difference is not significant ($P>.05$). This again suggests that the genetic improvement of crossbreds based on the selection of the same trait in purebreds would be effective.

From evidence of the response curve, selection differentials and genetic parameter estimates, it is predicted that response to selection will be continued in generations immediately ahead. There is very little sign of slow down of the rate of response.

8. Comparison of Progress in S and SE Performance

As has been pointed out before, the main objective of this study was to investigate the relative magnitude of selection in the S population on performance being reflected on the SE population. The issue can be examined in terms of the regression of performance on time expressed as deviations of population means from the control (Table XI). The regression coefficient for nine generations of selection (from

cycle 6 to 15) was 83.23 ± 7.30 for the S population and 32.10 ± 5.49 for the SE population. The regression coefficients for both populations were highly significant ($P<.01$). This indicates that there is a real genetic improvement in both populations. If gene effects were completely additive, response in SE should be one-half as large as in the S line. This can be examined by comparing one-half of the regression coefficient of S with that of SE. One-half of S regression coefficient is 41.6 ± 3.65 comparing with 32.10 ± 5.49 is slightly higher, but this is still well within the sampling error. This result is in good agreement with the reports of Rahnefeld (1961), but not with Boylan (1962) in comparing the performance of crossbreds and purebreds. Owing to the fact that the results of the above two workers were two different periods of the same experiment, it may suggest that the agreement will be good in the early stage of the selection experiment but it departs from one-half in the later period. This probably results from the greater effect of non-additive genetic variance in the later period of the selection.

### 9. Correlated Response in Egg Count

Egg count was carried along through the experimental period as a means to measure the change of fitness. A reduction of fitness in long term selection experiments was reported by Mather and Harrison (1949), Falconer (1953) and

other workers. The issue can be examined in terms of the time trend in egg count.

The mean egg counts and age of S and E populations are presented in Table XIX. Crossbred (SE and ES) records were not included in the means because it is felt that dams mated to different sires may have different production.

The time trend in egg count was estimated in terms of regression on cycle number of the difference between mean egg count in the S and E populations, respectively. Deviations of mean egg count in the E line are shown in Table XX and plotted in Figure 4. The estimate of regression on time was $-1.80 \pm .41$ eggs per generation and was statistically significant. The result suggests that there is natural selection operating against the trait so selected at the present stage. In other words, egg count is negatively correlated with increasing pupal weight.

This conclusion conflicts with those obtained from expected and effective selection differentials. But, if the situation is further examined, it is obvious that both results are justified because the number of offspring saved per mating was restricted to five for each sex in the S population and therefore the natural selection against the number of offspring per mating is not clear at this stage.

Despite the fact that the correlated response of infertility in terms of decreasing egg production, the rate

TABLE XIX

Mean Egg Count (48 Hour) and Age at Egg Count for Control (E) and Purebred (S) Population

| | S Line | | | E Line | | |
|---|---|---|---|---|---|---|
| Cycle | N | Age | Egg Count | N | Age | Egg Count |
| 6 | 52 | 34.56±.17 | 24.52±1.61 | 23 | 29.00±.56 | 8.91±1.64 |
| 7 | 52 | 33.29±.65 | 24.38±1.64 | 22 | 32.59±.38 | 9.77±2.09 |
| 8 | 54 | 31.28±.34 | 27.80±2.00 | 28 | 26.18±.41 | 9.89±1.66 |
| 9 | 54 | 27.52±.18 | 23.04±2.01 | 28 | 23.04±.36 | 10.82±1.42 |
| 10 | 54 | 17.43±.11 | 22.13±2.00 | 27 | 17.66±.35 | 15.15±1.82 |
| 11 | 53 | 18.04±.31 | 25.38±2.02 | 27 | 15.30±.34 | 17.59±2.20 |
| 12 | 53 | 16.51±.21 | 13.81±1.62 | 27 | 16.48±.33 | 14.00±2.03 |
| 13 | 54 | 20.67±.30 | 17.83±1.71 | 28 | 19.11±.27 | 8.43±1.47 |
| 14 | 54 | 26.39±.33 | 9.31±1.12 | 24 | 20.75±.75 | 9.67±1.59 |
| 15 | 62 | 20.31±.32 | 8.19±1.07 | 32 | 17.28±.30 | 5.13±0.77 |

TABLE XX

Mean Egg Count for S Population Expressed as Deviation From Control (E)

| | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|---|---|
| Deviation | 15.61 | 14.61 | 17.91 | 12.22 | 6.98 | 7.79 | -.19 | 9.40 | -.36 | 3.06 |

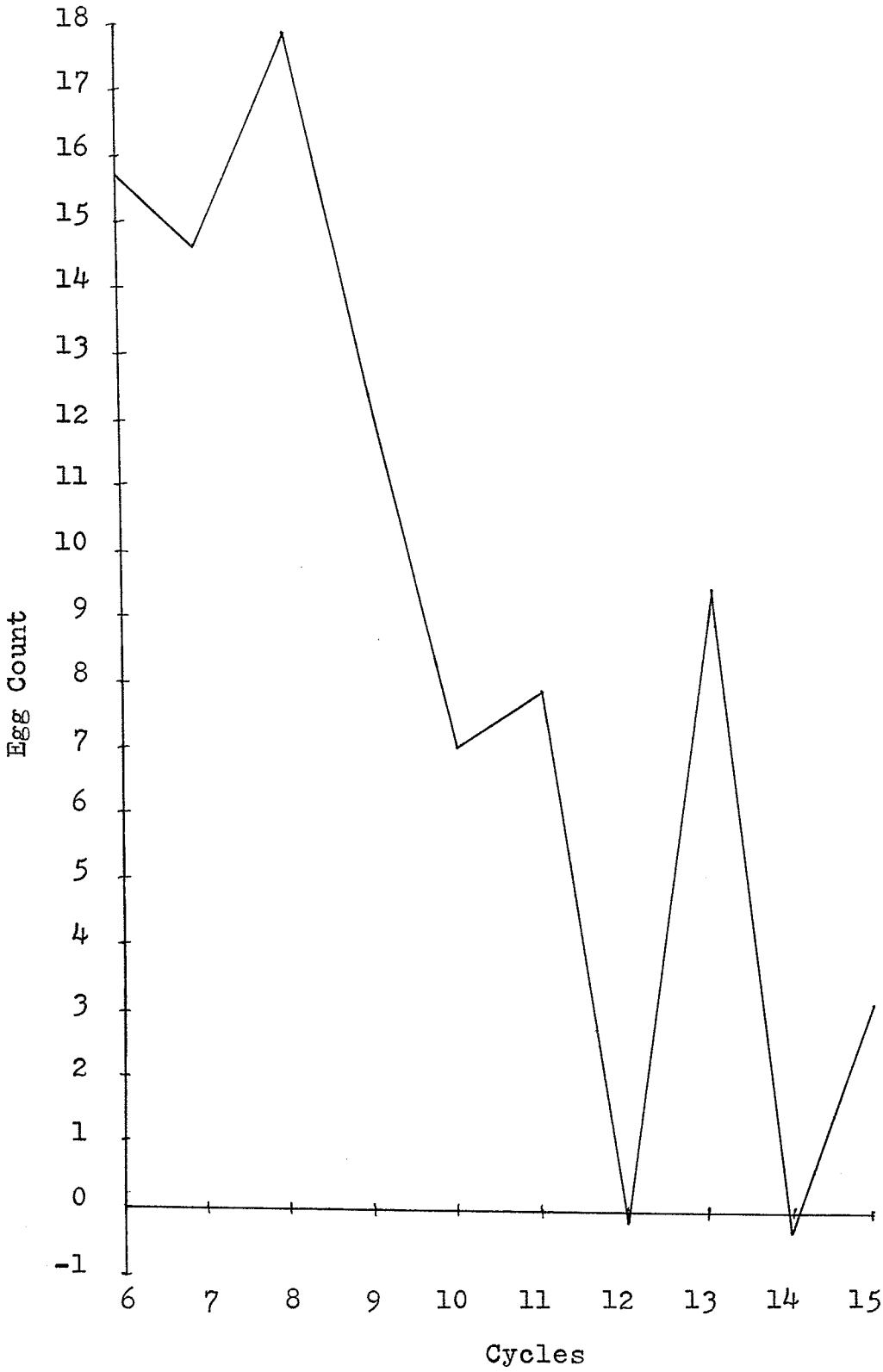



Figure 4. Mean Performance for Egg Count (48-hour) for S Population Expressed as Deviations from Control (E)

of response to selection is not likely to decline, because this force is too weak in counterbalance the magnitude of selection. Thus, the prediction made before that the response to selection will be continued is still valid.

## SUMMARY

The results of nine generations of selection with flour beetles, Tribolium castaneum, were reported in this study. The analysis of data included 13,461 animals of which 5,143 beetles were from the purebred population (S), 3,045 beetles were from the crossbred population (SE), and 2,781 and 2,492 beetles were from the inbred parent line populations (C and E respectively).

The cumulated effective selection differentials which had been weighted by the number of offspring produced were 370, -148 and 2311 ugm. for C, E and S populations respectively. In terms of their respective standard deviations (s), these quantities were equivalent to 1.65s for the C line, -.84s for the E line and 11.05s for the S line.

Information on genetic variances and selection differentials in the control line E indicated that genetic variability was low. Heritability of pupal weight in this line was estimated to be .029 $\pm$ .026. Analysis of genetic variance and selection differentials suggested that the C line contained a substantial amount of additive genetic variance and hence was not used as a control population. Heritability of pupal weight was estimated to be .286 $\pm$ .024.

The estimate of heritability of pupal weight in the purebred population (S) obtained from the components of

variance and parent-offspring regression was .237 ± .015. The realized heritability was .32. Some evidence indicated that the heritability estimate was probably under estimated.

The sire component of variance was estimated to be 3699 ± 1170 ugm. for purebreds (S) and 4807 ± 1037 ugm. for crossbreds (SE), while the genetic covariance was estimated to be 2269 ± 767 between the two populations. The higher genetic variance in the crossbreds suggested that the same sire might contribute a larger effect on crossbreds than purebreds. The estimate of genetic correlation between purebreds and crossbreds was .69 ± .20. The high genetic correlation indicated that selection based on purebred performance would be relatively effective in improving the crossbreds.

Agreement between predicted and observed response in the S population was not completely satisfactory although the difference was not statistically significant. Taken at face value the difference between observed and predicted response might be due to the under estimate of heritability. Agreement between the predicted and observed response was good in the crossbred population. The observed progress in crossbred population was lower although not significantly less than one-half of the purebred population indicating that gene action was predominantly additive.

The average genetic improvement was estimated to be 83.23 ± 7.30 ugm. and 32.10 ± 5.49 ugm. per generation for

purebred and crossbred populations respectively. Total change over nine generations of selection for pupal weight was about seven and three times their respective additive genetic standard deviation for purebred and crossbred populations. Evidence from various sources suggests that response to selection will be continued in generations immediately ahead.

The estimate of genetic correlation suggested that a high genetic correlation existed between the sexes for pupal weight, although some other evidence showed that the correlation was probably less than perfect.

The correlated response of egg count (during a 48-hour period) indicated that a negative relationship existed between pupal weight and egg count. This evidence led to the conclusion that natural selection worked against the trait under selection, although the magnitude was not large enough to retard response to selection at the present stage.

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