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STUDY OF THE EFFECTS OF DIFFERENT BASE  
POPULATIONS ON THE SIZE AND VARIABILITY  
OF SHORT-TERM RESPONSES TO SELECTION IN  
DROSOPHILA

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# I. INTRODUCTION

## I. INTRODUCTION

In the last decade or so the importance of the choice of a base population for selection experiments has gained recognition. Concurrent with this, there has been a surge of research activity in selection utilising heterogeneous hybrid foundation stocks for both laboratory animals and larger domestic species. The growing popularity of selection within crossbred base population is based on the premise that by crossing together different populations or strains to form a foundation stock, greater genetic variability is made available thus allowing a greater genetic response. There is also the additional advantage of greater viability of hybrid individuals. Yet, comparatively few experiments have been carried out specifically to evaluate the importance of base populations and particularly the relative merits of selection within "purebred" populations and "crossbred" populations in terms of size, trend and variability of response. James (1966) stressed the vital role of choosing the right base population for animal breeding schemes. Results from his theoretical considerations point in favour of selection from hybrid stocks derived from two or more populations as opposed to selection from a single but genetically superior population.

There is definite need for reliable and more conclusive evidence on this important aspect of selection and it is primarily for this purpose that the present investigation is undertaken. The selection experiment is designed to provide data amenable to detailed analysis of the variability of responses within and between populations and the relationship of the response to the genetic nature of the foundation stocks. The present experimental design consists of concurrent and

identical two-directional mass selection for abdominal bristles in two laboratory strains of Drosophila melanogaster of diverse origins and in the hybrid population formed by crossing them. Within each selection line a number of replicates are carried in order to assess the variability of response.

In this present thesis the work is carried out in the following order: The first part deals with the formation of the hybrid stock and also the evaluation of the population parameters of the three different foundation stocks. This is followed by preliminary experiments where the heritabilities of the two original strains are determined and the phenotypic variances partitioned into their various components. The main part of the thesis is the short-term selection experiment which lasts for fourteen generations. The high and low responses from the three populations are analysed in detail for significant heterogeneity of average response rate and realised heritability within each selection line and between selection lines. The patterns of two-directional responses are examined and the usefulness of the simple additive prediction theory is tested. The last section consists of a series of experiments - relaxation of selection, chromosome assays and tests for the presence of recessive autosomal lethals - carried on some of the selection replicates in an attempt to throw light on the underlying genetic situation responsible for the observed responses.

## II. REVIEW OF LITERATURE

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Different workers at various times have remarked on the variability of selection response even when similar selection was practised on the same species for the same character. The aim of this review is to examine closely past literature on directional selection experiments in an attempt to see how consistent or inconsistent the results are and what are the factors contributing to the variability of selection response. The review is divided into two parts - the first part being on patterns of directional selection response and the second part is devoted to factors affecting selection response.

### A. PATTERNS OF SELECTION RESPONSE

An artificial selection experiment consists essentially of selecting certain individuals to be used as parents at the expense of all the other individuals in the population and then controlling the mating of these selected individuals. The empirical aim of the breeder or experimenter is to change a phenotypic character (or characters) of a population by selection. The mode of selection may be divided into three main classes - directional, disruptive and stabilising selection. This review is concerned solely with directional selection.

The basic effect of selection is to change the genetic properties of the population. Selection favours certain alleles and as a result the frequency of these favoured alleles increases. It seems fitting to start with a brief description of the pattern of selection response that

is expected from the simple quantitative selection theory based on the concept of additive genetic variance. This selection theory originated from the work of Wright (1921b), Haldane (1924-1927) and Fisher (1930). The basic premises of the theory are that the genetic variance of a quantitative character is governed mainly by a large number of additive genes with small effects, that interaction between the genes at different loci and between the genes and the environment do not contribute significantly to the genetic variance, that most of the genes are at intermediate frequencies and that differential effects of natural selection on genotypes are negligible. Under these conditions selection would increase the frequency of certain genes leading to an increase in homozygosity as these alleles gradually become fixed. Selection response would be maximal and approximately linear during the early generations of selection when most of the genes are at intermediate frequencies and genetic variance near its maximum. As selection continues, more and more of the favoured genes become fixed and as a result the response declines very gradually and asymptotically. The selection limit is reached when all the favourable alleles become fixed and no additive genetic variance remains in the population. At the selection limit, no further response can be obtained and any variation remaining in the population is due to environmental influence on the individuals and is therefore not heritable. The expected response based on this selection theory would be symmetrical for the upward and downward direction of selection. This then is the pattern of selection response based on simple premises.

In actual fact, when selection responses from different experiments are examined, they very rarely conform to the pattern expected from the simple statistical model. Consequently alternative theories of gene

action have been advanced to interpret the different response patterns. The variety of selection responses observed is not surprising considering the complex genetic control of different quantitative characters in different organisms.

The theory of polygenic balance along chromosomes was first proposed by Mather (1941). Prior to Mather, the idea of gene balance along chromosomes had been suggested by Goodale (1937, 1938). He carried out selection for increased head spotting in mice as well as for increasing body weight. To explain the results obtained he suggested that three types of genes affecting the selection trait (+, - and 0) were present in the base population. The + gene which increases the expression of the selection trait was pictured as being linked with a - gene (or 0 gene) and arranged in alternating series on the chromosomes. Since the effects of the + genes are balanced by the - genes, little variation is found in the unselected base population. Crossing-over and recombination rearranges the genes and the + genes which favour the expression of the character are subsequently selected.

The main experimental evidence for the theory of balanced polygenic combinations could be accredited to the work of Mather and his collaborators (1941, 1943, 1949). This theory was put forward to account for the irregular patterns of long-term selection response which have been observed in some of their selection lines as well as in previous experiments by earlier workers (Payne, 1918; Sismanidis, 1942). The irregular response pattern consisted of alternating periods of low response or stability lasting for a few generations being followed by a period of sudden and rapid response. This is in contrast to the steady declining response which is expected from the additive selection theory. The polygenic theory is based on the assumption that in an unselected base population, metrical traits are under the control of stabilising natural

selection where phenotypic intermediates are favoured. The idea of + and - genes affecting a quantitative character has been adopted. The linked combinations +- and -+ are intermediate and balanced and thus retained in the population while the unbalanced ++ and -- combinations which give rise to extreme genotypes tend to be eliminated by stabilising natural selection since they are less fit. During selection the balanced polygenic combinations may be broken down by crossing-over but some time is needed for crossing-over to produce the right combinations and this would result in the period of delayed responses. With the sudden release of genetic variation through recombination there is the concomitant accelerated response to selection. Though the theory of linked polygenic combination and recombination of + and - genes seems too simple, it does offer some explanation for the observed accelerated response after several generations of apparent stability and also the observed decline in fitness of the more extreme phenotypes in the later generations of selection.

Strong evidence supporting the theory of polygenic balance was given by Thoday and Boam (1961) who selected for high sternopleural chaetae in Drosophila. Three of their lines (dpl, dp2 and dp6) showed remarkable similarity in their pattern of accelerated responses. Selection was not carried out concurrently so that the trend could not be due to environmental influences. They suggested four possible reasons for the unexpected sudden increase in selection response - mutation contamination, gene interaction and lastly recombination. With the evidence at hand, they reckoned that the most plausible explanation is the occurrence of a recombinational event. The pattern of response was interpreted along the same lines as Mather and his co-workers.

That selection response is the result of linkage and recombination



offers a better explanation for accelerated response rather than the effects of a large number of additive genes. However it has been pointed out by Mather that the polygenic balance theory is most applicable to species like Drosophila where the number of chromosomes is small and the frequency of crossing-over is low in females often because of the presence of chromosomal inversions and no crossing-over occurs in the males. Thus linkage would exert a greater effect in Drosophila than it would in other species with larger chromosome numbers and less obstruction to crossing over. However recently Wright (1969) has pointed out some weaknesses of Mather's hypothesis, for example the assumption of the occurrence of complete dominance and alternating series of + and - alleles, as the results from his theoretical considerations of this problem gave little evidence for the prevalence of such situations.

Fraser and Hansche (1965) by genetic simulation studies showed that irregular selection responses of alternating periods of rapid and slow response could be attributed to a change in linkage relationships in polygenic systems brought about by crossing-over during selection. But this occurs only when population size is small. They also reported that a similar pattern could occur if a few recessive genes having large effects on the selected character were present at low frequencies in the base population, or if suitable gene interactions are present such as that suggested by Robertson and Reeve (1953) where some minor genes were transformed into major genes due to the change in the genetic background brought about by selection.

Asymmetrical selection responses have been observed in numerous selection experiments contrary to the expected symmetrical two-way selection response based on simple premises. Asymmetry is the result of response in one direction being greater than the response in the opposite

direction of selection. Response may be greater in the upward direction (Mather and Harrison, 1949; Clayton, Morris and Robertson, 1957; and Sang, 1961), or it may be greater in the downward direction (Falconer, 1953; Rasmuson, 1955; Clarke, Maynard Smith and Sondhi, 1961; Sheldon, 1963).

Falconer (1953, 1960) has proposed several situations which could give rise to asymmetry in selection experiments. Scale effects may cause asymmetry. If this is the cause, it is often possible to remove the asymmetry by appropriate transformation of the raw data to another scale. If positive correlation between the population mean and variance is observed in the data, then a scale transformation is called for. A common and useful method is the logarithmic transformation which converts the arithmetic to the geometric scale. Another method of correcting scale effects is to obtain the ratio of the selection response to the cumulated selection differential which is known as the realised heritability (Falconer, 1954). This has been recommended because factors like scale effects or natural selection affecting selection responses are expected to affect the selection differential in similar proportion and direction. Hence the ratio would be free from such bias and has been frequently used to gauge the genetic response from selection.

Two genetic situations which may occur in the base population and are likely to cause asymmetry are directional dominance and directional gene frequency. Asymmetry due to directional dominance and inbreeding depression are related and they could cause considerable bias in small populations (Kojima, 1961). Decline of the mean on inbreeding shows that there must be directional dominance of the loci concerned but it does not discriminate between simple dominance and overdominance.

Directional gene frequencies occur in populations with previous

history of natural or artificial selection, so that genes favoured by previous selection are at higher frequencies than alleles less favoured. Selection will produce greater response towards the direction of the less frequent alleles. Zucker (1960) has placed importance on the effects of unequal initial gene frequencies in producing different patterns of response from different selection experiments in mice and rats where the same character, body size, has been selected. The patterns of response observed in selecting for this character include symmetry of response as well as positive and negative asymmetry.

When selection favours heterozygotes in one direction, asymmetry would be produced. Selection response in the direction where heterozygous extreme individuals are favoured will be limited but response in the opposite direction would continue till the favourable alleles become fixed. Clarke, Maynard Smith and Sondhi (1961) selected for fast and slow development rate in D. subobscura. This character was found to exhibit pronounced heterosis on crossing so that the highly heterozygous synthetic base population formed by intercrossing four wild stocks must have been close to the minimum time required for normal development. As a result, marked asymmetrical response was observed with poor response for faster development rate.

Natural selection for fitness may oppose more strongly artificial selection in one direction than the other direction and this could result in asymmetry. Its occurrence can be detected if the selected line declines in fitness as selection progresses or when the line on suspension of selection shows a marked tendency to regress to the population mean accompanied by improvement of fitness.

Latter (1965) examined the theoretical consequences of additive genes with large effects on selection for metric traits in a large popula-

tion. Results showed that pronounced asymmetry could result under conditions of high selection intensity and low initial frequency of genes with major effects in the foundation population. A formula to assess the size of asymmetry was given

$$S = \left( \frac{\Delta GH - \Delta GL}{\Delta GH + \Delta GL} \right)$$

where  $\Delta GH$  = High selection response

$\Delta GL$  = Low selection response

The parameter  $S$  lies in the range of +1 and -1 and will be zero in the case of symmetrical two-way response.  $S$  will be positive if + alleles which increase the expression of the character were present at low frequency and it will be negative if - alleles were present at low initial frequency. There is considerable evidence that a fair proportion of the genetic variance of metrical traits may be determined by a few genes with large effects (Thoday and Boam, 1961; Spickett and Thoday, 1966; Werhahn and Allard, 1965; Robertson, 1966; Law, 1966, 1967).

Linkage has been shown to affect both the rate and limits of selection response. Theoretical aspects of linkage effects have been dealt with by Cockerham (1956), Schnell (1963) and Lewontin (1964). Felsenstein (1965) studied linkage effects on directional selection (both natural and artificial) and showed that tight linkage could either enhance or inhibit the rate of response depending on whether positive or negative linkage disequilibrium was generated as a result of selection. Since negative disequilibrium has been demonstrated to result from artificial selection, tight linkage would be expected to slow progress from selection. Hill and Robertson (1966) from computer simulation studies showed that for a two-locus model, tight linkage could limit the total selection response in small populations.

## B. FACTORS AFFECTING SELECTION RESPONSE

A broad survey of selection experiments on different quantitative characters in different organisms reveals a spectrum of selection responses which is rather confusing and somewhat perturbing. Selection response is determined by the genetic nature of the organism and the character selected for together with the series of factors imposed by the experimenter. The main factors affecting selection response are the nature of the base population, the selection trait (or traits) and method of selection, the population size and selection intensity, mating system and finally the environmental conditions. Besides these variables there are of course the unknown and uncontrollable factors affecting each experiment. Each factor is considered separately in this review. However the author is fully aware that the different factors should not be separated each into its own compartment as all are inter-related in one way or other with the other factors. A particular selection response is the result of the joint action of all these factors. Nevertheless it is hoped that through the careful scrutiny of each factor a better understanding may be arrived at and perhaps then the factors could be reassembled together again in some sort of order to give a more coherent picture. The author suggests that results from selection experiments should be interpreted in the light of the factors determining the experiment and more particularly so when selection responses from two or more different experiments are compared. It should be noted that this review is rather biased because it is concentrated chiefly on literature of selection on laboratory animals like Drosophila, Tribolium and mice. There are two main reasons for this bias: firstly, because this aspect is of relevance to this thesis which is concerned with selection in Drosophila and secondly there are

fewer large-scale, critical selection experiments conducted on larger animals for reasons which are obvious such as the costliness and the time required for large projects.

1. Base populations

The importance of base populations has been largely overlooked in the past. This is indicated by the brief mention of the nature of the base populations in most literature on selection experiments and also by the negligence of interpreting the experimental results in relation to the base population employed. The aim in this section of review is to present the variety of base populations which have been used in past experiments and try to evaluate what effects they have had on the selection response.

It is fairly common to start selection from the stock at hand. For laboratory animals this would be simply the laboratory stock and for domestic animals it would be the production bred flock or herd. The laboratory stock of Drosophila is often derived from a single impregnated female or a group of individuals captured from the wild and subsequently maintained in the laboratory under standard conditions. Some laboratory stocks have been maintained as large cage populations with an average population size of 3000 to 5000 adult flies. Other Drosophila stocks have been kept in bottle cultures where the number of breeding individuals per generation is much lower, about 50 to 100 individuals (F.W. Robertson, 1955; Tantawy and Reeve, 1956; Sheldon, 1963). The other extreme is where the population size is greatly restricted to a few pairs of parents and in some cases a single pair of parents each generation (Rasmuson, 1952; Clayton and Robertson, 1964; F.W. Robertson and Reeve, 1953). Such laboratory strains of Drosophila, if maintained for a long time, would be

highly inbred and homogeneous.

Latter and Robertson (1962) selected for three quantitative characters, abdominal bristles, sternopleural bristles and wing length in D. melanogaster derived from a large population with the purpose of studying the decline in reproductive fitness due to artificial selection and inbreeding. Tantawy and Reeve (1956) reported an experiment conducted with similar objectives where they found that the fitness of the selection line was not greatly affected and only showed a sharp decline when the inbreeding coefficient  $F$  was over 75%. Latter and Robertson observed that for the range of  $F$  from zero to 85% in the selection line, the decline in fitness was sharp and linear. The discrepancies between the results of the two experiments could be related to the nature of the base populations used. The base population used by Tantawy and Reeve was maintained in bottle cultures while the base population used by Latter and Robertson was derived from a large cage population. The large cage population is expected to carry a greater load of deleterious recessives than the much smaller bottle population, due to the higher rate of inbreeding in the bottle population where more recessives would have been eliminated. Thus the rapid decline in reproductive fitness in Latter and Robertson's selection lines even during the early generations of selection and inbreeding could be attributed to the higher frequency of recessives in their base population.

Selection carried out on poultry have mainly used the production bred flock which consists of a few hundred birds as the base population (Lerner and Dempster, 1951; Dempster, Lerner and Lowry, 1952; Nordskog and Wehrli, 1963). Laboratory stocks again serve as the base populations for selection experiments on mice and rats (Kyle and Chapman, 1953; Chung and Chapman, 1958; Dalton, 1967). It is clear that with mice,

poultry and other larger animals it is rarely possible to maintain an unselected base population equivalent in size to that of a Drosophila cage population.

Insect species like Tribolium and Drosophila are quite different from mice and large domestic animals in that they could easily be captured from the wild and a large laboratory population built up from the original parents in a few generations because of their high reproductive rate. A newly derived laboratory strain is expected to contain greater genetic variation than a strain which have been maintained for a long time as a closed population. Rasmuson (1955) carried out identical selection on several strains of D. melanogaster derived from widely separated localities. Four of the strains were newly captured from the wild while two others have been maintained in the laboratory for close to thirty years. Selection for sternopleural bristle number was practised on all six strains while selection for abdominal bristle number was made on the four wild strains. The aim of the experiment was to investigate the difference of selection response between the wild strains selected for the same character and also the difference between the wild strains and the laboratory strains. Though there were differences between wild strains, some common features were observed. For sternopleural selection lines, the general pattern of response was asymmetry with greater response for upward selection. The general pattern for abdominal bristle selection of the wild strains was asymmetry again but here greater response was observed for downward selection. Selection for sternopleural chaetae on the two laboratory strains produced insignificant response in both directions. It would appear from the results that the wild strains gave greater selection response than the laboratory strains and this could be due to the greater genetic variation present in the recently captured strains.



The experiment however suffers from lack of replications for each of the selection lines as well as lack of controls, although it may be argued that practising identical selection on a number of different strains is a form of replication. The need for replication in this experiment is considerable since each selection line had a population size of two pairs of parents and consequently factors like random sampling could exert sizable effects on the variability of responses.

Rasmuson (1952) investigated the consequences of starting selection from different levels of inbreeding of a base population. Theoretically the degree of homozygosity in a line would be directly related to the number of generations of inbreeding and the more highly inbred a line, the less response it is expected to give. From the offspring of a pair of brother-sister mating, full-sib inbred lines were derived. Selection was commenced at four different inbreeding generations (5, 10, 15 and 20 inbreeding generations). Selection lines started from the 5th, 10th and 15th generation of inbreeding gave responses in both directions. In contrast selection in both directions was ineffective when practised on the line derived from the 20th inbreeding generation. This lack of response could be attributed to the small amount of genetic variation present in this line with the higher level of inbreeding. However the results are far from conclusive since all the full-sib selection lines, which would be considerably affected by both environmental variation and genetic drift, were not replicated.

The importance of the genetic nature of base populations in determining selection response is further illustrated by the work of Carson (1958). It has been demonstrated for Drosophila robusta that the genetic nature of the population is determined by the location from which the population was derived. Populations collected from the centre of the

species range contain various chromosomal inversions which confer heterozygosity and tend to inhibit crossing-over while marginal populations are more homozygous since they contain less inversions. Marginal populations are expected to show greater response to selection than central populations because crossing-over can occur freely with resulting release of genetic variability for selection to act on. Carson selected for a polygenic character - motility towards light on 25 strains of D. robusta. Each strain was derived from a pair of flies collected from the same locality. Fifteen strains were collected from the central area and ten from marginal areas. Eight of the ten marginal strains responded to selection while only seven out of the 15 central populations showed response. Moreover the size of response from central populations was only half of response realised in the marginal populations. The results could be considered to give strong evidence of the importance of the genetic nature of base populations in determining selection response. The validity of results from such experiments is largely determined by the accuracy in determining the species range. A question that is left open is whether the behaviour of a strain derived from a single pair of flies captured from a specific locality is representative of the population in that locality.

Hosgood, McBean and Parsons (1968) also stressed the importance of foundation populations. They selected for increased scutellar chaetae on four different base populations derived from sixteen strains of D. melanogaster. Each strain was derived from a single inseminated female and all females were collected from the same locality. This is in contrast to other experiments mentioned earlier where the different strains originated from widely separated localities. The four base populations used were - the strain with the highest mean scutellar bristle number, a hybrid population formed by crossing four strains with the

highest means, a hybrid population formed by inter-crossing all sixteen strains and lastly the strain with the lowest means. Remarkably variable response patterns were obtained from the four different foundation stocks. All lines with the exception of the line derived from the strain with the lowest mean responded to selection. The line derived from the strain with the highest mean gave the highest response. The variability of response is surprising considering that all the strains originated from females collected from the same locality and hence would have been regarded as from the same wild population. Hosgood et al. advocated pre-selection of suitable strains to act as base populations. However they pointed out that this may only be applicable where selection was for rigidly canalised characters such as scutellar chaetae used by them.

So far, in most of the literature reviewed, selection has been practised on closed populations i.e. populations which have been maintained without crossing to any other strains. But more often than not, foundation populations have been derived from crosses between two or more strains. There are different methods of forming crossbred base populations. The types of crossbred populations most commonly used are crosses between unselected, random-bred strains (Rasmuson, 1956; Zucker, 1960; Frahm and Kojima, 1966) or crosses between inbred lines (Falconer, 1953; Park et al., 1966; Wong and Boylan, 1970) or crosses between strains with some previous history of selection (Sang and Clayton, 1957; Bowman and Falconer, 1960). With insect species like Drosophila and Tribolium, the number of strains available is not as limited as with larger animals. The Tribolium base population used by Bartlett, Bell and Anderson (1960) was made from crosses between eight laboratory stocks from different localities. Martin and Bell (1960) formed a synthetic base population by interbreeding twelve inbred lines of Drosophila. The extreme example

came from Marien (1958), where 32 strains of D. pseudoobscura, each originating from a single impregnated female, were crossed en masse to form a base population for selection.

There is abundant literature on selection experiments utilising crossbred base populations. The primary object of crossing different lines or populations together to form a base population for selection is to provide greater genetic variability. Larger selection responses would be expected from a heterogeneous crossbred population than from a closed population, particularly if the closed population had been maintained for a long time using only small numbers of parents each generation. One feature which emerges from the review of selection experiments is that selection was either practised on the closed population (or populations) or on the crossbred base population. So far little attention has been focussed on carrying out identical selection concurrently on the crossbred population and on the original purebred closed populations from which the hybrid was derived. Critical experimental tests are badly needed along this line of research to evaluate the merits of using a hybrid base population for selection as opposed to using closed populations. One of the primary aims of this present thesis is to attempt to fill this gap in literature by carrying out identical and simultaneous selection on two closed populations of Drosophila (Oregon-R and +3) and on the crossbred population formed by crossing together the two original strains. A comparable experiment with respect to the base populations used was conducted by Richardson and Kojima (1965). However their results were not amenable for direct comparison of responses from the different populations since selection was not carried concurrently and different modes of selection were used on the "purebred" and "crossbred" populations.

A breeder or experimenter may subject the base population to some

kind of treatment prior to selection. Lately many experiments reported have used X-ray treatment on their base populations in the hope of inducing new and perhaps useful genetic variation. Irradiation has proved to be useful for plant breeding but so far its application to animals has not met with much success mainly because the high dosage which is needed to effect genetic changes cannot be tolerated by the animals (Clayton and Robertson, 1964; Abplanalp, Lowry, Lerner and Dempster, 1964; Roberts, 1967).

James (1966) pointed out the importance of the choice of a suitable base population in animal breeding projects. He made a theoretical analysis and comparison of two methods of selecting foundation populations. If  $N$  is the number of populations or strains available for selection, the first method is to choose from the  $N$  populations one population with the highest breeding value and selection is subsequently practised on this genetically superior base population. The second type of foundation population is formed by interbreeding superior individuals selected from the  $N$  populations and selection is carried out on this hybrid population. The relative merits of the two types of base populations are related to the parameter  $\sigma$ , which is the standard deviation of the breeding values among the available populations. For the first method to give greater genetic gains, the value of  $\sigma$  has to be greater than 
$$\frac{h \log N}{r(1.25 + \log N)}$$

where  $r$  = correlation between estimated and true breeding values

$h$  = square root of heritability

Since present evidence indicates that it is unlikely that  $\sigma$  is large enough, he arrived at the tentative conclusion that the second method is superior. He carried the analysis further to give a relationship between genetic gains and the size of  $N$  on the assumption of the superiority of

the second method. The difference in genetic gains is given as :-

$$R(N_1) - R(N_2) = 0.8h^2 \sigma_p \log \left( \frac{N_1}{N_2} \right)$$

where  $R(N_1)$  = expected genetic response from Method 2 using

$N_1$  number of populations

$R(N_2)$  = expected genetic response from Method 2 using

$N_2$  number of populations

$h^2$  = heritability

$\sigma_p$  = phenotypic standard deviation

If  $N_2$  is twice the size of  $N_1$  the genetic gain will be increased by approximately  $\frac{1}{4} h^2 \sigma_p$ . The theory is based on the assumption that the genetic effects are additive and that genotype-environmental interactions are not significant. Its uses are limited until more refined methods are available for accurate assessment of breeding values of populations.

## 2. Selection traits

In domestic animals, selection has usually been practised to improve characters of economic importance like milk production, egg production, growth rates, etc. For laboratory animals, the early selection experiments reported were conducted simply to test what responses would be obtained but later selection have been performed to test the usefulness of selection theory. Consequently selection has been concentrated predominantly on characters which are easily measured like bristle number, body size and body weight in Drosophila, pupa weight in Tribolium and in mice and rats, body weight and litter size. To cite F.W. Robertson (1955), "It is obvious that metrical traits are not to be regarded as a class with common

characteristics about which we can generalise with equanimity."

A. Robertson (1955) and Falconer (1955, 1960) have broadly classified metric characters into three groups according to their functional relationship to reproductive or Darwinian fitness. It is this relationship which plays an important role in determining the response of a trait to artificial selection. The first category consists of characters which are considered to be major components of fitness (fitness characters), the second class consists of characters with moderate effects on fitness while the last group are characters with little or no direct effect on fitness. The genetic nature of a metric character is determined by its functional relationship to fitness. It seems proper here to consider the characteristics of the genetic variation of each class of trait in a population at equilibrium with its present environmental conditions. Genetic variation arises originally by mutation. In turn, this genetic variance is modified by the forces of natural selection and if the population is small by the additional effects of random drift. Thus the genetical architecture of quantitative traits is shaped by the forces of natural selection which may be stabilizing, directional or disruptive. Genetic variation could be partitioned into the additive and non-additive components. It is the amount of additive genetic variance present which determines the magnitude of response to artificial selection.

#### (1) Major components of fitness

These are characters like viability, fecundity and competitive ability which affect the fitness of an organism directly. In a population at equilibrium, these characters are expected to be close to their optimum due to the action of directional natural selection for optimum fitness. Fisher's fundamental theorem of natural selection states that the rate of

change of fitness of a population is proportional to the additive genetic variance remaining in it. Since these characters are maintained at the extreme for optimum fitness, there would be little additive genetic variance left in the population (A. Robertson, 1955). The genetic variation of fitness characters would be predominantly non-additive. Dominance would be prevalent and it would be towards the direction for greater fitness; hence it is directional dominance. Fitness characters are subjected to inbreeding depression. Artificial selection would be expected to yield a poor response in the upward direction and response would mainly be in the downward direction resulting in asymmetrical two-way response.

Falconer (1955) made a detailed analysis and comparison of selection responses of three traits in mice - body weight, lactation and litter size, in relation to the genetic properties of each trait. From the results of the selection responses and heritability estimates, there is evidence that lactation is closely connected to fitness while body weight and possibly litter size have moderate direct effects on fitness. Directional natural selection for lactation would be directed towards the high extreme. A marked asymmetrical two-way selection response was observed for lactation.

Hollingsworth and Maynard Smith (1955) considered the quantitative trait, developmental rate in Drosophila to be closely associated to fitness. In wild natural populations or in normal crowded laboratory stocks, food supply would be limited to some extent. Natural selection would favour rapid developmental rate as the faster developing individuals would be able to take greater advantage of the available food. However, when rapid development rate is too extreme, fitness is expected to decline (A. Robertson, 1955). Clarke, Maynard Smith and Sondhi (1961) selected for development rate measured as the time from egg deposition to eclosion in D. pseudoobscura. Though unselected controls were maintained con-



currently with selection lines their results would have been more reliable if replicates had been maintained, particularly since development rate has been observed to be greatly affected by environmental variations. However great pains were taken to standardise the culture conditions by introducing a fixed number of eggs which have been laid about the same time into each culture and ensuring that there was excess food supply. Marien (1958) also selected for developmental rate in the same species. Each selection line contained ten replicates which is a definite improvement on the single replicate of Clarke et al. However, the experiment suffered from the serious defect that there was no strict standardisation of culture condition. Clarke et al. estimated the heritability of development rate in the base population to be close to zero and showed that most of the genetic variation was non-additive. This condition would appear to be quite typical of fitness characters. Selection response in the direction of faster development was poor, greater response was observed for slow development rate. Contrary to expectations, crosses between fast and slow development lines showed no dominance effects so that the non-additive genetic variation must be due to epistatic effects instead. However, Hollingsworth and Maynard Smith (1955), selecting for the same character but under slightly different experimental conditions, observed heterosis in crosses between opposite selection lines - dominance was for rapid development rate. Sang and Clayton (1957) who selected for larval development rate in Drosophila reported similar findings.

The general conclusion is that fitness traits yield slight response in the upward direction using the conventional methods of selection. Unfortunately most of the characters of economic importance belong to this class and artificial selection aimed at improving these traits has not been enormously successful.

(11) Characters with moderate effects on fitness

It has been demonstrated for this group of characters that individuals around the population means have the highest fitness. The genetic variation of such characters has been moulded mainly by stabilising natural selection (Mather, 1966) and the phenotypes deviating in either direction from the intermediate have lower fitness either because they are metric deviants or because they are genotypic deviants (A. Robertson, 1956; Latter, 1960). A proportion of additive genetic variance would be present in these traits and instead of directional dominance, ambidirectional dominance at gene loci affecting the character would prevail. Because traits with moderate effects on fitness have intermediate heritabilities, artificial selection is expected to yield a response in both directions. However the extreme phenotypes in the selection lines would exhibit deterioration of reproductive fitness. There would be some effects of inbreeding depression but less than that suffered by fitness characters. Many metric traits fall into this category. Karn and Penrose (1952) and Jayant (1966) reported that birth weight of man has a central optimum with fitness declining with deviations from this central optimum. Lack (1954) and Perrins (1964) noted that for swifts, the highest number of young birds were raised from clutches of intermediate size. Other traits which appear to be under stabilising selection are litter size of pigs (Darlington and Mather, 1949) and body weight of Drosophila (Sheldon, 1963).

Lerner and Dempster (1951) selected for increased shank length in poultry for eleven generations. Selection was effective for the first seven generations and it was noted that increase in shank length was accompanied by decrease in reproductive fitness. The longer-shanked pullets produced fewer eggs than unselected pullets and also fewer of the

eggs hatched. Suspending selection resulted in rapid regression towards the mean together with rise in the hatchability rate. The results provide strong evidence that intermediate shank length was associated with high fitness and that deviation in either direction from the intermediate resulted in decline in fitness.

There is still some controversy as to whether bristle characters in Drosophila have adaptive value. It has been noted that strains of D. melanogaster collected from widely separated geographical localities have very similar sternopleural chaetae number (Rasmuson, 1952). This could be regarded as evidence of stabilising natural selection maintaining the character at an intermediate optimum value. A recent investigation by Kearsey and Barnes (1970) demonstrated that individuals with average sternopleural bristle numbers have highest fitness and that the greater the deviation from the population mean the more drastic the reduction in reproductive fitness. Barnes (1968) conducted similar experiments with sternopleural chaetae and reported similar findings.

(iii) Characters with little direct effect on fitness

A. Robertson named these characters trivial or peripheral. Mather (1966) refers to them as non-fitness characters. Abdominal bristle of Drosophila is an oft quoted example of a neutral character. Because such traits have little or no direct relationship to fitness, neither stabilising nor directional natural selection would be important in determining the nature of genetic variation. Instead spontaneous mutation would play a major role in maintaining genetic variability. Durrant and Mather (1954) and Clayton and Robertson (1955) reported a spontaneous mutation rate of roughly 0.01 units of genetic variance per generation for abdominal bristle number. On a long-term basis this could contribute

significant amount of genetic variation. Characters belonging to this category in contrast to fitness characters have high heritabilities and are not affected by dominance or inbreeding depression. Artificial selection practised on peripheral characters would be expected to produce sizable response in both directions. Decline in fitness would only be expected under prolonged selection. The lower fitness of the extreme phenotypes in the selection lines may not be due to the change in the mean of the character itself but could be due to the pleiotropic action of the genes on other characters or to the greater homozygosity of the selection lines.

The comprehensive selection experiment carried out by Clayton, Morris and Robertson (1957) gives strong evidence that the abdominal bristle number is close to being a neutral metric trait. The heritability of the character in the base population estimated by different methods was consistently around 50%. Additive genetic variance constituted 85% of the genetic variance. The observed selection responses were in accord with expectations. Spectacular responses were obtained in both directions of selection and decline in fitness was encountered only in some selection lines during the later stages of long-term selection. Suspending selection resulted in slight regression towards the population mean although reversed selection indicated that genetic variance still existed. The results give support to the hypothesis that for neutral characters, natural selection is not opposing artificial selection in any direction and that the character has no adaptive value.

Some workers have expressed doubts as to whether neutral characters do in fact exist in nature. Breese and Mather (1960) analysed the third chromosome of Drosophila for polygenic systems affecting abdominal bristle character and reported that abdominal bristle character has some adaptive value. Further they argued that since the phenotypic variance of

abdominal bristle character in unselected strains of Drosophila was much less than the potential variance (Mather and Harrison, 1949; Rasmuson, 1955), its range in natural populations must have been restricted by stabilising natural selection.

### 3. Methods of selection

The above review shows how metric traits differ on the underlying scale by differences in their genetic structure which have arisen through an evolutionary history of mutation and natural selection. Obviously the genetic nature of a metric character also plays an important role in determining which method of selection is most suitable for it.

Theoretical expectations of response from different selection methods in the field of applied animal breeding have been developed mainly by Lush and his co-workers (1942, 1945, 1947) from the basic principles of population genetics. Useful accounts of the different methods of selection, their expected responses and relative merits of the different methods have been well covered by Lush (1945), Lerner (1958) and Falconer (1960a). A further review of these aspects would be redundant.

The conventional methods of individual selection, family selection, within-family selection, etc., bring about genetic gains by utilising the additive genetic variation available in the base population. Hence they are most suitable for highly heritable peripheral traits and also for characters with moderate direct effects on fitness. Individual selection has proved to be extremely effective in bringing about large responses in both high and low direction of selection for abdominal bristle character in Drosophila (Clayton et al., 1957). The method of selection based on individual or family merit is particularly effective even for long-term selection when the population size is fairly large and the selection

intensity high. For example, the high abdominal bristle selection line of Frankham, Jones and Barker (1968) with a population size of 40 pairs of parents and a high selection intensity of 10% was still responding at the 50th generation of selection.

Winter (1929), Woodworth et al. (1952) and Leng (1961) carried out one of the most extensive long-term selection experiments for the chemical content of maize. Individual selection for high and low oil and protein content was practised. After 61 generations of continuous selection, the high protein and high oil selection lines were still responding with no apparent signs of plateauing, thus showing the effectiveness of this method of selection.

The method of mass selection though suitable for plants and rapidly reproducing small animal species has its drawbacks when applied to larger animals where the total population size is limited both by the low reproductive rate and by the costs of maintaining the animals. If mass selection is practised on small populations, the rate of inbreeding within the selection line would be high and with it is the accompanying undesirable effects of deterioration of reproductive fitness. So mass selection practised on small populations, though advantageous in giving rapid response in the early generations of selection, presents difficulties on a long-term basis. Selection experiments on mice and rats have usually employed the method of within-family selection (Falconer, 1953; Zucker, 1960; Dalton, 1967). Although this method of selection gives smaller response, it has the advantage of minimising the rate of inbreeding within small population because under such a selection scheme, the effective population size is twice the actual population number. A further advantage is that the influence of maternal effects is minimised.

Clayton et al. (1957) tested different methods of selection,

individual, full-sib family and half-sib family, and compared the observed response with the predicted. In general, for short-term selection, the observed responses were in accord with predicted responses. The individual selection method gave the largest response and half-sib family selection the least response. The smaller responses from family selection is due to the lower selection differential and the smaller phenotypic standard deviation for families.

The genetic nature of fitness traits has been discussed earlier on. Review of the literature of selection experiments on fitness characters using the method of individual selection or family selection produced relatively poor response particularly in the upward direction. This, as has been pointed out, is expected since such characters have low heritabilities and a considerable proportion of their genetic variation is non-additive. The genetic nature of non-fitness traits which have been subjected to long-term selection bears some resemblance to that of fitness characters. Animal breeders have generally laid emphasis on methods of selection such as index selection, progeny testing, the use of records and pedigrees which are aimed at getting increased response through the maximum utilisation of available additive genetic variation. Plant breeders on the other hand have directed their attention along largely different lines by attempting to obtain response from traits with low heritability using methods of selection capable of exploiting non-additive genetic variance, particularly overdominance or heterosis. Shull (1908, 1909) initiated a method for plant breeding based on inbreeding and hybridisation. This has been developed by East and Hull and applied especially to corn. The success of this method of breeding in producing the famous hybrid corn need not be further elaborated. This method of inbreeding and crossing of inbred lines, though so suitable for plant

species like maize has very limited uses for animal breeding. The obvious reason is the tremendous costs and great length of time required for building up highly inbred lines of large domestic animals. However, it has been applied with some success to poultry and pigs. Two subsequent methods of selection for specific combining ability were developed primarily to improve the yield of hybrid corn. The first devised by Hull (1945) is known as recurrent selection and the second proposed by Comstock, Robinson and Harvey (1949) called the reciprocal recurrent selection is a modification of the method of recurrent selection.

Bell, Moore, Bohren and Warren (1952) gave theoretical considerations to the possibilities of using the methods of selection devised by plant breeders to improve the economic traits of poultry. They argued that since the conventional methods of selection, when practised on economic characters with low heritability in closed production flocks, appear to be giving very little response, other methods of selection for specific combining ability may prove to be more effective. One of the disadvantages of recurrent selection (RS) and reciprocal recurrent selection (RRS) when compared with mass selection is the longer time needed for each cycle of selection. Another disadvantage is the lower selection intensity, since the test-cross progenies maintained each generation are not included for selection. Dickerson (1952) suggested that for low heritability traits, mass selection method should be used during the early generations of selection and only when it becomes ineffective should the method of selection for cross-performance take its place.

Bell, Moore and Warren (1955), Rasmuson (1956) and Kojima and Kelleher (1963) carried out selection on D. melanogaster to test the usefulness of the selection method for specific combining ability. They selected for egg production - a trait which is considered to be closely



related to fitness. Bell et al. reported the heritability of egg production in unselected inbred stocks to be around 5 - 15% and observed marked heterosis on crossing. Kojima and Kelleher estimated the heritability for egg production in the two cage populations they used to be close to zero. In all three experiments, response obtained by mass selection on the closed population was compared with the response from reciprocal recurrent selection (RRS). Kojima and Kelleher termed the selection on closed population as purebred selection and RRS as crossbred selection. The results from the three experiments were somewhat disappointing and not in agreement. Bell et al. observed that purebred selection produced the greatest response during the early cycles of selection but RRS proved to be superior as selection progressed and maintained its superiority till the end of 40 cycles of selection. But the advantage of RRS over purebred selection was slight. Rasmuson's selection was carried for 20 cycles. The general trend during the entire period was for RRS to be slightly superior over purebred selection. Both Bell et al. and Rasmuson made no attempt to analyse the selection response in detail or to test for the significance of the difference in response from the two methods of selection. Kojima and Kelleher reported a definite advantage of RRS over the closed population selection. No general conclusions could be reached from the results of these three experiments with similar objectives. The difference in outcome of each experiment could be due to two causes. Firstly, different methods of purebred selection were used. Bell et al. practised full-sib family selection reinforced by individual selection within selected families, Rasmuson used half-sib family selection and Kojima and Kelleher's method was full-sib family selection. Thus, the method used by Bell et al. would be expected to give greater response and could be the cause of the observed larger response of purebred selection over crossbred selection

during the early cycles of selection. Secondly, the nature of the base populations for each experiment was different. Kojima and Kelleher utilized two cage populations for purebred and crossbred selection while Rasmuson and Bell et al. used heterogeneous synthetic base populations derived from crossing together several unrelated stocks. RRS will manifest greater advantage over mass selection only when practised on traits with low heritability using base populations containing little genetic variation.

Choice of a method of selection is no simple matter. Factors such as the selection traits, the nature of the base population, the finance and facilities available and others have to be considered very carefully before embarking on any selection scheme. It should be noted that the usual selection methods for breeding large domestic animals have been largely neglected in this section of review mainly because this would not have much direct bearing on the subject of this thesis.

#### 4. Population size and selection intensity

Selection consists essentially of choosing certain individuals from a population to serve as parents of the next generation. The number of selected parents constituted the population size and the proportion of individuals selected is referred to as the selection intensity. These two factors are related to each other and have considerable effect on selection response. A. Robertson (1966) noted that "... in a majority of laboratory selection experiments carried out with populations of fairly small size, the limits to selection are artifacts of the intensity of selection and the population size rather than the basic properties of the initial population."

The intensity of selection determines the size of the selection

differential. Higher selection intensity gives a larger selection differential which in turn gives a greater response to artificial selection. For laboratory species like Drosophila and Tribolium with high reproductive rate and low costs of maintaining large numbers of individuals, the intensity of selection is not limited by the number of individuals available for selection but rather by the labour and time involved in the measurement of the selected character. For larger animals, both the population size and the intensity of selection are limited by the low reproductive rate and the costs of maintaining the total population.

As A. Robertson has pointed out, in most artificial selection experiments, the population size is small. This has two main genetic consequences. Firstly, it increases the rate of inbreeding within the population and secondly, it leads to an increase in non-directional genetic drift (Crow, 1954; Gowe et al., 1959; Kimura and Crow, 1963). Both effects cause a rise in the level of homozygosity of the population. It is clear from this, that the amount of genetic variation in a small closed population would be lower than in a large outbred population.

In practice not all the selected individuals contribute equally towards the progeny of the next generation. In most cases then, the effective population size is smaller than the actual population size. This is due to the differences in fertility and viability among selected individuals and also due to the differential effects of natural selection. Furthermore, selected individuals tend to be more closely related than expected, particularly when highly heritable characters are selected for (A. Robertson, 1961). These two factors would cause further increases in the rate of inbreeding of a selection line or population. Crow (1954) made a theoretical investigation of the effects of small population size and derived a formula for the effective population number from the variance

of family size ( $\sigma_K^2$ ). The approximate value of  $N_e$  when the mean family size is two is given as :-

$$N_e = 4N/(2 + \sigma_K^2)$$

where  $N$  = actual population number

A. Robertson (1961) used a different approach to the problem of inbreeding and restricted population size. He proposed a formula for predicting  $N_e$  using the parameter ( $\sigma_S^2$ ) which is the variance of selective advantage between families. When applied to artificial selection for a quantitative character using full-sib families and based on the assumption that there is no difference in selective value between full-sib progeny groups, the ratio of actual to effective population number is given as :-

$$N/N_e = 1 + 2\bar{i}h^2[1 - h^2\bar{i}(\bar{i} - x)]$$

where  $\bar{i}$  = standardised selection differential

$h^2$  = heritability

$x$  = abscissa of the unit normal curve where the perpendicular cuts off the proportion of animals selected to be parents.

It is found that the higher the heritability of the selected character, the smaller the effective population size.

In selection experiments where the population size is greatly restricted, the deleterious effects of inbreeding in causing degeneration of reproductive fitness are usually encountered. Concurrent selection and inbreeding have been investigated by Rasmuson (1952), Tantawy (1956), and Sinnock (1970) on various quantitative traits in Drosophila. It is found that when additive genetic variation is present selection within highly inbred lines can be effective but there is the loss of many of the

inbred selection lines. Selection response proved to be highly variable. The general trend observed is asymmetrical two-way response with greater response downwards which is the direction of decline caused by inbreeding depression.

Large discrepancies between observed responses from inbred populations and responses predicted from the mass selection theory are the usual case. Kojima (1961) dealt with the theoretical consequences of the effects of small population size and dominance on selection response, and compared it to the response predicted from the mass selection theory based on mass selection practised on an infinite population. The main conclusion arrived at is that considerable deviation from the usual prediction equation would occur as a result of the combined effects of dominance and small population size.

In the present author's opinion the effects of population size and selection size on response could be studied in three ways. The first two are fairly straightforward. The first method is to compare the effects of different population sizes using the same intensity of selection. The second method is a comparison of different selection intensities with identical population size in each selection line. So for these two methods of comparison, the population size or selection intensity is varied by varying the total number of individual scored. The third method involves both population size and selection intensity and it stems from keeping constant the number of individuals scored for each selection line. This third method is most applicable to large domestic animals where the number of animals available for selection is limited so that the only way to vary selection intensity is to vary the proportion of individuals selected to be parents and vice versa for changing population size. In other words, the higher the selection intensity, the smaller the popula-

tion size.

The work of Frankham, Jones and Barker (1968) is to date the most comprehensive and detailed study of the effects of population size and selection intensity on selection responses. Selection was made for high and low abdominal bristle number in D. melanogaster. Both short-term (12 generations of selection) and long-term (50 generations) selection response have been analysed and discussed in terms of actual gain, selection differentials and realised heritabilities. A factorial experiment was set up involving three population sizes (10, 20 and 40 pairs of parents) and five selection intensities (10, 20, 40, 80, 100%). Altogether there were 15 different selection lines. The number of replicates carried for the selection lines ranged from one to five. Lines with the smallest population number which are most affected by random drift having the highest number of replications. The results obtained are valuable and interesting and so will be reviewed in some detail. When the responses of lines with different population sizes but the same intensity of selection are examined the trends are quite apparent. The size of the response is directly related to the size of the population, and the same trend is found in both short-term and long-term selection. Divergences between replicates within selection lines are noted after the first few generations of selection and it would appear that the smaller the population size the greater the discrepancies between replicates. In the second comparison, where the population size is constant for each selection line but the selection intensity varied, the results showed that the higher the intensity of selection the greater the selection response. The reason is quite obvious, greater selection differentials are produced by higher selection intensities since a greater number of individuals are scored. Here again both the short-term and long-term trends are much the same

except that differences between lines with different selection intensities become more pronounced in the later stages of selection. For the third method of comparison where the total number of individuals scored each line is kept constant but the proportion of the individuals selected is varied, the trends of short-term selection response are different from the long-term trends. For short-term selection, the line with the highest selection intensity and consequently the smallest population size gave the most rapid response. The magnitude of response seems to be determined by the selection intensity and not the population size. But a different trend emerged for long-term selection. Although the high selection line still maintained its superiority, the line with the lowest selection intensity but the largest population size soon overtook the moderate selection line and almost caught up with the high selection line towards the end of long-term selection. The possible reasons for the reversal of trends had been discussed by Rumball (1966). Among the fifteen selection lines, the line with the largest population size and highest selection intensity was clearly the most superior. Further useful information could be obtained from the data of Frankham et al. had they carried the analysis of results further to include the variability between replicates within selection lines instead of just noting the divergence between replicates and simply pooling the replicate means to give the average value for a selection line. This would have yielded valuable evidence on the part played by the two factors, population size and selection intensity, on the variability of selection responses within and between selection lines.

Experiments with similar objectives but on a smaller scale have been conducted by other workers. The results obtained are generally in agreement with the findings of Frankham et al. Clayton, Morris and Robertson (1957) investigated the differences in selection responses from selection

lines at different selection intensities but with the same population size. The results for short-term selection showed that the line with the highest selection intensity gave the greatest response and the weaker selection line gave the least. If the results obtained by Frankham et al. were the general rule then had Clayton et al. continued the selection, the most intensely selected line would still be expected to give the greatest response.

De Fries and Touchberry (1961) carried out two-directional selection for body weight in D. affinis at two intensities of selection. They used the minimum population size of a single pair of parents and as this necessitated high replications, they carried ten replicates for each selection line. With the data, they were able to assess the variability within and between replicates of each selection line. However the effects of the two selection intensities were largely ignored. The small population size was responsible for the significant intra-replicate variation as well as inter-replicate variation and also for the inter-generation fluctuations of selection responses. The magnitude of selection responses was also affected since the smaller the population size the greater the chances of some favourable genes being lost through random sampling and other less favourable genes becoming fixed in the lines. Tantawy (1956) provided further evidence on the effect of population size on the size of selection response. Short-term selection was made for long and short wings in D. melanogaster using three different population sizes but the same intensity of selection. Results obtained were in accordance with expectations. For constant selection intensity the size of selection response is positively correlated with the population size.

Rumball (1966) made a detailed study of the joint effects of population size and selection intensity. This corresponded to the third



method of comparison mentioned earlier where the total number of individuals measured was fixed and selection intensity varied by varying the proportion of individuals selected. The effects of three selection intensities were studied - high selection intensity with two pairs of parents, moderate intensity with four pairs of parents and weak selection intensity with eight pairs. From his literature review and subsequent discussion it would appear that he failed to make the distinction between the two methods for comparing selection intensities, one where the population size is constant at all selection intensities and the other where the population number is negatively correlated with selection intensity. For the first method, the rate of inbreeding would be the same in lines with different selection intensities but for the second method the line with the highest selection intensity would have the highest inbreeding rate because of the greatest restriction in population size. This is one of the few experiments where each selection line is well-replicated (six replications). For each selection line he estimated the within and between replicate variance components for every generation. The latter component gives a measure of the heterogeneity of responses within a selection line, and the line with the higher selection intensity exhibited the greatest heterogeneity between replicates. The trends of response during the twenty generations of selection proved to be interesting. The high intensity selection line gave the greatest response during the early generations of selection, the moderate intensity selection proved to be superior during the middle period of selection while the line with the weaker selection took the lead towards the end of the selection programme. The reversal of ranks could be due to the greater rate of reduction of genetic variation in the higher selection intensity lines.

Martin and Cockerham (1961) carried out genetic simulation studies

on the computer to trace the selection response from a range of genetically simulated populations. The simulated populations were characterized by parameters like the number of gene loci, type of gene action, the recombination fraction, population size and selection intensity. Using an additive model and where the population number is restricted, it is possible to obtain selection responses similar to that observed by Rumball (1966) and Frankham et al. (1968) where the lines with highest selection intensity gave most rapid response initially but the rate soon declined and the less intensely selected lines eventually proved to be superior. Thus for long-term selection with small population size, less intense selection is likely to produce the highest response in the long run.

#### 5. Mating systems

Essentially there are two main methods of mating selected individuals - randomly or non-randomly. Under the random mating system the parents are mated together purely by chance. This system of mating is commonly used for species like Drosophila where all the parents are mated en masse in a single culture bottle. For large domestic animals, one method of achieving random mating is to use a table of random numbers for assigning mates. Non-random mating can be made in different ways. Individuals may be mated together on the basis of genetic similarity (inbreeding) or somatic resemblance (phenotypic assortative mating). Dissimilar individuals may be mated together based on dissimilar genotypes (outbreeding) or somatic non-resemblance (phenotypic dissortative mating).

The theoretical consequences of different systems of mating on the genetic composition of a large population in equilibrium have been worked out by Wright (1921) in a series of papers entitled "Systems of

Mating." Under inbreeding and phenotypic assortative mating the genetic variance will be greater than under random mating. Associated with this increase in genetic variance is the rise in the homozygosity of the population. Under outbreeding and phenotypic dissortative mating systems the genetic variance will be lowered with little change in homozygosity of the population.

Breese (1956) compared the effects of phenotypic assortative mating with inbreeding by selfing and random mating on two traits, flowering time and flowering height in Nicotiana rustica. An increase in genetic variance was reported for the assortatively mated line. This increase could be explained in terms of increase in gene combinations having extreme expressions at the expense of gene combinations exhibiting intermediate effects. Assortative mating system by making more genetic variation for selection to act on could be a means of producing greater selection response. Similar findings were reported by James and McBride (1958) from their experiment on poultry.

One of the few experiments designed to compare the relative effectiveness of selection using phenotypic assortative mating and random mating was conducted by McBride and Robertson (1963). Selection was made for high abdominal bristle number in Drosophila, which is known to be a highly heritable trait. Three sets of selection lines were set up. Within each set was an assortatively mated line and a randomly mated line, the latter acting as a control. Individual selection was practised on two sets and index selection was used on the third set. All the three assortatively mated selection lines gave consistent greater response than their randomly mated selected control. However the advantage was small and no attempts were made to test for significance. The increase in response could be traced to the increase in genetic variance and selection differ-

entials in the assortatively mated lines. This is in accord with theoretical expectation. The smallness of the advantage is likely to be due to the greater rate of inbreeding resulting from assortative mating. They pointed out that assortative mating system could only help to increase selection response for highly heritable traits.

The main disadvantage of assortative mating system, particularly where selection intensity is high, is the rapid increase in inbreeding and the deterioration of reproductive fitness in the selection line. Though rapid response might occur during the early generations of selection, the selection limit would be lower due to the greater reduction in effective population size (A. Robertson, 1961).

Wilson, Kyle and Bell (1965) carried out an experiment to evaluate the merit of different systems of mating on selection responses of a highly heritable trait, pupa weight, in Tribolium. Selection was practised for only six generations since most of the effects of the mating systems should appear during the first few generations of selection. The experiment was divided into a mass selected group and a randomly selected group. Within each group, five different mating systems mentioned earlier were tested. The response from the different selection lines within each group appear to be remarkably similar over the six generations of selection. Wilson et al. reported that the average response of the mass selected assortatively mated line was slightly greater than the mass selected randomly mated line but that the difference was not statistically significant. Nevertheless, on that basis they claimed that the results were in line with theoretical expectation and that assortative systems of mating could help to bring about greater response for traits with high heritabilities. The present author finds it difficult to accept their conclusions based on such weak experimental evidence.

To end this section, the simple words of Wright (1921) seem appropriate "... all mating systems have their advantages and disadvantages."

## 5. Environment

The question of what is the most suitable environment in which to carry out a selection experiment has not been fully worked out, although it is recognized that the environment can exert a considerable effect on the trends as well as limits of the selection response.

In simple terms, a phenotype is said to be the result of its genotype, the environment and their interaction. Lerner (1950) has given a simple model for partitioning the phenotypic variance.

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + 2r_{GE}\sigma_G\sigma_E + f(GE)$$

where  $\sigma_G^2$  = genetic variance

$\sigma_E^2$  = environmental variance

$r_{GE}$  = genotype-environment correlation

$f(GE)$  = genotype-environment interaction

In usual selection experiments where the environment is kept as uniform and optimal as possible and where randomisation and effective controls are incorporated in the experimental design, the last two terms in the above equation may be neglected. The main purpose of maintaining control stocks is to separate the environmental and genetic effects in a selection line and this is based on the assumption that the selection lines and the controls are closely related and therefore react similarly to changes in the environment. Bray, Bell and King (1962) have drawn attention to the importance of genetic-environment interactions in

circumstances where the genetic content of the selection line has deviated considerably from that of the controls due to the effects of selection or to random genetic drift. Under such conditions, the control is no longer effective and considerable error could arise if selection responses were measured as deviations from the controls.

Often one is interested in the performance of a selected population not only in the environment in which selection was carried out but in a variety of environments. Falconer (1960) has pointed out, "The existence of genotype-environment interaction may mean that the best genotype in one environment is not the best in another." The question of such interactions is of tremendous importance in applied plant and animal breeding where the practice of importing and exporting superior breeds is becoming increasingly popular.

Hammond (1947) discussed at length the implications of genotype-environment interaction to livestock breeding. One of the conclusions reached is that greater genetic response is possible in an environment which is most favourable to the expression of the selected character. Individuals selected under such favourable conditions when transferred to other environments would perform better than individuals which have been similarly selected in less favourable conditions. He added that this would occur on condition that other characters required in the new environment are present in the selected animals. His thesis drew the attention of other workers to the problem of genotype-environment interactions.

The problem of evaluating the genotype-environment interactions had been tackled by Falconer (1952). He reasoned that if the same character selected in two different environments resulted in genetic differences then it could be regarded as two separate traits. The

genetic correlation between the two traits gives a measure of the interaction. He derived a formula by the method of path coefficients to compare the response of a selection line in its own environment (direct response) with its response in a different environment (correlated response).

$$r_G = \frac{\text{Correlated response}}{\text{direct response}} \frac{h_1 \bar{i}_1}{h_2 \bar{i}_2}$$

$$1-r_G = \text{genetic-environment interaction}$$

where  $r_G$  = genetic correlation between the two traits  
 $h_1$  and  $\bar{i}_1$  = square root of heritability and standardized selection differential in environment where direct response is measured  
 $h_2$  and  $\bar{i}_2$  = square root of heritability and standardized selection differential in the environment where correlated response is measured

The statistical procedure is based on the assumptions that genotype-environment correlation is insignificant and that the variation within environments is much smaller than the variation between environments. Falconer pointed out that only in rare occasions when the heritability in the alternative environment is much higher than the heritability in the original environment would the correlated response be equal or greater than the direct response.

A simple classification of genotype-environment interaction has been given by McBride (1958). He termed small genetic differences as intra-population genotypes and large differences as inter-population genotypes. Similarly, small environmental differences are termed micro-environments and large differences as macro-environments. The

four main classes of interaction are intra-population genotypes and micro-environments (Type A), intra-population genotypes and macro-environments (Type B), inter-population genotypes and micro-environments (Type C) and lastly inter-population genotypes and macro-environments (Type D). Classification of interactions have also been made by Haldane (1946), Mather and Jones (1958) and Dunlop (1962).

Many selection experiments have been carried out by various workers to study different aspects of genotype-environment interactions. The effects of different types of nutrition is most commonly studied since the experimenter can easily vary both the quantity and quality of the diet. Falconer and Latyszewski (1953) conducted a simple experiment on mice with the purpose of testing the validity of Hammond's thesis. Nine generations of selection were made for high 6-week body weight on two planes of nutrition - full diet and restricted diet. The quantity of food in the latter diet was 75% of the normal intake. At the 5th, 7th and 8th generations part of the selected stocks were transferred to the alternative environment and the correlated response measured. The results were contradictory to Hammond's views, as the mice selected under stringent conditions performed well in both environments whereas those selected on a full diet, when shifted to the poor diet, did worse than the contemporaneous mice selected on the restricted diet. Falconer (1960) repeated the experiment on a larger scale and with selection for decreased growth rate as well. Reciprocal transfers were made each generation. The results confirmed his earlier findings and he concluded that "... if good performance under a variety of conditions is desired then selection should be made under conditions least favourable to the desired expression of the character; if an increase is desired then selections should be made under conditions that reduce the character and vice versa." The pattern



of selection response was observed to be affected by the nature of the environment. An almost symmetrical two-way response was obtained under optimal conditions of full feeding while an asymmetrical response, greater in the downward direction, was obtained from selection on the restricted diet. Falconer pointed out that two characters were actually selected for in the experiment for body weight - mice on full diet were selected for higher appetite while those on restricted diet were selected for efficient food utilisation. Similar findings were reported by Fowler and Ensminger (1960) selecting for rate of gain in swine on full and restricted diet.

Dalton (1967) repeated Falconer's (1960) experiment. The design was improved as unselected controls were maintained for each selection line and diet differences were greater. Responses were estimated on deviations from controls and would be corrected to some extent for environmental variation and inbreeding depression. For both diets, the direct and correlated responses were not significantly different, indicating the absence of genotype-environment interactions. Since no genetic advantage was gained from selection in any particular environment, for practical purposes the best environment would be the most economical and efficient one. Young (1953) and Dalton and Bywater (1963) also reported non-significant genetic-environment interaction from their investigations. Frahm and Kojima (1966) selected for body weight in D. pseudoobscura under high and low larval density conditions. Body weight was found to be inversely correlated to larval density. No apparent genotype-environment interactions were observed. Under high larval density conditions, asymmetrical response was obtained with smaller upward response while the pattern was more symmetrical for selection under low larval density conditions. The greater upward response under low density conditions could be due to a higher optimum body weight under

less competitive conditions and also due to the wider range of phenotypes available for selection since the more extreme phenotypes would manage to survive under these less competitive conditions.

Park, Hansen, Chung and Chapman (1966) studied the influence of three diets - full diet, limited diet and limited protein on selection responses of 9-week body weight in rats. The results indicated that each selection line was superior over the other two lines in the environment appropriate to its selection. Hence, they advocated that selection is best practised under the environment in which the improved stock will subsequently live. However, the line selected on full feeding environment showed greater ability to adapt to other environments and this is contrary to the findings of Falconer (1960) and Fowler and Ensminger (1960). Comparable results were reported by F.W. Robertson (1960), Korkman (1961) and Bradford (1968).

Druger (1962) selected for long and short wings in D. pseudoobscura at two different temperatures - 25°C and 16°C. Temperature of 25°C favours short wings while 16°C favours longer wings. For each generation of selection, a sample of stock selected at 25°C was transferred to 19°C and 16°C. Similarly, transfers were made from the 16°C stock to 19°C and 25°C. The results were in agreement with the findings of Falconer and his co-workers in that the best overall performance was obtained by selection in conditions least favourable to the expression of the character. Hence, selection for long wings at 25°C produced individuals with greater transmitting ability than long-winged flies selected at 16°C. Similarly, short-winged flies selected at 16°C were more adaptable to other environments than those selected at 25°C. A very similar experiment using two different temperatures was conducted by Lawrence (1964). He found that genotype-environment interactions were important in the high sternopleural

selection lines but not significant for the low selection lines.

Chapman (1967) has reviewed work on genetic-environment interactions in laboratory and domestic animals. In view of the contradictory evidence presented by different workers he concluded that the safest measure is to carry out selection under the conditions in which the improved stock is destined to live. A general principle he proposed is that genetic-environment interactions are unlikely to be important except where inter-population genotypes and macro-environments are involved.

To round up this review, it seems worthwhile reiterating that the vital role each factor plays in shaping the selection response of each experiment cannot be over-emphasized. Since each factor can be varied in so many different ways, it is not so surprising after all to observe the variability of selection response from the same character in the same species. A. Robertson (1958) has already sounded a clear warning on the dangers and difficulties in extrapolating the results from one species to another and has discussed the reasons for it. The present author wishes to add that from the present review there is evidence that there are considerable dangers in extrapolating the results of selection on a character from one population to another, even within the same species.

### III. MATERIALS AND METHODS

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#### A. ORGANISM AND CULTURE METHODS

Drosophila melanogaster was the organism used in this present thesis. Its popularity as an organism for selection and genetical studies is because of its short life-cycle, high reproductive rate as well as the ease and economy with which it can be maintained in large numbers. Furthermore, there are special genetic strains and techniques for genetic analyses of the populations.

Throughout the present selection experiment, the stocks were cultured in quarter-pint cream bottles containing a standard food medium of oatmeal, syrup and yeast with Nipagin-M as a mould and bacteria preventative. All the cultures were kept in an incubator maintained at  $25 \pm 1^{\circ}\text{C}$ . The availability of incubator space was one of the main limiting factors of the size of this experiment.

Throughout the study, great care was taken to prevent the contamination of the Drosophila stocks by moulds, bacteria or semi-parasitic mites. The incubator and area around it were disinfected fortnightly with a dilute solution of benzyl benzoate. At no stage of the experiment were any serious diseases observed.

## B. ABDOMINAL BRISTLE CHARACTER

The aim of this thesis is to study the response from parallel mass selection on different base populations and the quantitative character used is the sum of the bristles on the 4th and 5th abdominal sternites. This trait has been chosen because it is known to respond well to two-directional selection, and suffers little from inbreeding depression and it can be easily scored under a high-power binocular microscope. It has been used by other workers for selection studies (Mather and Harrison, 1949; Rasmuson, 1952, 1955; Clayton et al., 1957; McBride and A. Robertson, 1963). The abdominal bristles are a group of microchaetae found on the sclerotised sternital plates. The females being larger than the males have about 20% more bristles than males but in other species like D. virilis, the males have higher bristle numbers than the females. Sclerotisation of the cuticle is normally accompanied by chaetae formation so that the presence of chaetae on the abdominal sternites is considered to be a secondary product of sclerotisation. The function of the sternital plate itself is clearly a skeletal one, that is, to give shape and rigidity to the abdomen and for the attachment of abdominal muscles. However, the functions of the abdominal sternital bristles are not clear. Since each bristle is innervated by a peripheral bi-polar nerve cell lying just below it (Stern, 1938; Lees and Waddington, 1942), it probably has a sensory function. Clayton et al. (1957) suggested a practical use for these bristles, to prevent the fly from sticking to moist food surfaces. As the abdominal bristle character appears to have little adaptive significance, natural selection would not be directed on the character itself but on its pleiotropic effects on other characters such as the underlying peripheral nervous system and the size and hardness of the

sternites and these two latter characters play an important role in the control of the shape and movement of the abdomen (Reeve and F.W. Robertson, 1954).

Mather and Harrison (1949) have demonstrated that genes affecting abdominal bristles are distributed over all the large chromosomes. Under optimal environmental conditions, the genetic correlation between sternites is found to be close to one and the environmental correlation on the other hand is virtually zero (Reeve and F.W. Robertson, 1954). This means that genes affecting bristles on one sternite exert almost identical effects on other sternites. Heritability estimates of the bristle character in the base population made by Reeve and F.W. Robertson (1954) and Clayton et al. (1957) showed that about 50% of the phenotypic variance is due to genetic variation which is mainly additive, that environmental variance common to sternites contributes only about 5% of phenotypic variance and the rest is due to developmental effects peculiar to each sternite. Sheldon (1963) on the other hand reported lower additive genetic variance (about 25%) as well as lower variance due to developmental error (25%). The abdominal bristle character does not appear to be affected by inbreeding (Rasmuson, 1952) nor does it exhibit heterosis (Clayton et al., 1957). Mather and Harrison (1949) reported that the character is not affected to any great extent by the quality of nutrition since a difference of less than one chaeta was found between the means of flies raised on fresh food medium and those cultured on stale food heavily contaminated with moulds and yeasts. However, environmental conditions like overcrowding and increased temperature which reduce body size also cause correlated reduction in bristle number (Rasmuson, 1952; Reeve and F.W. Robertson, 1954). Because of these properties, this character has been classified as a neutral or peripheral one (A. Robertson, 1955).

## C. BASE POPULATIONS

### 1. Description of base populations

The two wild-type stocks of D. melanogaster, Oregon-R and +3, used in this thesis were from diverse origins. The Oregon-R strain was obtained from Victoria University, Wellington while the +3 came from Auckland University. Both strains have been bottle-cultured for several years and it is not known where they were originally from. The stocks had no previous history of selection for abdominal bristles or any other character.

The Oregon-R and +3 both served as base populations for this present selection experiment. They were also crossed to initiate a synthetic population which formed the third base population and was designated as the "Cross". This Cross was formed by making reciprocal crosses of the two original strains to form the  $F_1$  generation. Approximately equal numbers of males and females randomly selected from each of the reciprocal  $F_1$  crosses were inter-crossed in all possible ways giving the  $F_2$  generation. Selection from the Cross population was started on the  $F_3$  population which was obtained by random mating the  $F_2$  flies.

### 2. Results and discussion

The mean abdominal bristle numbers of the parent strains (Oregon-R and +3) and the  $F_1$  reciprocal crosses for the two sexes separately are given in Table 1. The difference between the means of two lines was tested for statistical significance using the standard "t" test. The level of significance is expressed as the probability that the difference between the two population means is due to chance. The probability level is given between each pair of means.



Table 1: Mean abdominal bristle number of D. melanogaster by strain, reciprocal crosses and sex

| Population                    | Abdominal Bristle number         |                                  |
|-------------------------------|----------------------------------|----------------------------------|
|                               | Females                          | Males                            |
| Oregon-R                      | 36.15 $\pm$ 0.14*<br>(P < 0.001) | 30.77 $\pm$ 0.13*<br>(P < 0.001) |
| +3                            | 38.87 $\pm$ 0.15*                | 33.05 $\pm$ 0.13*                |
| Midparent                     | 37.51 $\pm$ 0.11 <sup>+</sup>    | 31.91 $\pm$ 0.10 <sup>+</sup>    |
| F <sub>1</sub> (♂Or-R x ♀ +3) | 39.05 $\pm$ 0.14*<br>(P < 0.005) | 32.03 $\pm$ 0.12*<br>(P < 0.001) |
| F <sub>1</sub> (♀Or-R x ♂ +3) | 39.69 $\pm$ 0.14                 | 35.02 $\pm$ 0.12*                |
| Average F <sub>1</sub>        | 39.37 $\pm$ 0.10 <sup>+</sup>    | 33.52 $\pm$ 0.10 <sup>+</sup>    |
| Heterosis (%)                 | 5.0%                             | 5.0%                             |
| F <sub>2</sub>                | 39.69 $\pm$ 0.19*                | 33.46 $\pm$ 0.17                 |

\* Means based on 400 observations  
+ Means based on 800 observations

The difference between the means of the two parent strains (Oregon-R and +3) was found to be highly significant (P 0.001) with the +3 strain having higher means. Results from the F<sub>1</sub> reciprocal crosses yield some useful information about the nature of the genes affecting the abdominal bristles. Heterosis was measured as the difference between the average of the F<sub>1</sub> means and the mid-parent value and was expressed as a percentage of the mid-parent value. The average F<sub>1</sub> means exceeded not only the mid-parent value but also the mean of the +3 strain with the higher bristle number. The heterosis for both male and female data was 5%. This finding does not conform to the previous claims that

abdominal bristle number has no effect on fitness and thus shows no heterosis on crossing (A. Robertson, 1955; Falconer, 1955). However, heterosis shown is low compared to that of over 200% exhibited by fitness traits like egg production and viability (Boylan and Wong, 1965). Rasmuson (1952) made reciprocal crosses between a number of unselected highly inbred lines of D. melanogaster and reported about 5% heterosis among the  $F_1$  females but no heterosis for the males.

Comparison of the means of the  $F_1$  reciprocal crosses gives information on the role of the sex-chromosomes in determining abdominal bristles. Greater differences between the  $F_1$  means for the male data than for the female data indicate the prevalence of sex-linked effects. Results presented in Table 1 showed a difference of 0.55 bristles between the means of the reciprocal crosses in the female data and this difference though small was significant ( $P < 0.005$ ). However, a much greater difference of 2.99 bristles was found in the male data ( $P < 0.001$ ) and this difference could be due to sex-linked effects. It was noted that the abdominal bristle number of  $F_1$  males from the cross which received the Y chromosome from the +3 strain with the higher population means was higher. This evidence points to the presence of genes located on the Y chromosome favouring bristle character. This finding is consistent with that of Rasmuson (1952).

Vetukhiv (1953, 1956, 1957) carried out a series of experiments to investigate the effects of crossing together wild-type populations of D. pseudoobscura on fitness traits like viability, fecundity and longevity. His results showed that for these fitness traits, there was marked heterosis in the  $F_1$  generation but breakdown of heterosis in the  $F_2$  generation, with the  $F_2$  means often being lower than the parental populations means. The  $F_1$  heterosis was interpreted as being due to superiority conferred by

heterozygosity and the  $F_2$  breakdown as due to the disintegration of co-adapted genetic systems by segregation and recombination. Results from this present experiment give evidence that this phenomenon is not exhibited by neutral traits like abdominal bristles.

The two original strains, Oregon-R and +3, and the  $F_3$  of the Cross serve as base populations for simultaneous mass selection. The statistical parameters of these base populations are given in Table 2. The Cross has the highest population mean, the +3 intermediate and Oregon-R the lowest.

| Table 2: Parameters of the base populations |                                         |                                         |                                         |                                         |                                         |                                         |
|---------------------------------------------|-----------------------------------------|-----------------------------------------|-----------------------------------------|-----------------------------------------|-----------------------------------------|-----------------------------------------|
| Parameter                                   | Oregon-R                                |                                         | +3                                      |                                         | Cross ( $F_2$ )                         |                                         |
|                                             | Females                                 | Males                                   | Females                                 | Males                                   | Females                                 | Males                                   |
| Mean abdominal bristle number ( $\mu$ )     | 36.15 <sup>+</sup><br>0.14 <sup>-</sup> | 30.77 <sup>+</sup><br>0.13 <sup>-</sup> | 38.87 <sup>+</sup><br>0.15 <sup>-</sup> | 33.05 <sup>+</sup><br>0.13 <sup>-</sup> | 39.69 <sup>+</sup><br>0.19 <sup>-</sup> | 33.46 <sup>+</sup><br>0.17 <sup>-</sup> |
| Phenotypic variance ( $\sigma_p^2$ )        | 7.84                                    | 6.50                                    | 9.33                                    | 7.08                                    | 14.23                                   | 11.67                                   |
| Standard deviation ( $\sigma$ )             | 2.80                                    | 2.55                                    | 3.06                                    | 2.66                                    | 3.77                                    | 3.41                                    |
| Developmental error ( $\sigma_D^2$ )        | 1.55                                    | 1.52                                    | 2.21                                    | 1.65                                    | 1.80                                    | 1.67                                    |
| Coeff. of variation ( $\sigma/\mu$ )        | 7.7%                                    | 8.5%                                    | 7.9%                                    | 8.1%                                    | 9.5%                                    | 10.2%                                   |

The phenotypic variance appears to be correlated with the population means. The females with higher abdominal bristle number than males have higher phenotypic variance. Similarly, the +3 strain with higher mean than Oregon-R has higher phenotypic variance. The phenotypic variance of the  $F_2$  is strikingly greater than both the parent lines; it is about twice the phenotypic variance of the Oregon-R strain and about  $1\frac{1}{2}$  times that of

the +3 strain. Although the phenotypic variance of  $F_1$  of the Cross is of the same order of magnitude as the parent populations, the  $F_2$  shows a great increase in phenotypic variance due to segregation and recombination and a much greater range of phenotypes is observed among the  $F_2$  progeny. On the underlying genetic scale, crossing of two (or more) different populations results in the pooling together of genes to form a larger common "gene pool." Thus, the genetic variation within the "crossbred" population would be expected to be greater than the genetic variation within each of the "purebred" parental populations. On this basis, the Cross population is expected to give greater response to selection than either of the parental strains. However, if the quantitative character is controlled by a large number of genes, the increase in genetic variance in the Cross would not be much. Recent investigations by various workers have shown that the genetic variation of quantitative characters are controlled by relatively fewer loci, with large effects, than previously thought (Thoday, Gibson and Spickett, 1964; A. Robertson, 1966; Werhahn and Allard, 1965; Law, 1966, 1967).

The Oregon-R and +3 base populations would be in linkage equilibrium, since they have been maintained by random-mating for a long time but the  $F_3$  of the Cross would still be in linkage disequilibrium. Although the Cross is expected to give greater selection response because of greater genetic variance, this response could be slowed down if the disequilibrium was due to tight linkages (Martin and Cockerham, 1960). For this reason, Kojima and Kelleher (1963) suggested that the hybrid base population should be randomly mated for a few generations to establish linkage equilibrium before commencing selection.

A high proportion of the non-genetic variation of abdominal bristles is due to developmental variation, that is, accidents of development affecting

each sternite differently and only a small proportion is due to environmental variation affecting both sternites. The developmental variance, estimated from the variance of difference between the two sternites, constitutes about 20-25% of this phenotypic variance in all three base populations of this experiment.

By using these three different base populations for selection, it is hoped that this investigation would provide some answers to the important question of the effects of base populations in determining the magnitude of response, as well as the variability of response within populations.

IV. HERITABILITY ESTIMATES OF THE  
OREGON - R AND +3 BASE POPULATIONS

#### IV. HERITABILITY ESTIMATES OF THE OREGON - R AND +3 BASE POPULATIONS

##### A. INTRODUCTION

Prior to the start of the selection experiment, heritability estimates were made on the Oregon-R and +3 base populations. Heritability, in the narrow sense, is defined as the fraction of the total phenotypic variance which is additively genetic (Lush, 1949). Methods for estimating heritability are based on resemblance between related individuals. The usual methods of estimation are by parent-offspring regression, half-sib correlation, full-sib correlation and analysis of variance of diallel crosses. Preliminary knowledge of this genetic parameter has two important uses. Firstly, it could serve as a guide to the choice of the most appropriate method of selection. For highly heritable traits, mass selection based on individual merit would be suitable but for lowly heritable traits, more reliance should be placed on selection based on family means or on progeny tests. On the other hand, if a considerable proportion of the genetic variation is non-additive, a crossbred mating scheme such as reciprocal recurrent selection would be expected to produce greater response than intra-population selection. The second function of heritability is to predict response to selection.

There is a large volume of literature on heritability estimates for a wide variety of quantitative characters in different organisms. However, only a short review of literature on heritability estimates for abdominal bristles will be presented.

F.W. Robertson (1954) made a study of the quantitative inheritance of bristles on the 3-5th abdominal sternites in males and on the 3-6th sternites in females. He reported that under optimal conditions, about 40% of the phenotypic variance of bristles on one sternite is due to additive genetic variance, the rest is due almost entirely to accidents of development. The true environmental variance was found to be almost zero. Clayton et al. (1957) made heritability estimates for the abdominal bristles on the 4th and 5th abdominal sternites using the parent-offspring regression, full-sib and half-sib analysis. The three independent estimates were highly consistent and gave an average heritability of 0.52. The full-sib heritability estimate was only slightly higher than the other two estimates, indicating that the abdominal bristle character is not greatly affected by dominance, epistatic deviations or maternal effects.

Sheldon (1963) employed a restricted form of the diallel cross using two sires and two dams block matings to estimate the heritability in the base population as well as in the individual selection lines during the 13th, 23rd and 33rd generation of selection. This method of estimation is superior to the others mentioned earlier, as the data permits the estimated genetic variance to be sub-divided into its additive and non-additive components. By carrying out the diallel cross at regular intervals during the selection programme, the trend in the additive and non-additive genetic variance could be followed. The results obtained indicated a general trend of decline in heritability during the selection and a rise in non-additive genetic variation in the selection lines.

This method of restricted diallel cross will be used in the present thesis to estimate the genetic parameters in the base populations. The diallel cross, also known as the polyallel cross, is essentially a mating scheme in which a sample of individuals is randomly drawn from a population and progeny are produced by mating every male to every female in the sample.



From the analysis of variance of the diallel cross, it is possible to separate out the additive genetic variance contributed by the sire and by the dam (general combining ability) as well as the non-additive genetic variance due to interaction between the sire and dam (specific combining ability). Since the number of possible crosses increases rapidly with the increase in the number of parents, it is obvious that an organism like Drosophila, with a short life span, would not be able to complete the full diallel programme if too many crosses are involved. Consequently, the restricted diallel cross involving two sires and two dams was adopted in this present experiment (Lerner, 1958 p.61). This restricted diallel cross was used by Sheldon (1963) in Drosophila studies and also by Rumball (1966) for heritability estimates of pupa weight of Tribolium. It should be noted that the use of the diallel cross to gain information about the genetic parameters of a population is based on the following assumptions (Griffing, 1956; Kempthorne, 1957): (a) The sample of individuals to be used for the cross is drawn at random; (b) The base population is randomly mated and at equilibrium; (c) Normal diploid segregation occurs and (d) Linkage is absent.

In addition to the analysis of variance of the diallel cross, the data could also be used to allow independent estimates of heritability by the parent-offspring regression analysis. The different methods of estimation are subjected to different amounts and kinds of bias. Sheridan et al. (1968) has given a summary of the variance components to be expected in the heritability estimates obtained from the regression analysis and the diallel analysis. This is repeated in Table 3 for ease of reference.

Comparison of the different heritability estimates provides a simple way of evaluating the importance of sex-linked effects and additive x additive epistatic variance. The analysis of the diallel cross also permits the interaction between sire and dam to be estimated and this term

**Table 3: Expected composition of the heritability estimates derived from the parent-offspring regression analysis and the diallel analysis**

| Estimate                                                                                                                                                                    | Genetic Component |               |          |               |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------|---------------|----------|---------------|
|                                                                                                                                                                             | $V_A$             | $V_{AA}$      | $V_{AS}$ | $V_D$         |
| Sire-son                                                                                                                                                                    | 1                 | $\frac{1}{2}$ |          |               |
| Sire-daughter                                                                                                                                                               | 1                 | $\frac{1}{2}$ | 1        |               |
| Dam-son                                                                                                                                                                     | 1                 | $\frac{1}{2}$ | 1        |               |
| Dam-daughter                                                                                                                                                                | 1                 | $\frac{1}{2}$ | 1        |               |
| Paternal half brother                                                                                                                                                       | 1                 | $\frac{1}{4}$ |          |               |
| Paternal half sister                                                                                                                                                        | 1                 | $\frac{1}{4}$ | 2        |               |
| Maternal half brother                                                                                                                                                       | 1                 | $\frac{1}{4}$ | 2        |               |
| Maternal half sister                                                                                                                                                        | 1                 | $\frac{1}{4}$ | 1        |               |
| Sire x Dam interaction ( $\varnothing$ progeny)                                                                                                                             |                   | $\frac{1}{8}$ |          | $\frac{1}{4}$ |
| Sire x Dam interaction ( $\sigma$ progeny)                                                                                                                                  |                   | $\frac{1}{8}$ |          | $\frac{1}{4}$ |
| $V_A$ = additive autosomal variance<br>$V_{AA}$ = additive x additive autosomal variance<br>$V_{AS}$ = additive sex-linked variance<br>$V_D$ = autosomal dominance variance |                   |               |          |               |

( $\sigma_I^2$ ) includes one-quarter of the dominance variance,  $\frac{1}{8}$ th of the additive x additive epistatic variance and smaller fractions of higher order epistatic variance.

## B. MATERIALS AND METHODS

To produce the flies needed for the diallel cross, 15 culture bottles with five pairs of parents in each, were set up. Sufficient male and virgin female progeny emerging from these cultures were collected. The method of restricted diallel cross adopted is very simple and involves two sires and two dams per block mating. The block matings were replicated as often as possible. A simple diagram given by Lerner (1958) shows the mating scheme within each block.

| Sire<br>Dam | A | B |
|-------------|---|---|
| a           |   |   |
| b           |   |   |

— each cell represents a single cross

The timing procedure for this diallel cross given by Sheldon (1963) was used. The diallel programme can be divided into the first mating and the second mating. Referring to the diagram given above, for the first mating sire A is mated to dam a and similarly sire B to dam b. For the second mating, sire A is mated to dam b and sire B to dam a. Sheldon reported that there must be a period of at least one week between the first and second mating, to ensure that the progeny from the second matings were indeed sired by the second male introduced to each of the females.

All the matings of the diallel cross were made in quarter-pint bottles which were the same as those used during the selection experiment. Before making the crosses, the sires and dams were scored for bristle number to furnish part of the data needed for the parent-offspring

regression analysis. As many paired matings as possible were set up and it was found that the main limiting factor was the lack of available space in the incubator. The parents of the first matings were left together for two days, after which the males were removed and stored separately in 3" by 1" storage vials, leaving the females in the culture bottles. Six days after removal of the sires, the second matings were set up in fresh culture bottles. The parents were left in the bottles for four days and then discarded. From each single cross five male and five female progeny were scored.

For a block mating to be successfully completed, all four matings within each block had to give a quota of five male and five female offsprings for scoring. The failure of some of the crosses could be due to one of the following causes; death of one of the four parents before the full diallel programme was completed (often the death was accidental with the fly being trapped on the moist food surface or in cracks in the food medium), sterility of either the male or female parent and lastly low fecundity of the females, where insufficient progeny were produced for scoring. From observations of the single pair matings, differences between the reproductive fitness of the Oregon-R and the +3 strains were noted. Of the 75 block matings set up for the Oregon-R, only 31 blocks were successfully completed giving a failure rate of about 60%. For the +3 base population, of the 75 block matings, 45 blocks yielded complete data so that the failure rate was 40%. The failure of the single crosses in the +3 stock was due almost entirely to death of one or more of the parents (accidentally or otherwise) and rarely to sterility or low fecundity. The incidence of sterility and low reproductivity was higher for the Oregon-R stock. From these observations, it would appear that the +3 strain had higher reproductive fitness than the Oregon-R strain. This

suspicion was partly confirmed from observations of the Oregon-R and +3 selection lines, where several of the Oregon-R selection replicates at various times were nearly threatened with extinction due to low viability and sterility, while the +3 selection replicates were almost completely free from such problems.

## C. RESULTS

The parent-offspring regression analysis used data from the completed first matings of the diallel cross. The diallel analysis employed data from the block matings whose first and second matings were successfully completed, giving the number of progeny required for scoring. The Oregon-R analysis had fewer degrees of freedom due to a higher incidence of failure of single crosses, so that their estimates would be subjected to greater sampling error than the +3 heritability estimates.

1. Oregon-R base population(i) Parent-offspring regression analysis

The heritability values and standard errors were obtained using the standard formulae given by Becker (1964). The results given below are based on 92 single pair matings, with five male and five female offsprings scored for abdominal bristles from each mating.

Table 4: Parent-offspring regression estimates of heritability for abdominal bristle number in the Oregon-R base population

| <u>Heritability estimate</u> |   |      |            |
|------------------------------|---|------|------------|
| Sire-son                     | : | 0.34 | $\pm$ 0.10 |
| Dam-son                      | : | 0.42 | $\pm$ 0.13 |
| Sire-daughter                | : | 0.45 | $\pm$ 0.14 |
| Dam-daughter                 | : | 0.40 | $\pm$ 0.11 |
| Average                      | : | 0.40 |            |

The dam-son and sire-daughter regression estimates of heritability were corrected for inequality of male and female phenotypic variances by multiplying the former by the ratio of standard deviation of abdominal bristles in the females to that in the males and by multiplying the latter by the ratio of the male standard deviation to the female standard deviation (Clayton et al, 1957). The importance of sex-linked effects can be evaluated by comparing the sire-son regression heritability estimate, which is free of sex-linked effects, with the other regression estimates. Examination of the results in Table 4 shows that the sire-son regression estimate is smaller than the other three heritability estimates, thus indicating the prevalence of sex-linked additive variance. However, the reliability of this conclusion is marred by the high sampling errors of the heritability estimates.

(ii) Diallel analysis

The main advantage of this method of estimation is that not only the additive genetic variance can be evaluated but also the non-additive variance, due to interaction between sire and dam. The ratio of the interaction variance over the total phenotypic variance ( $\sigma_I^2 / \sigma_P^2$ ) could give an indication of the size of non-additive genetic effects. The results of the diallel analysis are summarised in Table 5.

The heritability estimates from the diallel cross are obtained by multiplying the intraclass correlations by four and this means that the sampling errors are similarly multiplied by four. This could have accounted for the large sampling errors, as well as the discrepancies between the four heritability estimates. The paternal half-brother heritability value is lower than the paternal half-sister as well as the maternal half-brother. This could be taken as an indication of sex-linked effects. Both additive x additive epistatic variance and dominance

Table 5: Analysis of variance of the diallel cross in the Oregon-R base population

| Source of variation                                                                                                                                                                                                                                                    | df        | Components of mean square                 | df  | Mean Square                                           |                                                                                   |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------|-------------------------------------------|-----|-------------------------------------------------------|-----------------------------------------------------------------------------------|
|                                                                                                                                                                                                                                                                        |           |                                           |     | Females                                               | Males                                                                             |
| Between sires within blocks                                                                                                                                                                                                                                            | k         | $\sigma_W^2 + 5\sigma_I^2 + 10\sigma_S^2$ | 31  | 11.92                                                 | 9.10                                                                              |
| Between dams within blocks                                                                                                                                                                                                                                             | k         | $\sigma_W^2 + 5\sigma_I^2 + 10\sigma_D^2$ | 31  | 10.65                                                 | 11.68                                                                             |
| Sire x dam interaction                                                                                                                                                                                                                                                 | k         | $\sigma_W^2 + 5\sigma_I^2$                | 31  | 8.95                                                  | 4.37                                                                              |
| Residual                                                                                                                                                                                                                                                               | $4(n-k)k$ | $\sigma_W^2$                              | 496 | 7.12                                                  | 5.72                                                                              |
| $h_S^2 = \frac{4\sigma_S^2}{\sigma_W^2 + \sigma_I^2 + \sigma_D^2 + \sigma_S^2}$ $h_D^2 = \frac{4\sigma_D^2}{\sigma_W^2 + \sigma_I^2 + \sigma_D^2 + \sigma_S^2}$ $\frac{\sigma_I^2}{\sigma_P^2} = \frac{\sigma_I^2}{\sigma_W^2 + \sigma_I^2 + \sigma_D^2 + \sigma_S^2}$ |           |                                           |     | $h_S^2$<br>$h_D^2$<br>$\frac{\sigma_I^2}{\sigma_P^2}$ | $0.32 \pm 0.12$ $0.27 \pm 0.12$<br>$0.16 \pm 0.10$ $0.42 \pm 0.13$<br>0.04   0.00 |

appeared to be insignificant in the Oregon-R base population, as indicated by the negligible interaction term and also by the sire-son regression heritability estimate being smaller than the paternal half-brother heritability estimate.

The weighted average heritability was found to be  $0.32 \pm 0.11$  and there was some evidence that part of the additive genetic variance was contributed by the sex chromosomes.



## 2. +3 base population

The data from the diallel cross of the +3 base population were analysed in the same way as the Oregon-R population.

### (i) Parent-offspring regression analysis

The results are based on 96 single pair matings with five male and five female offsprings scored from each mating. The heritability estimates are summarised in Table 6.

Table 6: Parent-offspring regression estimates of heritability for abdominal bristle number in the +3 base population

| <u>Heritability estimate</u> |   |      |            |
|------------------------------|---|------|------------|
| Sire-son                     | : | 0.52 | $\pm$ 0.10 |
| Dam-son                      | : | 0.49 | $\pm$ 0.13 |
| Sire-daughter                | : | 0.16 | $\pm$ 0.13 |
| Dam-daughter                 | : | 0.44 | $\pm$ 0.11 |
| Average                      | : | 0.40 |            |

The regression heritability estimates are consistently high except for the sire-daughter estimate. There appears to be no evidence of sex-linked additive effects.

### (ii) Diallel analysis

The results are presented in Table 7. There is greater difference between the four estimates in the +3 population than the Oregon-R population. The negative heritability estimate of  $h_S^2$  from the female progeny should be noted, although the value is not far from zero. Due to large

| Table 7: Analysis of variance of the diallel cross in the +3 base population |     |                  |                 |
|------------------------------------------------------------------------------|-----|------------------|-----------------|
| Source of Variation                                                          | df  | Mean square      |                 |
|                                                                              |     | Females          | Males           |
| Between sires within blocks                                                  | 43  | 10.41            | 10.59           |
| Between dams within blocks                                                   | 43  | 14.96            | 18.55           |
| Sire x dam interaction                                                       | 43  | 11.65            | 5.90            |
| Residual                                                                     | 688 | 6.87             | 5.83            |
| $h^2_S$                                                                      |     | -0.06 $\pm$ 0.05 | 0.24 $\pm$ 0.09 |
| $h^2_D$                                                                      |     | 0.16 $\pm$ 0.08  | 0.66 $\pm$ 0.13 |
| Interaction ( $\sigma_I^2 / \sigma_P^2$ )                                    |     | 0.12             | 0.02            |

statistical sampling errors for the heritabilities, it is expected that some of the estimates would be too high and others too low and so the negative value should be accepted as a valid estimate (Kojima and Kelleher, 1963). The high value of 0.66 for  $h^2_D$  from the male progeny could be better regarded as due to sampling error rather than bias caused by sex-linked effects. The interaction variance component in the +3 base population is slightly higher than in the Oregon-R base population.

All the heritability estimates were averaged to give the overall heritability of the +3 base population and in so doing it is hoped that the errors due to sampling would be cancelled to some extent. The average heritability was found to be  $0.37 \pm 0.11$ . There was no evidence of sex-linked effects in this base population.

## D. DISCUSSION

Sheldon (1963) compared the different components of variation in abdominal bristle number in the Kaduna base population of Clayton et al. (1957) with his own Oregon-R C base population. It would be of interest to extend this comparison to include other base populations. This information could show to some extent how well estimates of heritabilities made in one population extrapolate to others. Table 8 gives the components of phenotypic variance in base populations used by Clayton et al. (1957), Sheldon (1963), Sheridan et al. (1968) and the two original populations utilised in the present selection experiment.

| Table 8: Components of variance for abdominal bristle number in different base populations |                                    |                   |                                     |                             |           |
|--------------------------------------------------------------------------------------------|------------------------------------|-------------------|-------------------------------------|-----------------------------|-----------|
| Source of Variation                                                                        | Clayton<br><u>et al.</u><br>(1957) | Sheldon<br>(1963) | Sheridan<br><u>et al.</u><br>(1968) | Present populations<br>Or-R | +3        |
| Additive genetic                                                                           | 0.52                               | 0.20-0.25         | 0.20-0.25                           | 0.30-0.35                   | 0.35-0.40 |
| Non-additive genetic                                                                       | 0.09                               | 0.00-0.05         | 0.20-0.30                           | 0.00-0.05                   | 0.05-0.10 |
| Developmental error                                                                        | 0.35                               | 0.25              | 0.35-0.55                           | 0.25                        | 0.25      |
| True environmental                                                                         | 0.04                               | 0.45-0.55         | 0.00-0.05                           | 0.30-0.40                   | 0.20-0.30 |

Clayton and Sheridan's stocks were maintained as large cage populations for several years while Sheldon's and the two present populations have been cultured in small containers. From Table 8, it can be seen that the Oregon-R, +3 and Sheldon's Oregon-R C stocks are fairly comparable, with

the two present base populations bearing greatest similarities in their genetic composition. On the other hand, the cage populations utilised by Clayton and Sheridan resembled each other with respect to their large developmental error and the almost negligible true environmental error. The higher environmental variance shown by the "bottle" base populations as opposed to the cage populations could be explained to some extent on the grounds that they are partially inbred populations due to restriction of population size (Kojima and Kelleher, 1963) and consequently show greater environmental variance being less well buffered. Sheldon pointed out that increase in environmental variance should theoretically be accompanied by an increase in variance due to developmental error. However, the developmental errors of the bottle base populations were no greater than that of the cage populations and at present no satisfactory explanation could be found to account for this situation.

There was some evidence of sex-linkage in the Oregon-R population but not in the +3 population. Sex-linked effects have been reported by Sheldon (1963) and also by Sheridan et al. (1968). On the other hand, there was some indication of non-additive genetic variance in the +3 population but none in the Oregon-R population. However, these results are by no means conclusive because of the high sampling errors and the variability of the heritability estimates.

Since the two present foundation stocks have high heritabilities, mass selection based on individual merit should be effective in producing the desired response. In a later section, the estimated heritabilities will be compared with the realised heritabilities and similarly the predicted response with the observed. This would add further evidence to the practical usefulness of the additive prediction theory.

## V.   S E L E C T I O N   E X P E R I M E N T

## V. S E L E C T I O N   E X P E R I M E N T

### A.     M A T E R I A L S   A N D   M E T H O D S

The design of this selection experiment is directly related to the aims of this thesis. The primary objective of this thesis is to make a comparative study of the high and low selection response from three different populations of D. melanogaster. Thus, the experiment aims at supplying data for the detailed analysis of :-

(a) The variability of selection response (including average rate of response, phenotypic variation and realised heritability) between replications within the high and low selection lines of each of the three populations.

(b) The variability of selection response between the three populations for each direction of selection and also between the high and low selection responses of each population.

To achieve the above aims, the experimental design needs to incorporate two important features; high replications within each selection line and an appropriate control for each population.

#### 1.     Replications

In brief, the experiment consisted of two-directional selection carried out simultaneously on the Oregon-R, +3 and Cross base populations as well as the maintenance of unselected controls. Each selection line is replicated. Initially, the total size of the experiment needed to be

determined and this was dictated mainly by the time and labour involved in the collection of virgin flies and scoring of the abdominal bristles. A simple trial was carried out to gauge roughly how many individuals could be scored a day, so that if a period of say three to four days was allowed for counting in each generation, the total size of the experiment could be assessed approximately.

The primary aim of this investigation is to study the variability of response between replicates within selection lines. The preliminary information needed here is the approximate number of animals required for each replication in order to detect differences between replicate means within each generation. The formula used for estimating the order of size of each replicate is given in Sokal and Rohlf (1969, p.247).

$$n = 2 \left( \frac{\sigma}{\delta} \right)^2 (t_1 + t_2)^2$$

where  $n$  = number of animals required per replication

$\sigma$  = true standard deviation (expressed as percentage of the mean)

$\delta$  = true percentage difference it is desired to detect

$\alpha$  = significance level

$P$  = probability of getting significant result

$t_1$  and  $t_2$  = values from 2-tailed t-table with  $\infty$  degrees of freedom and corresponding to probabilities of  $\alpha$  and  $2(1-P)$ , respectively

Assuming  $n$  to be large, the degrees of freedom needed for  $t_1$  and  $t_2$  are set at infinity. In order to detect 5% differences between replicates at the 5% level of significance with 90% probability of getting significant result,  $\delta$  has the value of 5% and  $P = 0.90$ .  $\sigma$  which is the coefficient of variation is about 8%. The values of  $t_1$  and  $t_2$  are found to be 1.96 and 1.28 respectively. The substitution of all these

values in the equation gave the solution of 53 individuals for each replicate. Since the two sexes have different means and variances, their data are always presented and analysed separately so that the value  $n$  applies to a single sex at a time.

After careful considerations of the various factors, the following experimental design was decided on. Four replicates were carried for each high and low selection line of the three populations. From each replication, 45 males and females were scored each generation and the nine most extreme pairs were selected to be parents of the next generation. Higher replications within each selection line would have been desirable. However, in the present instance where the total size of the experiment is limited, an increase in replication number could only be achieved by decreasing the number sampled and selected within each replicate in order to retain a 20% selection intensity. The author considers this to be unwise since too small a population size would be affected by large sampling vagaries, resulting in exaggerated differences between replicates (De Fries and Touchberry, 1961). Besides, the higher inbreeding rate in smaller populations could cause serious problems of decline in fitness and often even loss of some of the replicates before the selection programme was completed (Marien, 1958).

## 2. Control

Since interest in this thesis includes comparison of selection responses between the different populations and between different generations, controls are needed to evaluate the true genetic response. Such controls are based on the principle that the selection line and its control population are similar in genetic make-up and react in much the same way to changes in the environment. Under this condition, subtracting



the mean of the control population from the mean of the selection line would be expected to give an unbiased estimate of the genetic response of the selected line. Bray et al. (1962) have pointed out that since the basic effect of selection is to change the array of gene frequencies of the population, the selection line tends to deviate from the control in its genetic content and this could cause bias in the correction for environmental effects because of genotype-environment interactions. However, in short-term selection experiments, it is likely that such interactions would be negligible (Richardson and Kojima, 1968).

Bray (1966) has given a definition for an ideal control population: "... one in which no change in gene frequency or genotypic frequency occurs from generation to generation and which is genetically related to the lines under treatment." This means that under constant environmental conditions, the mean and genetic parameters remain unchanged from generation to generation and in theory this could only be achieved in a population of infinite size. In practical situations, all control populations are restricted in size and so would be subject to influences such as genetic drift or natural selection (Gowe, Robertson and Latter, 1959). Robinson and Bray (1965) worked out the theoretical consequences of the effects of two restrictions - equal family size and no sib-mating - in populations of different sizes, in reducing the variability due to genetic drift. Bray (1961, 1965) investigated this experimentally and reported that both the theoretical and experimental results indicated that restriction against unequal family size was a much more powerful tool in helping to maintain a genetically stable control population than restriction against inbreeding.

With regard to the choice of suitable control for this present experiment, since selection responses from three different populations

are to be studied, a single control for all three populations would not suffice. It is necessary therefore to have an Oregon-R control for the Oregon-R high and low selection lines, and similarly +3 and Cross controls for their respective populations. The type of control decided on for each population is a randomly mated, unselected line with 30 pairs of parents maintained in each generation. Although it is desirable to maintain controls of larger sizes and with restrictions imposed to reduce genetic drift, the lack of facilities and the pressure of work from the selection experiment itself made this impossible. To help to minimise the rate of inbreeding in each population, six bottles were set up per control with five pairs of parents in each bottle. Each bottle contributed equally to the parents of the next generation. One hundred females and 100 males, equally sampled from the six bottles within a control, were scored each generation.

This control, though simple, was considered to be adequate for the present short-term selection experiment utilising a highly heritable trait which is not expected to be greatly affected by inbreeding depression or fluctuations in the environment. However, more elaborate controls would be needed for long-term selection experiments or for selection using fitness traits which are sensitive to minor fluctuations in the environment.

### 3. Selection procedure

To initiate the selection experiment, 20 cultures in quarter-pint cream bottles were set up simultaneously for each of the three populations (Oregon-R, +3 and  $F_3$  of the Cross). When the progeny started to emerge, collections were made twice daily, more or less equally from the 20 bottles of each population, to ensure virginity of the females. These

progeny served as the base for the selection lines as well as for the controls. When sufficient numbers of progeny were collected, eight samples, each of 45 males and 45 females, were drawn from each base population to form the four replicates of the high selection line and low selection line of that population. The flies in each replicate were scored for abdominal bristles and the nine pairs with the highest (or lowest) bristle numbers were selected to be parents of the next generation. Throughout the selection experiment, three bottles, each with three pairs of selected parents, were set up for each replicate. The controls were set up at the same time by taking a random sample of 30 pairs of flies from each base population and assigning the flies at random into six bottles with five pairs in each bottle. The parents were left in the bottles for 4-5 days and then discarded, but those in the control bottles were removed after the third day to prevent too many eggs from being laid. The progeny emerging formed the first selection generation (G1).

A quota of 15 males and 15 virgin females were collected from each bottle and the males and females were stored separately in small food vials until ready for counting and selection. From the 15 pairs of flies scored per bottle, the three extreme pairs were selected and stored. The next three extreme pairs were kept as reserves in case one of the parents died before mating. If a bottle failed to produce the full quota of flies, it was supplemented with extra flies from the other two bottles of the same replicate. In this way, the size of the replicates was kept constant from generation to generation. This method of within bottle mass selection has the advantage of minimising inbreeding rate within a replicate, although it does mean that the selection differential and consequently the response is lower. It took at least five days to

complete scoring the flies of the six selection lines. Matings of all the lines were made on the same day. The selected flies from the three bottles in each replicate were pooled and randomly divided into three groups and set up in three culture bottles.

For each control population 100 females and 100 males, equally sampled from the six bottles, were counted and 30 pairs were selected at random to serve as parents for the next generation.

The plan of the experiment as well as the code designation for each selection replication and control are summarised in Table 9.

| Table 9: Experimental plan and its code designations<br>(Identification code: H, high selection; L, low selection;<br>C, Control; I, II, III, IV; Replication one to four respectively) |                |             |         |          |         |         |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------|-------------|---------|----------|---------|---------|
| Base population                                                                                                                                                                         | Selection line | Replication |         |          |         | Control |
|                                                                                                                                                                                         |                | I           | II      | III      | IV      |         |
| Oregon-R (Or-R)                                                                                                                                                                         | High selection | Or-RHI      | Or-RHII | Or-RHIII | Or-RHIV | COr-R   |
|                                                                                                                                                                                         | Low selection  | Or-RLI      | Or-RLII | Or-RLIII | Or-RLIV |         |
| +3                                                                                                                                                                                      | High selection | +3HI        | +3HII   | +3HIII   | +3HIV   | C+3     |
|                                                                                                                                                                                         | Low selection  | +3LI        | +3LII   | +3LIII   | +3LIV   |         |
| Cross (X)                                                                                                                                                                               | High selection | XHI         | XHII    | XHIII    | XHIV    | CX      |
|                                                                                                                                                                                         | Low selection  | XLI         | XLII    | XLIII    | XLIV    |         |

The generation interval for Sheldon's (1963) selection experiment was two weeks, whereas the average generation interval for this present experiment was three weeks. The extra week was needed for collecting the full quota of flies from each bottle as well as for scoring the larger number of flies each generation.

## B. SELECTION RESULTS

### 1. General observations

The three populations, Oregon-R, +3 and Cross, were selected for fourteen generations and this phase of the experiment lasted for about eleven months. At the end of the selection programme, all the replicates were relaxed for nine generations. The behaviour of the selection lines on relaxation would provide evidence of the magnitude of the forces of natural selection opposing artificial selection. A few problems arose during the selection experiment. In the first generation, the parents of the controls were inadvertently left too long in the bottles and this resulted in the cultures becoming far too crowded. The Oregon-R and the +3 controls consequently suffered from high mortality of the larvae and delayed emergence of the imago. The progeny were smaller in size and had depressed bristle scores. The Cross control, though subjected to similar overcrowding, did not show the same ill effects and this ability to withstand adverse conditions was probably due to its hybrid vigor.

During the eighth and eleventh selection generation, fluctuations of the temperature in the incubator occurred due to the break-down of the thermostat. This could have possible effects on bristle score (Rasmuson, 1952; Reeve and F.W. Robertson, 1954).

The major difficulty encountered in this experiment was the decline in viability and fertility of the low selection lines after a few generations of selection. The high lines were relatively free from such fitness problems. Invariably it took longer to collect the full quota of males and females required for scoring from each of the low replicates and consequently, the high selection lines were scored before the low lines but all the matings were made on the same day. This differential

reproductive fitness of the high and low selection lines has also been reported by other workers (Mather and Harrison, 1949; Clayton et al., 1957; Latter and Robertson, 1962).

At various times, the mutant "hairy", where the wings of the flies were slightly crumpled and had tiny hairs, appeared in the +3 controls as well as in some of the +3 high and low selection replicates. This mutant apparently has no effect on abdominal bristles (Bridges and Brehme, 1944) but it was deliberately selected out of the +3 population so as not to complicate matters.

## 2. Presentation of basic data

Since the means and variances of abdominal bristle number of the males and females are distinctly different, the data for the two sexes are presented and analysed separately. This separate treatment has the added advantage of allowing any differential responses of the two sexes to be evaluated.

The problem of choice of a suitable scale for biometric analysis has already been treated in fair detail by a number of workers. Rasmuson (1952) was the only one so far to use logarithmic transformations on her data on selection for bristle numbers. Her main purpose was to remove scale effects and she subsequently utilised the transformed data to carry out analysis of variance involving different sexes as well as different types of bristles (sternopleural and abdominal bristles). Other workers who have discussed the problem and applied scaling tests found strong evidence favouring the arithmetic scale (Cavalli, 1952; Reeve and F.W. Robertson, 1954; Clayton et al., 1957; Sheldon, 1963). In view of this, no transformation was made on the data from the present experiment.

(1) Response of mean bristle number

The interest of the experimenter or breeder is naturally focussed first of all on the changes in the population means as a result of selection. The mean abdominal bristle number of each replicate and control for each generation is given in Tables 10a and 10b. Figures 1 (a) - 1 (e) show the changes of the means of each replication of the Oregon-R, +3 and Cross populations over the fourteen generations of selection and the subsequent nine generations of suspended selection. In each figure, the means of the appropriate control are also incorporated. These graphs show readily the trends of changes as well as any anomalies in them. Before discussing the changes in the mean of each population, it is worthwhile to examine whether the two setbacks, over-crowding and fluctuations in temperature, which occurred during G1, G8 and G11 had affected the population means.

The means of the Oregon-R and +3 controls of G1 were about two bristles lower than their base population means and this was undoubtedly due to over-crowding of the cultures. In the following generation, when care was taken to remove the parents before excess eggs were laid, the +3 and Oregon-R means returned immediately to their original levels. The Cross control, which was observed to be unaffected by over-crowding, showed no decline in means. Clearly, to use the +3 and Oregon-R control means to evaluate the actual responses in G1 would result in considerable bias, with the high selection response being over-estimated and the low response under-estimated. It was decided that at least for this generation, the control means would not be used. Instead, the response of G1 would be obtained by averaging the divergence between the high and low selection lines.

Table 10(a): Mean abdominal bristle number of individual selection replicates and controls  
(female data)

| Rep      | High selection |       |       |       |       | Low selection |       |       |       |       | Control |       |
|----------|----------------|-------|-------|-------|-------|---------------|-------|-------|-------|-------|---------|-------|
|          | 1              | 2     | 3     | 4     | mean  | 1             | 2     | 3     | 4     | mean  |         |       |
| OREGON-R |                |       |       |       |       |               |       |       |       |       |         |       |
| Gen 0    | 39.22          | 38.42 | 37.13 | 39.31 | 38.52 | 0             | 39.60 | 37.98 | 38.31 | 38.00 | 38.47   | 38.20 |
| 1        | 38.11          | 39.33 | 39.42 | 39.42 | 39.07 | 1             | 36.91 | 37.38 | 38.09 | 38.40 | 37.70   | 36.87 |
| 2        | 38.71          | 41.58 | 40.42 | 40.64 | 40.34 | 2             | 36.36 | 37.02 | 38.02 | 36.93 | 37.08   | 38.73 |
| 3        | 40.22          | 42.07 | 39.58 | 40.82 | 40.67 | 3             | 34.69 | 37.18 | 36.96 | 37.31 | 36.54   | 38.82 |
| 4        | 40.25          | 40.88 | 39.33 | 39.05 | 39.88 | 4             | 34.05 | 36.42 | 36.28 | 36.18 | 35.73   | 37.68 |
| 5        | 39.75          | 41.98 | 40.10 | 40.42 | 40.56 | 5             | 34.15 | 34.42 | 36.00 | 35.30 | 34.97   | 38.32 |
| 6        | 40.28          | 42.58 | 40.67 | 40.62 | 41.04 | 6             | 34.75 | 33.32 | 35.53 | 35.35 | 34.74   | 38.50 |
| 7        | 40.28          | 42.07 | 39.75 | 40.42 | 40.63 | 7             | 32.68 | 33.63 | 35.05 | 33.87 | 33.81   | 38.03 |
| 8        | 40.95          | 40.68 | 40.00 | 41.53 | 40.79 | 8             | 32.37 | 33.15 | 35.43 | 34.50 | 33.86   | 38.47 |
| 9        | 41.25          | 42.60 | 41.22 | 41.05 | 41.53 | 9             | 31.68 | 33.23 | 34.95 | 34.03 | 33.47   | 37.92 |
| 10       | 40.62          | 41.70 | 41.10 | 41.62 | 41.26 | 10            | 30.03 | 32.70 | 34.37 | 33.42 | 32.63   | 37.76 |
| 11       | 40.88          | 41.90 | 42.52 | 41.70 | 41.75 | 11            | 28.77 | 31.58 | 34.68 | 33.78 | 31.95   | 38.48 |
| 12       | 41.13          | 41.73 | 41.88 | 41.18 | 41.48 | 12            | 27.42 | 31.15 | 33.45 | 32.57 | 31.15   | 38.02 |
| 13       | 41.03          | 41.63 | 41.52 | 41.93 | 41.53 | 13            | 28.25 | 30.40 | 32.48 | 32.38 | 30.88   | 37.96 |
| 14       | 41.29          | 42.73 | 41.64 | 42.20 | 41.97 | 14            | 27.78 | 31.24 | 32.40 | 32.78 | 31.05   | 37.14 |
| +3       |                |       |       |       |       |               |       |       |       |       |         |       |
| Gen 0    | 39.33          | 40.09 | 38.49 | 38.82 | 39.18 | 0             | 39.91 | 40.64 | 39.22 | 40.27 | 40.01   | 38.49 |
| 1        | 39.73          | 41.02 | 40.60 | 39.49 | 40.21 | 1             | 36.98 | 37.73 | 38.24 | 38.87 | 37.96   | 36.30 |
| 2        | 40.87          | 40.73 | 40.58 | 39.98 | 40.54 | 2             | 36.27 | 37.69 | 37.22 | 37.80 | 37.25   | 40.83 |
| 3        | 40.33          | 41.49 | 41.18 | 40.91 | 40.98 | 3             | 36.29 | 37.44 | 36.67 | 37.82 | 37.06   | 39.34 |
| 4        | 40.58          | 42.09 | 40.80 | 41.24 | 41.18 | 4             | 36.29 | 35.22 | 35.40 | 35.69 | 35.65   | 40.34 |
| 5        | 40.87          | 41.29 | 41.42 | 41.84 | 41.36 | 5             | 35.13 | 34.91 | 35.62 | 35.53 | 35.30   | 40.05 |
| 6        | 40.49          | 41.49 | 41.13 | 40.87 | 41.00 | 6             | 34.62 | 34.67 | 34.22 | 34.00 | 34.38   | 39.70 |
| 7        | 40.67          | 40.62 | 40.67 | 40.93 | 40.72 | 7             | 33.68 | 33.58 | 33.78 | 33.44 | 33.62   | 39.36 |
| 8        | 40.58          | 41.33 | 40.20 | 40.96 | 40.77 | 8             | 33.56 | 32.10 | 32.96 | 34.09 | 33.18   | 40.55 |
| 9        | 41.42          | 41.02 | 39.87 | 40.35 | 40.66 | 9             | 32.98 | 31.47 | 32.20 | 33.44 | 32.52   | 40.35 |
| 10       | 39.78          | 40.93 | 40.16 | 40.69 | 40.39 | 10            | 32.75 | 30.72 | 30.73 | 32.90 | 31.76   | 38.60 |
| 11       | 41.00          | 40.96 | 41.40 | 40.98 | 41.09 | 11            | 32.90 | 30.60 | 30.90 | 33.67 | 32.02   | 40.40 |
| 12       | 41.24          | 41.02 | 40.00 | 41.09 | 40.84 | 12            | 32.37 | 29.85 | 29.63 | 33.22 | 31.26   | 40.40 |
| 13       | 41.51          | 40.89 | 40.53 | 40.73 | 40.92 | 13            | 31.92 | 28.37 | 28.88 | 32.70 | 30.47   | 39.46 |
| 14       | 43.27          | 42.36 | 41.91 | 41.96 | 42.38 | 14            | 32.69 | 28.13 | 31.02 | 31.69 | 30.88   | 39.67 |
| CROSS    |                |       |       |       |       |               |       |       |       |       |         |       |
| Gen 0    | 39.89          | 38.80 | 38.60 | 39.80 | 39.27 | 0             | 41.18 | 38.47 | 40.60 | 37.82 | 39.51   | 41.92 |
| 1        | 40.24          | 39.93 | 41.11 | 40.20 | 40.37 | 1             | 37.71 | 36.91 | 37.20 | 35.64 | 36.87   | 39.53 |
| 2        | 42.60          | 41.02 | 42.29 | 42.31 | 42.06 | 2             | 36.20 | 37.22 | 37.11 | 35.38 | 36.48   | 40.61 |
| 3        | 45.33          | 43.67 | 42.51 | 45.13 | 44.16 | 3             | 34.89 | 38.11 | 35.67 | 34.84 | 35.88   | 41.48 |
| 4        | 44.87          | 42.76 | 42.00 | 43.09 | 43.18 | 4             | 33.64 | 35.38 | 33.69 | 33.58 | 34.07   | 40.13 |
| 5        | 45.44          | 44.40 | 42.22 | 45.11 | 44.29 | 5             | 32.47 | 35.16 | 34.29 | 33.25 | 33.79   | 39.84 |
| 6        | 44.89          | 45.62 | 44.51 | 45.98 | 45.25 | 6             | 32.22 | 33.78 | 33.91 | 32.97 | 33.22   | 39.42 |
| 7        | 44.69          | 44.73 | 44.69 | 46.69 | 45.20 | 7             | 31.17 | 33.36 | 33.02 | 32.97 | 32.63   | 39.29 |
| 8        | 45.49          | 47.76 | 45.38 | 47.16 | 46.45 | 8             | 30.85 | 33.93 | 33.23 | 32.17 | 32.55   | 39.76 |
| 9        | 46.16          | 49.25 | 46.20 | 48.62 | 47.55 | 9             | 30.45 | 33.72 | 33.10 | 31.33 | 32.15   | 38.23 |
| 10       | 47.11          | 48.16 | 46.20 | 48.84 | 47.58 | 10            | 29.68 | 31.72 | 31.87 | 30.58 | 30.96   | 37.83 |
| 11       | 49.28          | 50.00 | 47.17 | 48.98 | 48.86 | 11            | 29.03 | 32.38 | 31.88 | 31.05 | 31.09   | 39.11 |
| 12       | 50.58          | 50.28 | 47.71 | 51.22 | 49.95 | 12            | 30.13 | 32.17 | 32.05 | 29.07 | 30.89   | 38.22 |
| 13       | 50.18          | 50.62 | 47.72 | 51.00 | 49.88 | 13            | 28.50 | 30.37 | 31.25 | 27.98 | 29.53   | 37.68 |
| 14       | 51.96          | 51.27 | 49.58 | 52.71 | 51.38 | 14            | 28.44 | 30.87 | 31.24 | 27.69 | 29.56   | 38.30 |



Table 10(b): Mean abdominal bristle number of individual selection replicates and controls  
(male data)

| Rep      | High selection |       |       |       |       |    | Low selection |       |       |       |       | Control |
|----------|----------------|-------|-------|-------|-------|----|---------------|-------|-------|-------|-------|---------|
|          | 1              | 2     | 3     | 4     | mean  |    | 1             | 2     | 3     | 4     | mean  |         |
| OREGON-R |                |       |       |       |       |    |               |       |       |       |       |         |
| Gen 0    | 31.73          | 32.51 | 32.04 | 33.04 | 32.33 | 0  | 32.53         | 32.07 | 33.16 | 32.02 | 32.45 | 31.50   |
| 1        | 32.04          | 33.31 | 32.42 | 33.29 | 32.77 | 1  | 30.31         | 32.98 | 31.00 | 31.64 | 31.48 | 30.43   |
| 2        | 31.96          | 34.40 | 33.07 | 33.64 | 33.27 | 2  | 30.07         | 32.49 | 31.51 | 31.07 | 31.29 | 31.94   |
| 3        | 33.64          | 34.58 | 33.27 | 33.18 | 33.67 | 3  | 29.67         | 31.80 | 30.13 | 30.42 | 30.51 | 31.83   |
| 4        | 33.16          | 33.76 | 32.59 | 33.57 | 33.27 | 4  | 27.56         | 29.78 | 29.80 | 29.30 | 29.11 | 31.37   |
| 5        | 32.85          | 34.32 | 32.98 | 34.22 | 33.59 | 5  | 28.90         | 29.18 | 29.33 | 28.80 | 29.05 | 31.59   |
| 6        | 33.57          | 35.12 | 33.13 | 33.68 | 33.88 | 6  | 28.17         | 28.22 | 28.98 | 29.00 | 28.59 | 31.37   |
| 7        | 32.98          | 35.05 | 33.00 | 33.98 | 33.75 | 7  | 27.70         | 27.65 | 28.78 | 28.40 | 28.13 | 31.19   |
| 8        | 33.10          | 34.37 | 33.65 | 34.42 | 33.89 | 8  | 26.95         | 27.40 | 28.77 | 28.62 | 27.94 | 31.59   |
| 9        | 33.81          | 34.58 | 33.85 | 34.25 | 34.10 | 9  | 26.50         | 26.45 | 27.70 | 28.47 | 27.28 | 31.17   |
| 10       | 33.37          | 33.73 | 33.03 | 34.47 | 33.65 | 10 | 25.85         | 27.45 | 28.18 | 28.02 | 27.37 | 30.81   |
| 11       | 33.78          | 34.83 | 33.91 | 33.77 | 34.07 | 11 | 25.60         | 26.60 | 27.18 | 27.37 | 26.69 | 31.38   |
| 12       | 33.88          | 34.40 | 33.22 | 34.07 | 33.89 | 12 | 24.25         | 26.45 | 27.18 | 27.67 | 26.39 | 30.75   |
| 13       | 34.08          | 34.53 | 33.67 | 33.84 | 34.03 | 13 | 23.23         | 26.05 | 26.85 | 27.55 | 25.92 | 30.94   |
| 14       | 35.24          | 36.33 | 33.97 | 35.11 | 35.16 | 14 | 25.40         | 25.97 | 26.84 | 28.16 | 26.59 | 31.26   |
| +3       |                |       |       |       |       |    |               |       |       |       |       |         |
| Gen 0    | 33.20          | 34.33 | 34.24 | 33.56 | 33.83 | 0  | 31.78         | 32.89 | 33.04 | 33.04 | 32.69 | 33.50   |
| 1        | 33.47          | 34.42 | 34.02 | 33.60 | 33.88 | 1  | 31.06         | 32.22 | 32.07 | 33.27 | 32.16 | 31.94   |
| 2        | 33.98          | 34.71 | 34.82 | 34.47 | 34.50 | 2  | 30.91         | 31.60 | 31.31 | 32.27 | 31.52 | 34.39   |
| 3        | 33.60          | 35.29 | 33.93 | 34.33 | 34.29 | 3  | 29.16         | 30.31 | 30.38 | 30.78 | 30.16 | 33.72   |
| 4        | 33.87          | 34.71 | 34.96 | 34.56 | 34.53 | 4  | 29.20         | 29.40 | 28.31 | 30.76 | 29.42 | 33.73   |
| 5        | 34.53          | 34.53 | 35.04 | 34.71 | 34.70 | 5  | 28.40         | 28.73 | 28.31 | 29.40 | 28.71 | 33.50   |
| 6        | 34.89          | 34.51 | 35.51 | 34.53 | 34.86 | 6  | 27.67         | 28.31 | 28.11 | 29.33 | 28.36 | 33.94   |
| 7        | 33.53          | 34.13 | 34.78 | 34.27 | 34.18 | 7  | 27.22         | 27.58 | 27.67 | 28.40 | 27.72 | 33.90   |
| 8        | 33.80          | 34.09 | 34.47 | 33.78 | 34.04 | 8  | 27.92         | 26.56 | 27.18 | 28.44 | 27.53 | 34.43   |
| 9        | 34.82          | 34.69 | 34.40 | 33.70 | 34.40 | 9  | 27.45         | 25.98 | 26.78 | 27.51 | 26.93 | 33.80   |
| 10       | 33.38          | 34.38 | 35.02 | 34.02 | 34.20 | 10 | 27.12         | 26.33 | 25.50 | 27.87 | 26.71 | 33.60   |
| 11       | 33.75          | 34.24 | 34.50 | 34.27 | 34.19 | 11 | 26.62         | 25.65 | 25.25 | 28.38 | 26.48 | 34.42   |
| 12       | 34.30          | 34.12 | 34.24 | 34.20 | 34.22 | 12 | 26.57         | 26.13 | 25.58 | 27.78 | 26.52 | 34.07   |
| 13       | 35.69          | 34.87 | 35.07 | 34.24 | 34.97 | 13 | 27.00         | 25.98 | 25.45 | 27.53 | 26.49 | 32.91   |
| 14       | 36.42          | 36.49 | 35.73 | 36.31 | 36.24 | 14 | 27.29         | 26.91 | 26.20 | 27.24 | 26.91 | 34.33   |
| GROSS    |                |       |       |       |       |    |               |       |       |       |       |         |
| Gen 0    | 33.22          | 31.56 | 32.42 | 32.98 | 32.55 | 0  | 33.98         | 32.44 | 33.29 | 32.51 | 33.06 | 34.22   |
| 1        | 34.20          | 33.04 | 34.00 | 34.76 | 34.00 | 1  | 30.95         | 31.31 | 31.98 | 29.44 | 30.92 | 32.34   |
| 2        | 36.07          | 34.58 | 35.82 | 36.38 | 35.71 | 2  | 31.42         | 30.58 | 31.31 | 30.42 | 30.93 | 32.90   |
| 3        | 38.07          | 35.60 | 35.60 | 37.44 | 36.68 | 3  | 28.47         | 30.24 | 31.22 | 28.93 | 29.72 | 34.16   |
| 4        | 37.53          | 35.93 | 35.58 | 36.47 | 36.38 | 4  | 27.17         | 28.75 | 29.16 | 28.15 | 28.31 | 33.39   |
| 5        | 37.91          | 37.51 | 35.20 | 37.53 | 37.04 | 5  | 26.30         | 28.23 | 29.42 | 27.73 | 27.92 | 33.47   |
| 6        | 37.91          | 37.69 | 36.07 | 39.56 | 37.82 | 6  | 27.10         | 28.12 | 28.05 | 27.68 | 27.73 | 32.58   |
| 7        | 36.73          | 37.82 | 37.33 | 38.78 | 37.67 | 7  | 25.75         | 27.20 | 27.88 | 27.05 | 26.97 | 32.52   |
| 8        | 38.00          | 39.33 | 37.42 | 39.62 | 38.59 | 8  | 25.38         | 26.73 | 27.90 | 26.43 | 26.61 | 33.35   |
| 9        | 37.96          | 40.64 | 38.49 | 40.84 | 39.48 | 9  | 25.40         | 26.72 | 27.45 | 26.95 | 26.63 | 31.80   |
| 10       | 38.89          | 39.78 | 37.47 | 40.69 | 39.21 | 10 | 24.97         | 25.85 | 26.48 | 25.88 | 25.80 | 32.31   |
| 11       | 40.52          | 40.02 | 38.12 | 41.40 | 40.02 | 11 | 24.43         | 25.41 | 26.03 | 25.47 | 25.34 | 32.34   |
| 12       | 41.85          | 41.53 | 39.47 | 42.58 | 41.36 | 12 | 25.05         | 25.85 | 26.53 | 25.90 | 25.83 | 32.31   |
| 13       | 42.45          | 41.53 | 39.03 | 42.55 | 41.39 | 13 | 24.05         | 25.27 | 26.15 | 24.87 | 25.09 | 31.50   |
| 14       | 42.82          | 42.80 | 40.31 | 44.63 | 42.64 | 14 | 24.42         | 25.76 | 27.31 | 24.98 | 25.62 | 31.90   |

None of the selection lines or controls showed any aberrant trends during G8 and G11 when fluctuations of temperature occurred. In any case if the assumption of the absence of genotype-environment interaction was realised, the control would be able to cater for such shifts in the environment so that the validity of the actual responses obtained would not be affected.

The trends of the upward and downward response of each population will be discussed in detail since the primary aim of this thesis is to study and compare the responses from different base populations.

Oregon-R population: (Figs 1(a) and (b) ). The females and the males show very similar patterns of response to two-directional selection. Selection in the high direction produced poor responses from all four high replicates. Most of the response was obtained in the first three generations of selection, and from G4 to G14 the four replicates continued to give consistent but much weaker response. Divergences between the high replicates started as early as the third selection generation. As a result of generation to generation fluctuations of each replicate, no definite ranking was established among the replicates even after 14 generations of selection. A similar finding of divergence, but randomisation of response among replications, was observed by Frankham, Jones and Barker (1968) for 12 generations of high selection for abdominal bristles in their replicates with population size of ten pairs of parents and selection intensity of 20%. Their experimental set-up was comparable to the present experiment. On the other hand, Clayton et al. (1957) and Sheldon (1963) reported differences between replicates with a definite order being established in the early generations of selection and this was subsequently maintained, with the differences between replicates becoming larger as selection proceeded. Both Clayton and Sheldon used 20 pairs of parents for each replicate and

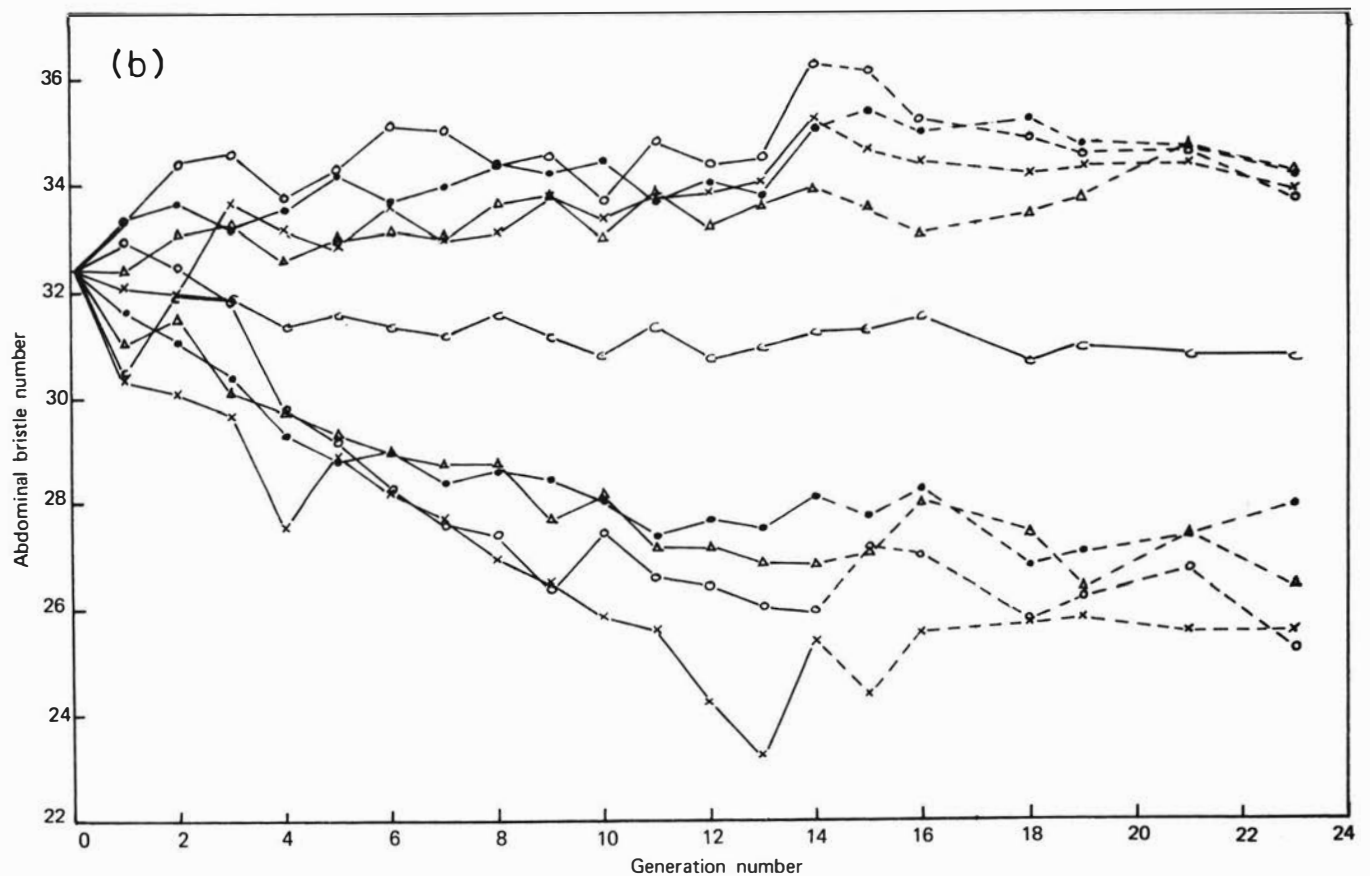
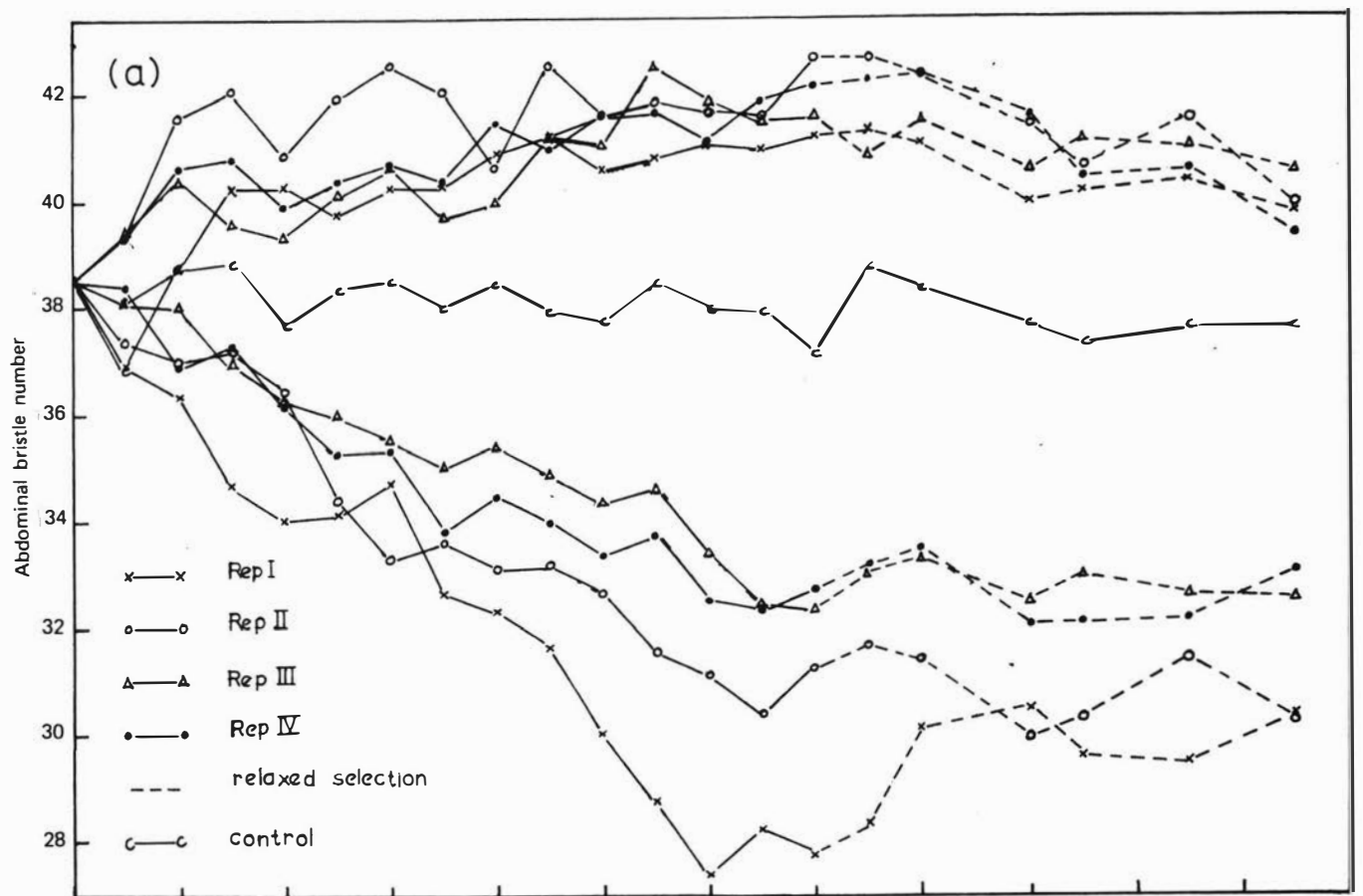


Fig. 1(a) Selection response of the Oregon-R population (female data).

Fig. 1(b) Selection response of the Oregon-R population (male data).

this larger population size could be the reason for the lack of randomness among their replicates. Another deviation from the observations of the above two workers was that the variation between the Oregon-R high replicates tended to become less instead of greater in the later generations of selection (G8 - G14).

The behaviour of the four Oregon-R low replicates was quite different from that of the high replicates and was more in line with the findings of Clayton et al. and Sheldon. From Fig. 1(a) it can be seen that except for the first replicate (Or-RLI), the responses from the other three replicates were in good agreement till G4. From then on, the replicates started to diverge with the differences between them becoming more pronounced as selection progressed. Furthermore, a definite order was established among the four low replicates. The difference between the replicate which gave the greatest and the one which gave the least response, Or-RLI and Or-RLIII respectively, was as much as 5-6 bristles during the last few generations of selection. Unlike the Oregon-R high replicates, the low replicates continued to give steady response till about G12. Then, the response abruptly declined during the last two generations. Since selection was terminated at G14, it was not possible to tell whether the decline in response rate during the last two generations was temporary as a result of some undetected environmental changes or whether it was permanent due to the exhaustion of usable genetic variation. On the whole, the low replicates showed less inter-generation fluctuations than the high replicates. The pattern of two-directional selection response from the Oregon-R population was asymmetrical, with greater response downwards. Latter (1965a) designated this as negative asymmetry and the pattern with greater upward response as positive asymmetry.

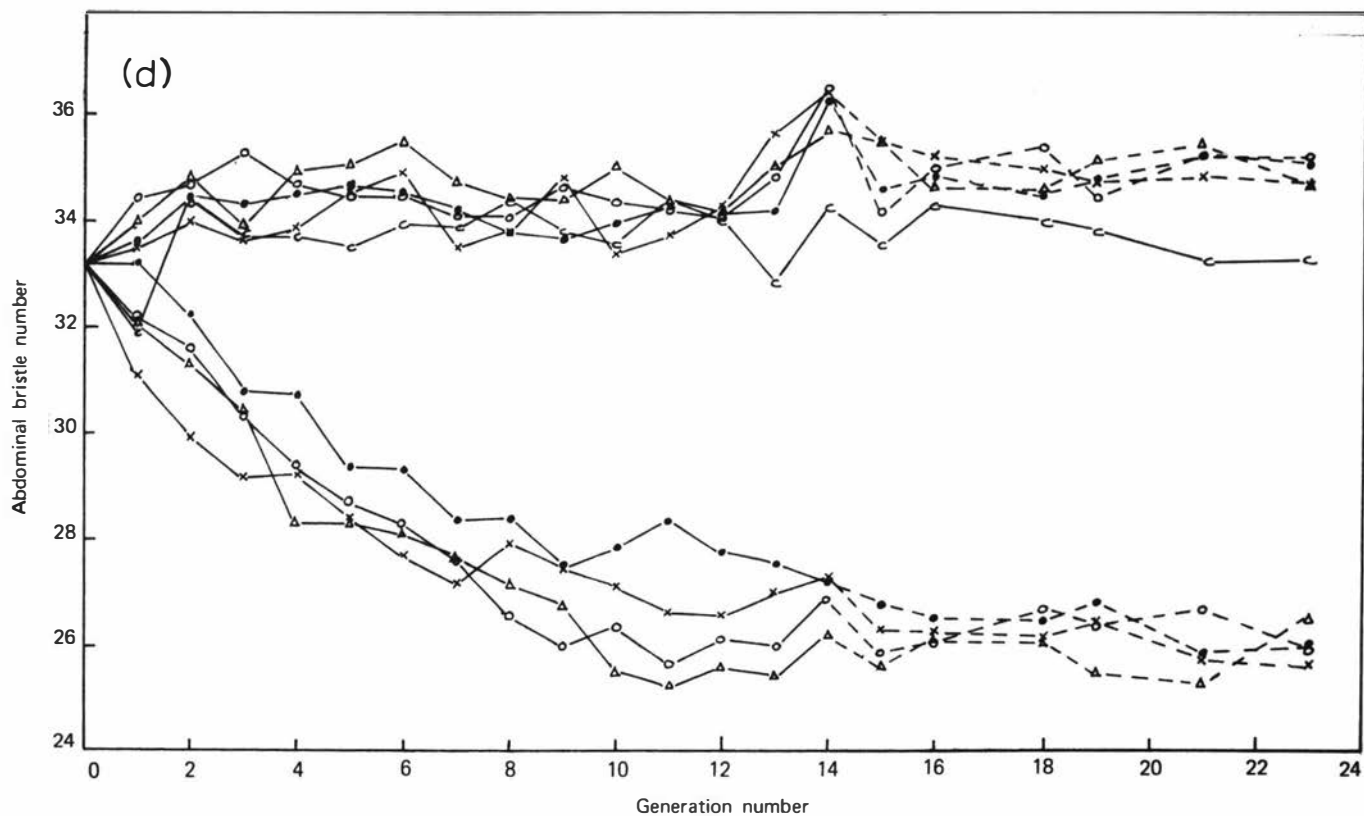
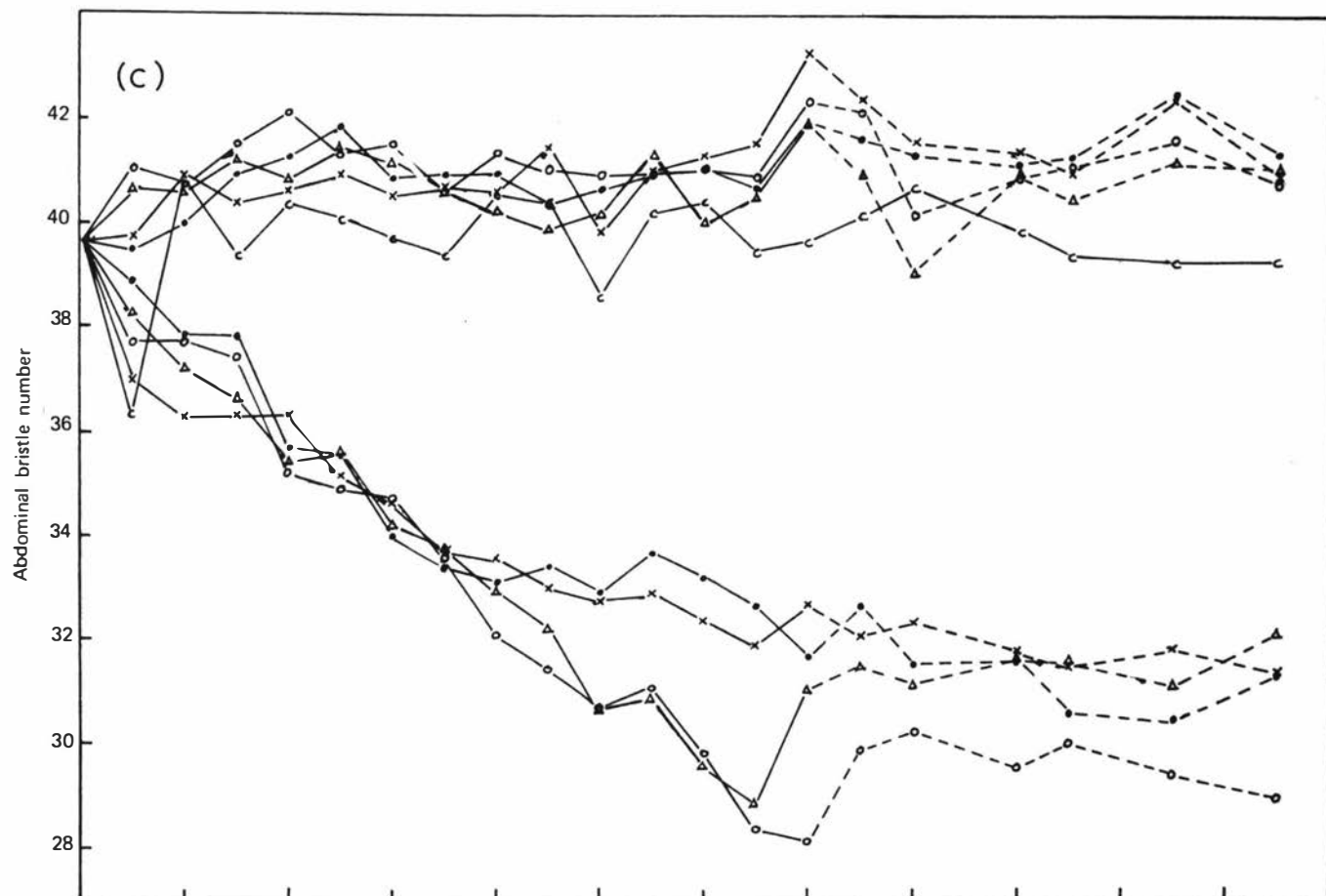


Fig. 1(c) Selection response of the +3 population (female data).

Fig. 1(d) Selection response of the +3 population (male data).

Except for the depressed G1 generation means, due to over-crowded culture conditions, the Oregon-R unselected control means fluctuated around its original base population mean and showed no apparent upward or downward trend over the 14 generations.

+3 population: (Figs 1(c) and (d) ). The striking feature of the two-way response from this population was the strong negative asymmetry. All four high replicates were remarkably resistant to the efforts of selection for high bristle number. What little response obtained occurred almost entirely in the first three generations of selection and from then on selection was virtually without any effect. From G7 - G12 some of the high replicates had means which were lower than that of the unselected +3 control in the corresponding generations. However, the average population mean of the high selection line was 0.5-1.5 bristles above the control means. The high replicates at G14 showed an unexpected rise of about two bristles but this was suspected to be due to environmental effects rather than true genetic response. It is clear that the heritability of about 35% estimated from the +3 base population had poor predictive value, at least for high selection responses.

The +3 low replicates responded reasonably well to selection. The behaviour of the males was a little different from that of the females. For the females, the agreement between the four replicates was good until G7. From then, the first and fourth replicates (+3LI and +3LIV) showed weaker response while the other two replicates continued to respond at the same rate. For the male data, all four replicates showed a similar trend over the 14 selection generations. However, this trend over the 14 generations was not linear but could be divided into a period of fair response (G1-G7) and a later period of poor response (G8-G14). Clayton et al. (1957) and Sheldon (1963) observed that the variation between

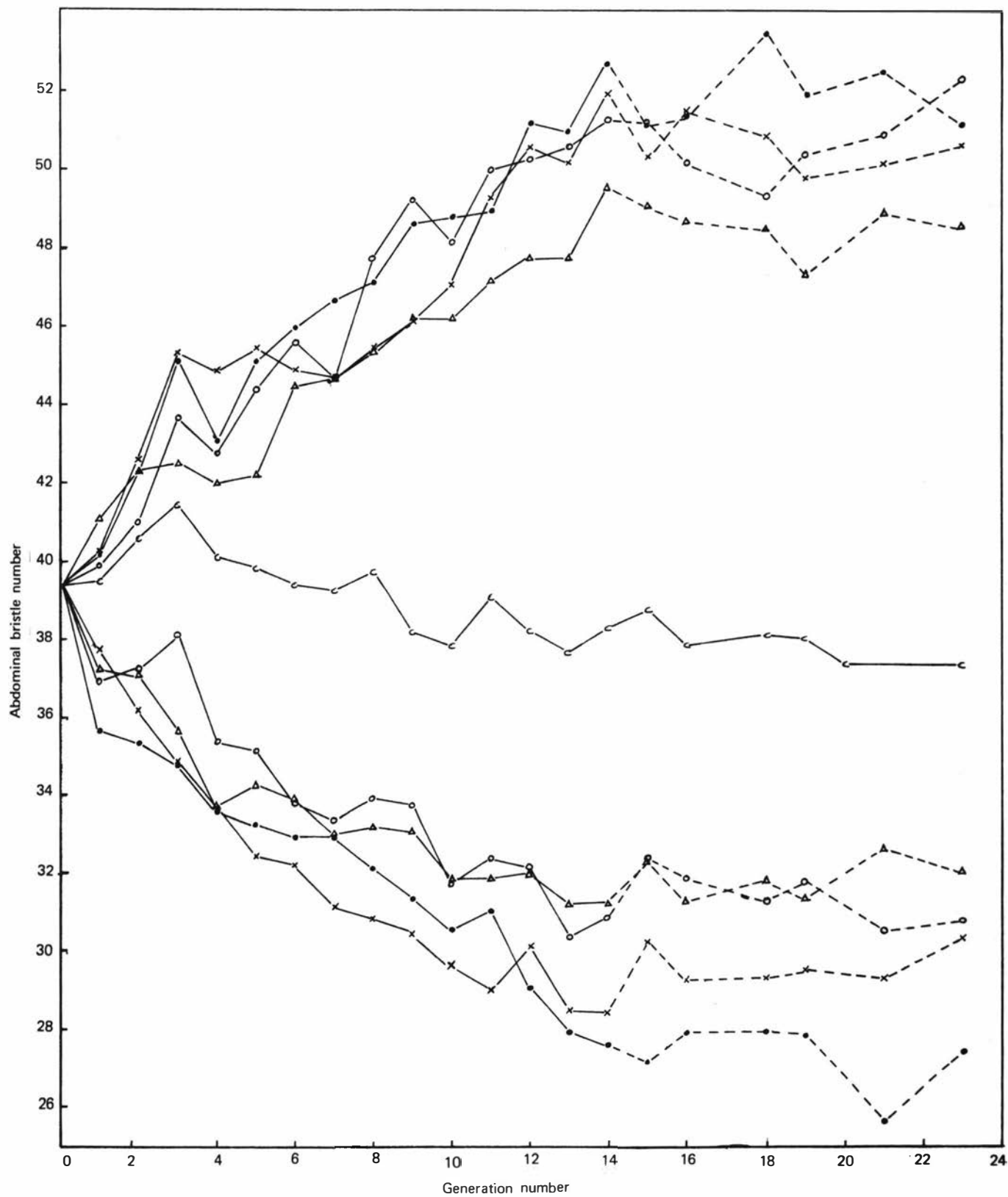


Fig. 1(e) Selection response of the Cross population (female data).

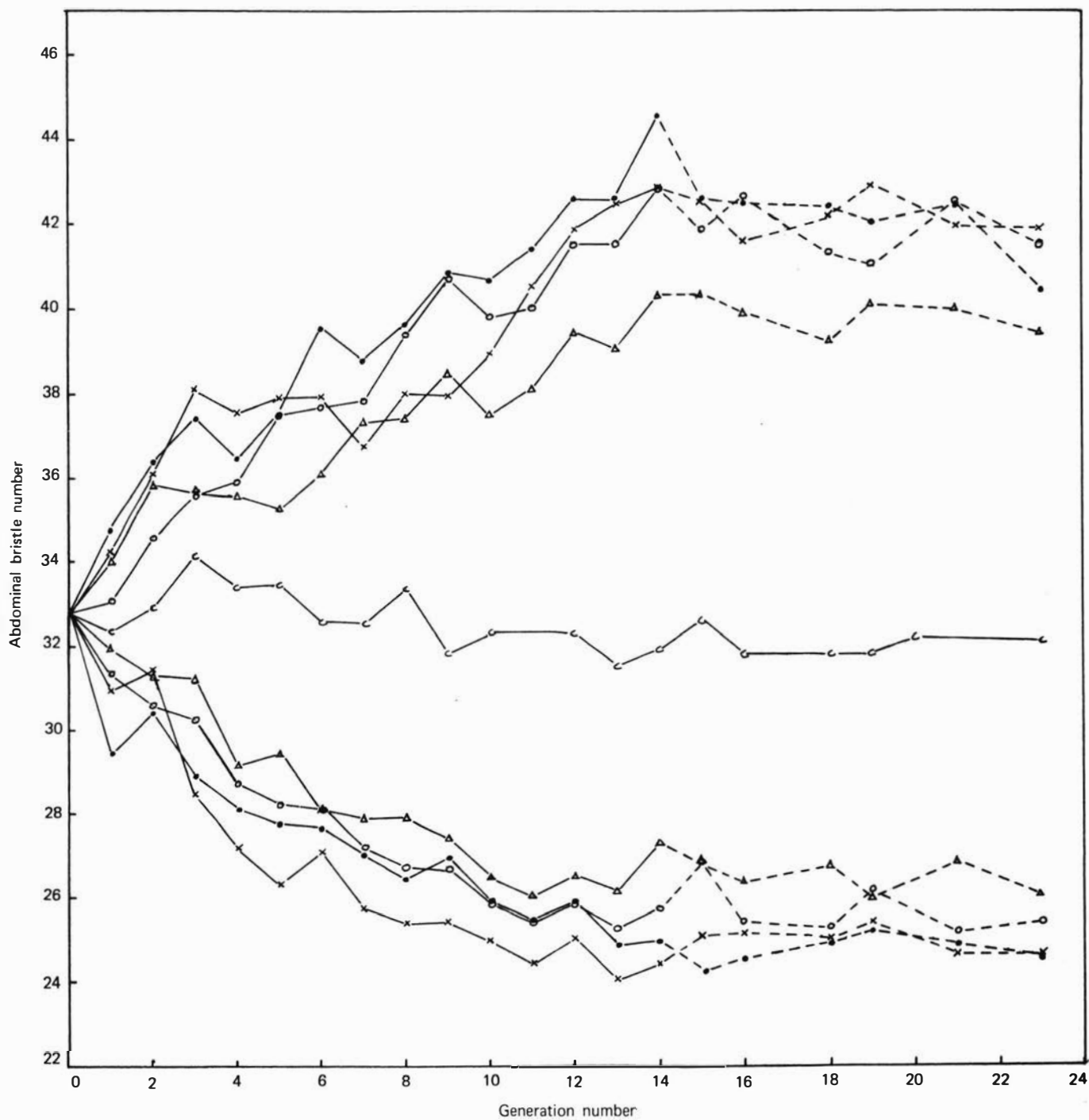


Fig. 1(f) Selection response of the Cross population (male data).



replicates was greater in the high selection line than in the low line. The reverse condition was found in the present +3 high and low lines. The +3 control, like the Oregon-R control, showed no apparent upward or downward trend and except for the lowered means at G1, no anomalies were observed.

Cross population: (Figs 1(e) and (f) ). Although the trend of response from the Cross low selection line was similar to the +3 and Oregon-R low lines, the response from the Cross high line differed markedly from the other two high lines. The response rate was greatest for the Cross high line, poor for the Oregon-R high line and almost zero for the +3 high line. One of the Cross high replicates (XHI) showed the typical "stairway" pattern of response, with a sudden cessation of response from G3 - G7 followed by renewed response. All the other Cross high replicates gave consistent response upwards and showed no signs of declining even at the end of 14 generations of selection. Differences between the four replicates were obvious from G4 and once again due to wide inter-generation fluctuations, no definite order was established between the replicates.

The trend of downward response from the Cross low line was similar to the +3 low line with the first seven generations giving greater response than the later generations. Here again, variation between the replicates was quite obvious, especially for the female data. The average high and low responses from the Cross population at the end of selection measured as deviations from the means of the control were 12 bristles and 9 bristles respectively. Thus, the two-way selection in the Cross population produced positive asymmetrical response.

The Cross control means over the 14 generations appeared to show a slight but definite trend downwards unlike the +3 and Oregon-R control means. It should be noted that the Cross control showed an unexpected

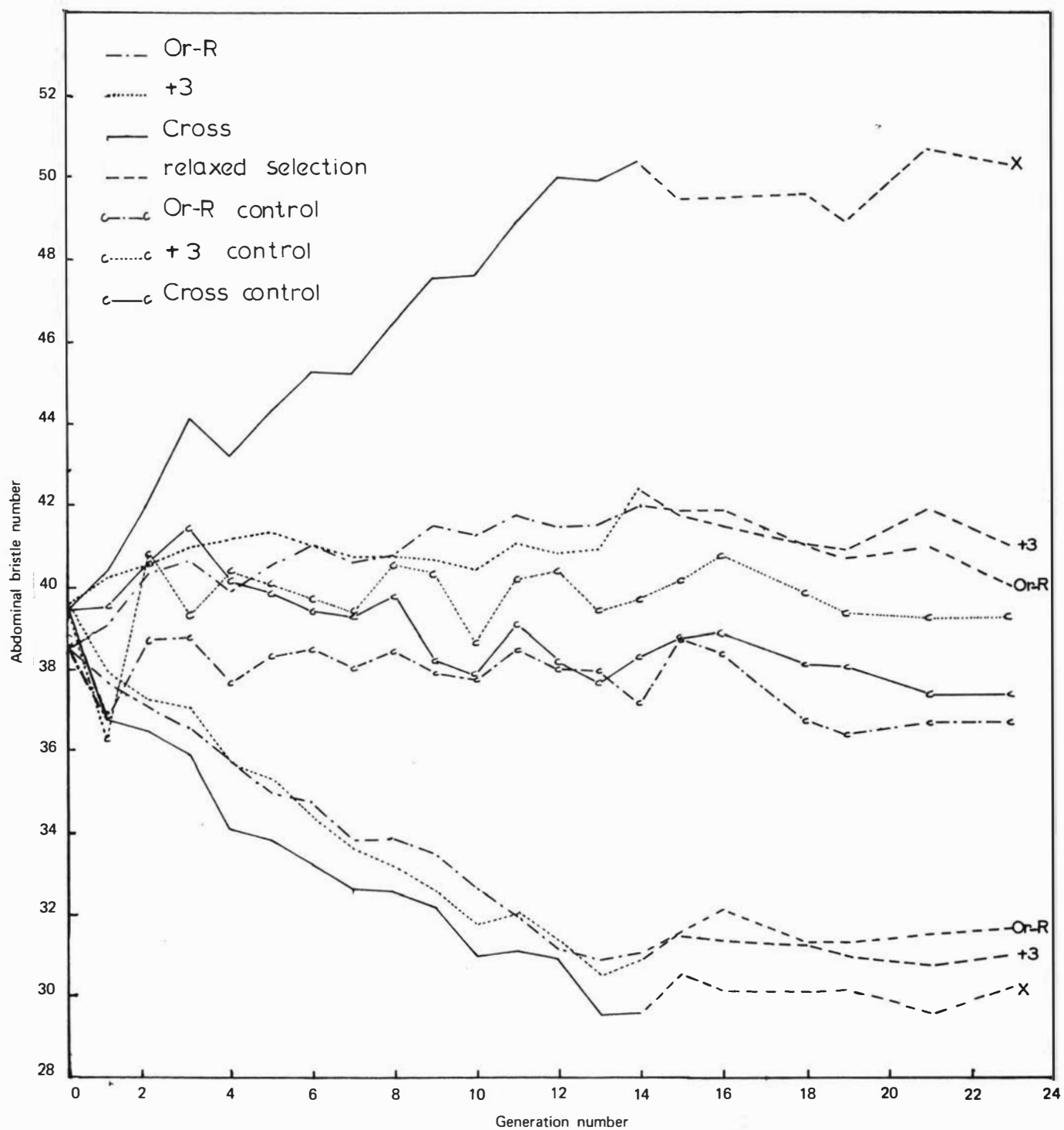


Fig. 1(g) Average selection response of the Oregon-R +3 and Cross populations (female data).

rise of about two bristles at G3 but no apparent reason could be found to account for the increase. From G4 onwards, the control means gradually declined and settled at a level of about two bristles below the original base population mean. In an earlier section on base populations (see Part III C), a small amount of heterosis was noted in the  $F_1$  and  $F_2$  of the Cross, and the slight downward trend observed during the subsequent generations of random inter-breeding could be due to the gradual breakdown of heterosis.

Discussion: Although individual replicates tend to show inter-generation fluctuation, which is no doubt due to causes like sampling or scoring errors as well as environmental variation, the average of four replicates, which gives the mean of a selection line, shows a fairly smooth upward or downward trend (Fig. 1(g)). The downward responses from all three populations showed very similar trends. If the total responses were measured as the deviation of the means of the selection lines from their respective control means at G14, the response from +3 and Cross low lines was about nine bristles while that from the Oregon-R low line was six bristles. Thus, the Cross low selection line contrary to expectations did not show obvious superiority over the low lines of the two parental strains.

The high selection lines unlike the low lines showed obvious differences in trend of response. The +3 high line gave virtually no response and at G14 the total response was two bristles, the total response of the Oregon-R was five bristles and the Cross high line 12 bristles. Thus, the total high response from the Cross was six times that of the +3 and 2.4 times that of the Oregon-R. Mainly because of the differential responses from the high lines, the three populations showed different patterns of two-way response with the +3 population giving strong negative asymmetry, the Oregon-R mild negative asymmetry and the Cross positive asymmetry.

Asymmetry has been observed in all previous selection experiments on abdominal bristles. Mather and Harrison (1949), Clayton et al. (1957) and Latter and A. Robertson (1962) reported greater upward response while Rasmuson (1955) and Sheldon (1963) found the opposite.

The graphs can depict clearly the trend of responses but they are not able to reveal the genetic situation which is responsible for the observed responses. Falconer (1960) has advanced a number of possible causes for asymmetry in two-way selection experiments, such as directional dominance, directional gene frequencies, selection for heterozygotes in one direction, inbreeding depression, maternal effects or difference in selection differentials in the high and low selection lines. In the case of asymmetry found in the Oregon-R, factors like inbreeding depression, directional dominance and maternal effects are not likely to be important (Rasmuson, 1952; Clayton et al., 1957). It was also unlikely that natural selection was opposing artificial selection in the high direction, since the Oregon-R high replicates had less problems with low fertility and viability than the low replicates. Furthermore, during the nine generations of relaxation following the 14 generations of continuous selection, the four Oregon-R high replicates regressed only about one to two bristles towards the unselected control means and this decline was probably due to the break-up of favourable epistatic combinations rather than due to the forces of stabilising natural selection. A possible cause of asymmetry was that selection for high bristles favoured lethal heterozygotes because of their higher fitness or higher bristle score. Lethal tests, to be carried out on some of the replicates at the end of the selection programme, would throw light on the possibility of this situation.

For the +3 population, it is unlikely that the factors pointed out by Falconer are responsible since the asymmetry occurred in the very early

generations of selection. A hypothesis has been put forward by Clarke, Maynard Smith and Sondhi (1961) to explain the marked asymmetrical response observed in selection for fast and slow developmental rate in D. subobscura. It is based on a model of inter-allelic epistatic interaction in that the phenotypic effect of a given gene substitution is dependent on the nature of its genetic background. Asymmetry is produced if the genetic background of a base population acts as a barrier to phenotypic expression in one direction and not in the other. In the context of this present experiment, it means that the +3 has a genetic constitution which inhibits the expression of genes for higher bristles and not for fewer bristles. However, an attempt to explain the asymmetry in the +3 population based on this hypothesis runs into difficulties since the assumption inherent in this model is that the genetic variance is made up largely of epistatic variation, whereas the non-additive genetic variance was estimated to be low in the +3 base population.

In recent years evidence has been accumulating that the genetic variance of a quantitative character may be due largely to the segregation of a few genes with large effects. Spickett and Thoday (1961) made chromosomal analysis of two of Thoday and Boam's (1961) lines selected for high sternopleural bristles. They successfully located three "genes" in one line and five in the other, which accounted for at least 80% of the genetic variation. Further evidence comes from chromosome analysis in wheat conducted by Werhahn and Allard (1965) and Law (1966, 1967). It is possible that the variation of abdominal bristles in the +3 population is largely controlled by very few additive genes with major effects so that once they are fixed in the early generations of selection, subsequent artificial selection applied in the high direction would fail to produce further response. Because of the aberrant behaviour of the +3 high line, the author decided to carry out subsidiary tests at the end of selection,

such as heritability estimation and crosses between +3 high and low lines, in attempt to throw light on the nature of the underlying genetic situation.

The response from the Cross high selection line was definitely superior over the high responses from the two original parent lines, Oregon-R and +3. The simplest explanation for the more rapid responses in the Cross is that different genes for higher bristles are fixed at different loci in the two original populations, so that crossing between the two resulted in an increase in genetic variability within the hybrid population. This greater genetic variability allowed more effective selection.

Reeve and F.W. Robertson (1952) proposed a hypothesis that genes with small effects in their normal genetic background may be transformed into major genes if the genotype has been modified by selection. The same principle could apply in the present case, where crossing between the +3 and Oregon-R strains produced a hybrid population with "different" genetic content than either of its original parental strains so that some genes with minor effects on bristle number may be changed to major genes in their new genetic background. Further evidence for the transformation of a normally minor gene to one with a large effect comes from Fraser (1963) in a selection experiment using D. simulans for decreasing number of bristles. Another hypothesis proposed to account for increases in response is that where genes from two or more populations are pooled together, it is possible that some genes with insignificant or neutral effects on the selected character in their usual background, when combined with other genes, may together exert a large effect and selection would favour the increase in frequency of the gene combinations (Fraser and Hansche, 1965).

In summing up, the hybrid population showed superiority over the two parental populations when selection was for increased abdominal bristles

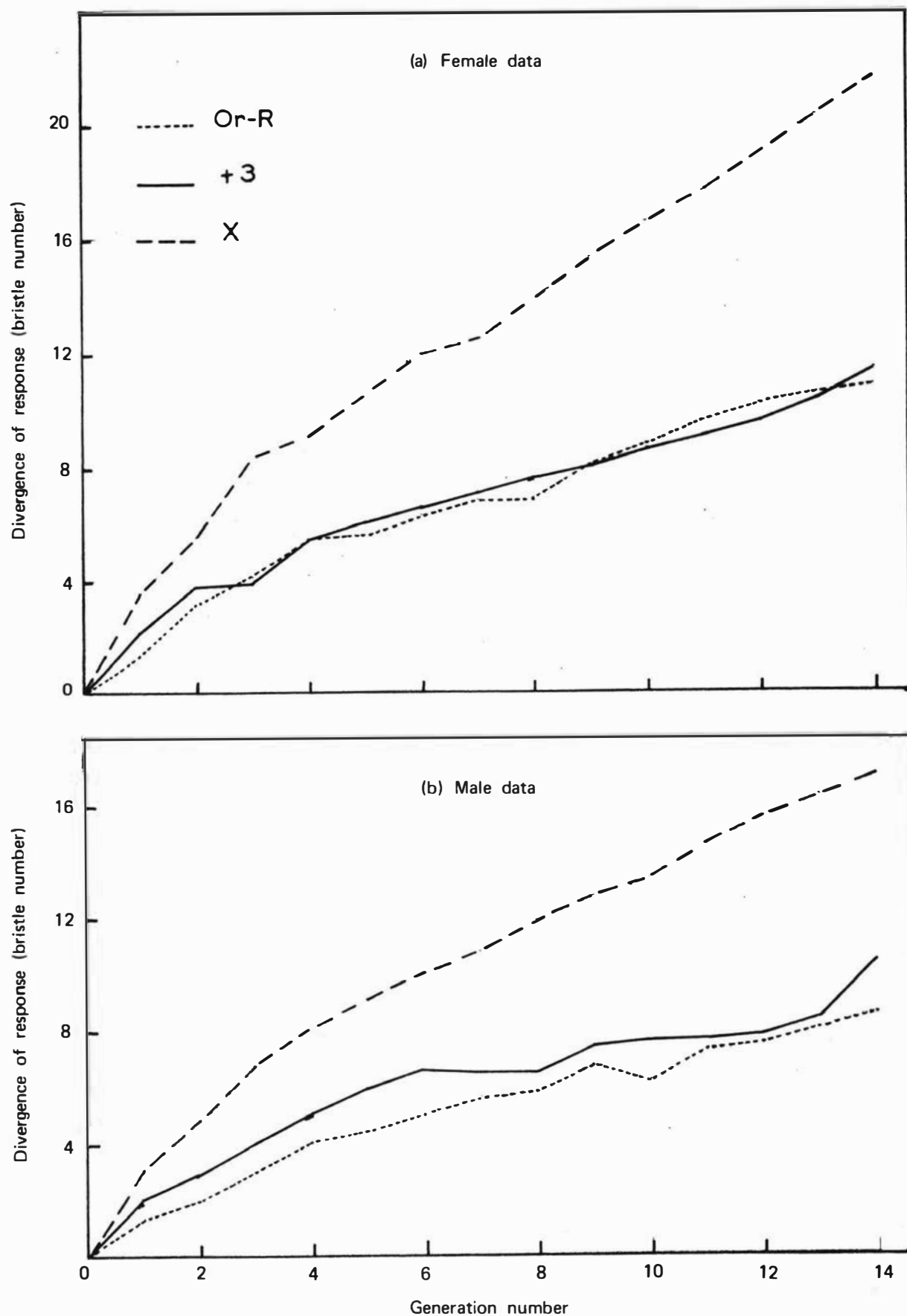


Fig. 2. Divergence of selection response between high and low selection lines. (a) Female data, (b) Male data.

Table 11(a): Phenotypic variances of individual replicates and controls (female data)

| Rep      | High selection |       |       |       |       | Low selection |       |       |       |       | Control |       |
|----------|----------------|-------|-------|-------|-------|---------------|-------|-------|-------|-------|---------|-------|
|          | 1              | 2     | 3     | 4     | mean  | 1             | 2     | 3     | 4     | mean  |         |       |
| OREGON-R |                |       |       |       |       |               |       |       |       |       |         |       |
| Gen 0    | 7.50           | 7.89  | 7.84  | 8.95  | 8.05  | 0             | 8.84  | 6.80  | 9.55  | 10.05 | 8.81    | 9.29  |
| 1        | 8.18           | 9.05  | 7.52  | 8.39  | 8.29  | 1             | 22.59 | 8.70  | 6.68  | 8.66  | 11.66   | 9.33  |
| 2        | 6.52           | 9.89  | 12.30 | 7.64  | 9.09  | 2             | 13.50 | 8.25  | 8.52  | 5.61  | 8.97    | 8.38  |
| 3        | 6.50           | 7.96  | 9.25  | 7.50  | 7.80  | 3             | 8.86  | 12.84 | 13.45 | 6.45  | 10.40   | 9.04  |
| 4        | 4.70           | 8.10  | 9.37  | 7.94  | 7.53  | 4             | 10.17 | 10.07 | 6.64  | 7.88  | 8.69    | 9.29  |
| 5        | 6.63           | 5.88  | 6.63  | 6.39  | 6.38  | 5             | 8.34  | 9.14  | 5.32  | 6.80  | 7.40    | 9.74  |
| 6        | 6.34           | 14.32 | 5.76  | 5.97  | 8.10  | 6             | 6.25  | 10.69 | 6.80  | 7.36  | 7.78    | 8.88  |
| 7        | 6.34           | 7.19  | 5.41  | 4.69  | 5.91  | 7             | 7.41  | 9.19  | 4.83  | 7.49  | 7.23    | 10.09 |
| 8        | 5.07           | 5.98  | 6.81  | 7.88  | 6.44  | 8             | 12.17 | 5.56  | 5.20  | 7.68  | 7.60    | 7.20  |
| 9        | 4.97           | 7.12  | 8.24  | 3.73  | 6.02  | 9             | 5.37  | 10.50 | 6.15  | 5.12  | 6.79    | 13.63 |
| 10       | 5.15           | 4.73  | 9.17  | 4.64  | 5.92  | 10            | 8.20  | 8.93  | 5.52  | 6.70  | 7.34    | 10.75 |
| 11       | 5.66           | 5.51  | 8.17  | 7.34  | 6.67  | 11            | 11.92 | 7.37  | 6.39  | 4.95  | 7.66    | 9.22  |
| 12       | 4.90           | 3.85  | 6.81  | 5.88  | 5.36  | 12            | 17.05 | 6.98  | 4.25  | 6.32  | 8.65    | 11.82 |
| 13       | 5.69           | 7.73  | 7.20  | 6.31  | 6.73  | 13            | 8.46  | 7.32  | 4.63  | 7.80  | 7.05    | 10.06 |
| 14       | 8.02           | 6.61  | 7.27  | 4.89  | 6.70  | 14            | 8.32  | 10.54 | 4.34  | 8.91  | 8.03    | 8.12  |
| +3       |                |       |       |       |       |               |       |       |       |       |         |       |
| Gen 0    | 3.91           | 5.55  | 5.30  | 5.34  | 5.02  | 0             | 7.50  | 10.00 | 9.45  | 7.34  | 8.57    | 7.89  |
| 1        | 6.75           | 5.11  | 7.61  | 6.11  | 6.40  | 1             | 10.80 | 7.25  | 8.41  | 9.25  | 8.92    | 9.08  |
| 2        | 4.30           | 7.93  | 5.93  | 7.43  | 6.40  | 2             | 11.11 | 8.91  | 9.14  | 8.70  | 9.47    | 6.08  |
| 3        | 7.68           | 5.70  | 8.11  | 5.68  | 6.79  | 3             | 5.29  | 8.43  | 10.27 | 6.16  | 7.54    | 7.05  |
| 4        | 6.16           | 5.86  | 7.16  | 6.41  | 6.40  | 4             | 9.07  | 13.27 | 4.57  | 6.64  | 8.39    | 8.46  |
| 5        | 2.84           | 3.84  | 3.48  | 4.59  | 3.69  | 5             | 7.30  | 10.27 | 6.11  | 4.57  | 7.06    | 9.65  |
| 6        | 4.75           | 6.66  | 4.89  | 5.11  | 5.35  | 6             | 5.70  | 10.77 | 5.64  | 7.68  | 7.45    | 10.05 |
| 7        | 6.23           | 6.66  | 3.73  | 6.52  | 5.79  | 7             | 6.14  | 5.98  | 8.86  | 6.02  | 6.75    | 8.47  |
| 8        | 6.61           | 7.36  | 6.64  | 6.55  | 6.79  | 8             | 6.29  | 6.20  | 6.32  | 3.45  | 5.57    | 6.31  |
| 9        | 5.70           | 5.39  | 4.43  | 4.37  | 4.97  | 9             | 5.39  | 7.89  | 6.72  | 4.07  | 6.02    | 8.98  |
| 10       | 5.28           | 7.07  | 4.23  | 6.70  | 5.82  | 10            | 7.07  | 8.07  | 6.64  | 5.14  | 6.73    | 7.09  |
| 11       | 7.07           | 4.04  | 7.31  | 5.50  | 5.98  | 11            | 7.24  | 7.02  | 7.85  | 6.12  | 7.06    | 7.74  |
| 12       | 7.59           | 5.43  | 5.26  | 4.46  | 5.69  | 12            | 5.73  | 10.64 | 5.90  | 4.47  | 6.69    | 8.26  |
| 13       | 8.30           | 4.31  | 6.78  | 5.61  | 6.25  | 13            | 4.93  | 9.29  | 12.54 | 4.59  | 7.84    | 7.53  |
| 14       | 8.70           | 8.07  | 6.41  | 8.41  | 7.90  | 14            | 6.27  | 11.13 | 6.75  | 7.14  | 7.82    | 6.06  |
| CROSS    |                |       |       |       |       |               |       |       |       |       |         |       |
| Gen 0    | 7.91           | 14.89 | 11.89 | 10.57 | 11.32 | 0             | 10.75 | 9.39  | 11.11 | 10.25 | 10.38   | 13.87 |
| 1        | 11.45          | 7.87  | 11.64 | 7.48  | 9.61  | 1             | 9.39  | 10.86 | 9.98  | 9.14  | 9.84    | 11.73 |
| 2        | 9.61           | 7.59  | 10.84 | 9.82  | 9.47  | 2             | 10.48 | 9.32  | 9.88  | 7.39  | 9.27    | 12.93 |
| 3        | 11.50          | 8.64  | 8.13  | 10.93 | 9.80  | 3             | 6.14  | 10.77 | 7.14  | 4.91  | 7.24    | 15.10 |
| 4        | 9.66           | 8.36  | 7.54  | 9.14  | 8.68  | 4             | 7.73  | 10.89 | 5.95  | 7.39  | 7.99    | 10.07 |
| 5        | 11.48          | 11.15 | 8.05  | 8.64  | 9.83  | 5             | 6.74  | 8.41  | 5.34  | 7.67  | 7.04    | 9.83  |
| 6        | 6.64           | 6.61  | 6.80  | 5.48  | 6.38  | 6             | 6.08  | 5.78  | 8.41  | 7.90  | 7.04    | 9.49  |
| 7        | 7.82           | 7.16  | 6.36  | 4.41  | 6.44  | 7             | 4.68  | 7.26  | 5.65  | 9.42  | 6.75    | 11.32 |
| 8        | 7.84           | 8.23  | 9.47  | 6.82  | 8.09  | 8             | 6.88  | 5.29  | 5.61  | 13.39 | 7.79    | 10.51 |
| 9        | 10.88          | 9.26  | 15.61 | 8.10  | 10.96 | 9             | 7.68  | 8.37  | 6.73  | 7.78  | 7.64    | 7.36  |
| 10       | 9.28           | 7.15  | 6.94  | 12.00 | 8.84  | 10            | 7.37  | 5.73  | 6.02  | 10.86 | 7.50    | 7.80  |
| 11       | 12.00          | 9.07  | 12.14 | 11.75 | 11.24 | 11            | 8.75  | 6.75  | 5.46  | 11.41 | 8.09    | 9.07  |
| 12       | 7.95           | 6.64  | 9.66  | 7.29  | 7.89  | 12            | 4.83  | 4.88  | 4.69  | 11.39 | 6.45    | 7.79  |
| 13       | 11.92          | 10.37 | 5.56  | 10.20 | 9.51  | 13            | 7.17  | 6.51  | 6.36  | 6.56  | 6.65    | 9.25  |
| 14       | 11.91          | 9.39  | 10.98 | 14.39 | 11.67 | 14            | 7.66  | 6.16  | 7.55  | 10.50 | 7.97    | 7.26  |



Table 11(b): Phenotypic variances of individual replicates and controls (male data)

| Rep      | High selection |      |       |       |      | Low selection |       |       |       |      | Control |       |
|----------|----------------|------|-------|-------|------|---------------|-------|-------|-------|------|---------|-------|
|          | 1              | 2    | 3     | 4     | mean | 1             | 2     | 3     | 4     | mean |         |       |
| OREGON-R |                |      |       |       |      |               |       |       |       |      |         |       |
| Gen 0    | 5.48           | 9.11 | 8.36  | 4.95  | 6.73 | 0             | 9.61  | 5.66  | 6.00  | 7.20 | 7.12    | 6.23  |
| 1        | 7.09           | 6.59 | 6.89  | 6.20  | 6.69 | 1             | 6.82  | 6.98  | 5.18  | 7.09 | 6.52    | 6.19  |
| 2        | 6.59           | 6.84 | 8.11  | 4.95  | 6.62 | 2             | 5.34  | 4.80  | 8.66  | 5.20 | 6.00    | 7.58  |
| 3        | 4.23           | 5.84 | 4.98  | 8.25  | 5.83 | 3             | 4.86  | 9.07  | 7.16  | 3.98 | 6.27    | 8.10  |
| 4        | 6.18           | 4.26 | 4.48  | 5.85  | 5.19 | 4             | 4.80  | 8.68  | 8.48  | 7.58 | 7.39    | 6.72  |
| 5        | 5.76           | 8.63 | 6.56  | 4.14  | 6.27 | 5             | 6.15  | 5.95  | 5.92  | 5.15 | 5.79    | 8.36  |
| 6        | 4.36           | 7.63 | 4.05  | 4.20  | 5.06 | 6             | 4.36  | 7.63  | 4.05  | 4.20 | 5.06    | 5.61  |
| 7        | 5.71           | 5.14 | 4.64  | 5.17  | 5.17 | 7             | 5.68  | 5.12  | 3.66  | 5.73 | 5.05    | 8.17  |
| 8        | 5.71           | 6.07 | 5.46  | 4.29  | 5.38 | 8             | 5.54  | 4.46  | 4.83  | 3.93 | 4.69    | 8.12  |
| 9        | 4.31           | 6.25 | 5.56  | 4.42  | 5.14 | 9             | 5.31  | 6.63  | 4.90  | 5.17 | 5.50    | 10.46 |
| 10       | 5.32           | 3.76 | 6.47  | 8.69  | 6.06 | 10            | 6.17  | 6.66  | 4.97  | 5.71 | 5.88    | 8.60  |
| 11       | 5.49           | 4.41 | 5.61  | 5.61  | 5.28 | 11            | 8.00  | 7.08  | 4.97  | 6.98 | 6.76    | 7.92  |
| 12       | 5.25           | 4.41 | 6.98  | 7.25  | 5.97 | 12            | 6.49  | 5.37  | 5.51  | 6.32 | 5.92    | 5.14  |
| 13       | 4.49           | 4.80 | 6.95  | 5.45  | 5.42 | 13            | 9.14  | 5.00  | 3.56  | 5.75 | 5.86    | 5.78  |
| 14       | 5.64           | 5.91 | 5.43  | 7.18  | 6.04 | 14            | 7.30  | 5.70  | 4.86  | 4.86 | 5.68    | 8.37  |
| +3       |                |      |       |       |      |               |       |       |       |      |         |       |
| Gen 0    | 5.16           | 5.00 | 7.41  | 6.29  | 5.97 | 0             | 7.41  | 5.98  | 7.50  | 5.25 | 6.54    | 6.64  |
| 1        | 6.89           | 4.34 | 5.98  | 5.98  | 5.80 | 1             | 7.84  | 8.18  | 12.16 | 8.66 | 9.21    | 5.25  |
| 2        | 6.98           | 5.39 | 7.16  | 6.07  | 6.40 | 2             | 8.77  | 7.89  | 6.45  | 8.80 | 7.98    | 5.41  |
| 3        | 6.16           | 4.20 | 6.11  | 3.50  | 4.99 | 3             | 7.68  | 7.32  | 5.75  | 9.18 | 7.48    | 7.54  |
| 4        | 5.43           | 5.16 | 5.50  | 4.16  | 5.06 | 4             | 7.02  | 6.25  | 3.50  | 7.41 | 6.05    | 8.12  |
| 5        | 5.07           | 5.66 | 5.32  | 4.11  | 5.04 | 5             | 4.61  | 6.75  | 3.91  | 4.70 | 4.99    | 6.01  |
| 6        | 4.18           | 3.25 | 3.75  | 4.70  | 3.97 | 6             | 5.05  | 5.64  | 4.82  | 6.55 | 5.52    | 5.68  |
| 7        | 4.02           | 2.66 | 3.14  | 7.57  | 4.35 | 7             | 4.27  | 3.57  | 5.91  | 6.07 | 4.96    | 6.80  |
| 8        | 5.25           | 5.32 | 2.93  | 4.41  | 4.48 | 8             | 4.00  | 4.49  | 4.98  | 5.34 | 4.70    | 7.14  |
| 9        | 6.34           | 4.14 | 4.25  | 4.97  | 4.93 | 9             | 3.18  | 3.24  | 3.80  | 5.96 | 4.05    | 7.82  |
| 10       | 3.46           | 3.75 | 5.84  | 5.06  | 4.53 | 10            | 4.61  | 4.23  | 4.97  | 3.81 | 4.41    | 4.26  |
| 11       | 5.30           | 3.82 | 6.61  | 5.31  | 5.26 | 11            | 4.78  | 4.07  | 6.15  | 4.54 | 4.89    | 5.52  |
| 12       | 5.24           | 5.25 | 3.81  | 3.94  | 4.56 | 12            | 4.66  | 4.08  | 4.42  | 5.05 | 4.55    | 4.70  |
| 13       | 9.59           | 3.81 | 3.89  | 6.52  | 5.95 | 13            | 3.49  | 5.24  | 5.51  | 7.88 | 5.53    | 5.54  |
| 14       | 7.66           | 5.34 | 6.98  | 4.55  | 6.13 | 14            | 3.11  | 4.95  | 4.61  | 6.82 | 4.87    | 5.72  |
| CROSS    |                |      |       |       |      |               |       |       |       |      |         |       |
| Gen 0    | 11.41          | 6.93 | 7.84  | 9.80  | 9.00 | 0             | 10.66 | 11.79 | 8.98  | 9.52 | 10.24   | 8.88  |
| 1        | 4.70           | 6.32 | 10.23 | 10.18 | 7.86 | 1             | 8.59  | 9.05  | 6.07  | 8.11 | 7.96    | 11.89 |
| 2        | 7.89           | 5.80 | 8.66  | 8.80  | 7.79 | 2             | 6.57  | 8.70  | 10.27 | 7.25 | 8.20    | 10.07 |
| 3        | 6.52           | 6.39 | 7.39  | 11.07 | 7.84 | 3             | 5.57  | 7.18  | 4.95  | 5.30 | 5.75    | 9.74  |
| 4        | 9.66           | 5.98 | 5.16  | 4.52  | 6.33 | 4             | 7.22  | 5.78  | 7.27  | 5.46 | 6.43    | 5.25  |
| 5        | 7.66           | 6.52 | 7.61  | 5.75  | 6.89 | 5             | 4.66  | 3.95  | 4.29  | 4.85 | 4.44    | 9.06  |
| 6        | 5.00           | 5.09 | 6.43  | 4.48  | 5.25 | 6             | 5.47  | 4.31  | 5.17  | 6.42 | 5.34    | 7.07  |
| 7        | 6.93           | 5.89 | 6.23  | 6.82  | 6.47 | 7             | 4.90  | 7.25  | 3.53  | 5.20 | 5.22    | 9.93  |
| 8        | 4.23           | 7.95 | 5.55  | 5.75  | 5.87 | 8             | 4.64  | 5.24  | 3.58  | 5.37 | 4.71    | 5.65  |
| 9        | 9.02           | 6.46 | 4.96  | 7.65  | 7.02 | 9             | 5.15  | 6.51  | 4.42  | 5.03 | 5.28    | 7.45  |
| 10       | 10.02          | 5.87 | 6.85  | 7.19  | 7.48 | 10            | 5.39  | 4.00  | 3.58  | 4.27 | 4.31    | 6.60  |
| 11       | 6.42           | 6.42 | 5.32  | 7.42  | 6.40 | 11            | 3.68  | 7.58  | 5.71  | 8.46 | 6.36    | 8.98  |
| 12       | 6.10           | 5.75 | 6.80  | 7.92  | 6.64 | 12            | 4.42  | 5.05  | 3.14  | 7.03 | 4.91    | 7.20  |
| 13       | 7.49           | 5.81 | 6.24  | 6.39  | 6.48 | 13            | 4.53  | 3.76  | 3.80  | 4.69 | 4.19    | 6.78  |
| 14       | 6.66           | 7.70 | 7.91  | 10.57 | 8.21 | 14            | 5.80  | 6.50  | 3.95  | 7.20 | 5.86    | 7.69  |

but when selection was in the low direction, the original +3 population gave as much response as the Cross while the Oregon-R's response was the lowest.

If total response from each population was measured as the divergence between the high and low selection lines (Fig. 2), the Cross was clearly superior over the two parent lines. The trends of the divergence of selection response from the females of the +3 and Oregon-R populations were remarkably similar. For the males, the divergence of the +3 population was consistently greater than that of the Oregon-R by an average of 0.5 bristles.

#### (ii) Phenotypic Variance

According to selection theory based on the additive model, selection is expected to bring about the gradual fixation of favoured alleles leading to the reduction of genetic variability and this in turn is reflected in the decline in the phenotypic variance of the selected character. However, this expected decrease in phenotypic variance within selection lines has not often been realised in actual experiments. Some of the high and low replicates of Clayton et al. (1957) were characterised by sudden and spectacular increases in phenotypic variability in the later generations of selection, with the high level being maintained even when response had ceased. This phenomenon has been found to be due mainly to selection of heterozygotes for lethal genes. Sheldon (1963) reported slight reduction in phenotypic variance within three of his four replicates selected for abdominal bristles for 30 generations. Frankham, Jones and Barker (1968) and Rathie and Barker (1968) found that the majority of replicates selected for high abdominal bristles on a long-term basis showed no consistent changes in phenotypic variance.

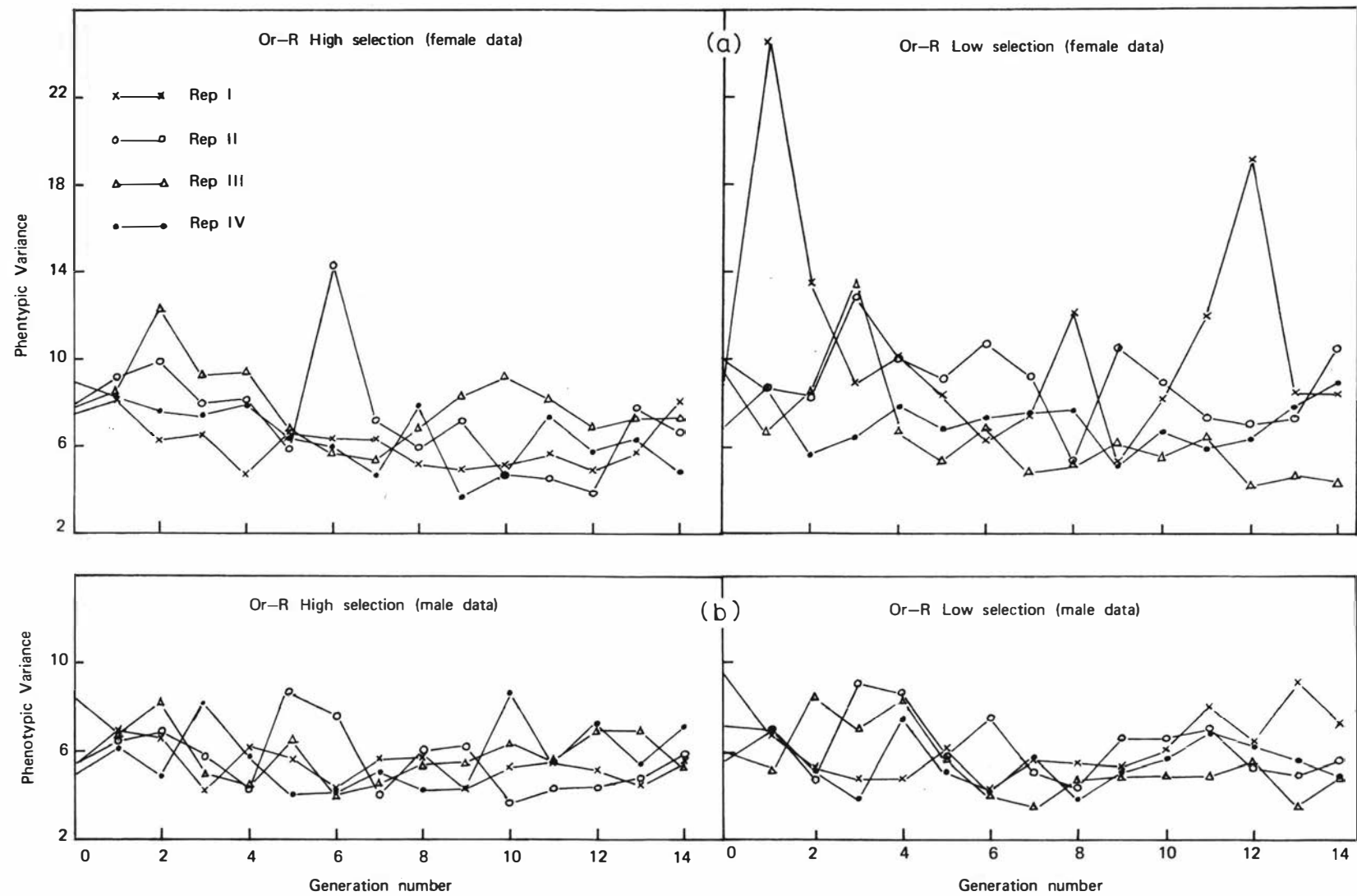


Fig. 3. Phenotypic variances of individual replicates of Oregon-R (a) female data, (b) male data.

It is the purpose here to survey how selection has affected the variability within each of the replicates of the Oregon-R, +3 and Cross selection lines and also the heterogeneity of variance within selection lines and between different lines. The phenotypic variances for each selection replicate and control are presented in Tables 11(a) and 11(b). Figs 3(a) - (f) show the phenotypic variance of each high and low selection line for each replication, generation and sex. These graphs depict clearly the trend within each replication and also whether the four replicates within a selection line show any similarity in pattern over the 14 generations.

Oregon-R population: The females of each high and low replicate appear to show greater generation to generation fluctuations than the males. Similar observations of the differential behaviour of the two sexes to selection have been made by Clayton et al. (1957) and Sheldon (1963) and the former authors regarded this to be a physiological rather than a genetic effect. The four Oregon-R high replications within each generation were averaged to give the generation mean of the high line. The generation mean of the Oregon-R high line showed a slight but definite downward trend till G7 and from then it remained at that level till the end of selection. From as early as G3, the phenotypic variance of the high line was lower than that of the Oregon-R unselected control. This apparent reduction in phenotypic variability was accompanied by a decline in selection response of the Oregon-R high line and could reflect the exhaustion of genetic variability as a result of gene fixation.

The four low replicates showed greater heterogeneity of variance than the high replicates. The Or-RLI females exhibited a sudden and sharp increase in variance at G2 and G11 but no similar rise was observed among the males of the corresponding generations. Since on both

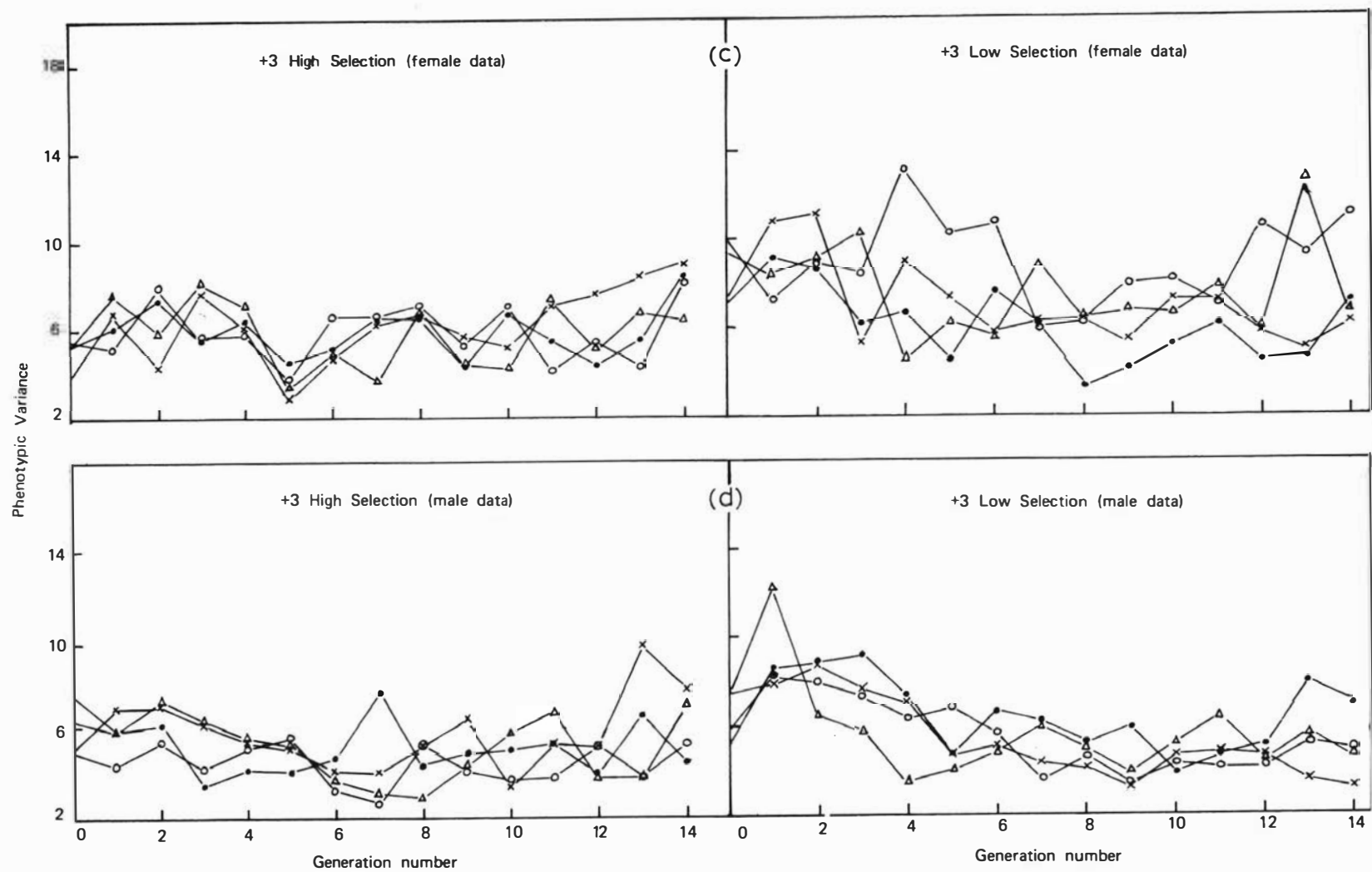


Fig. 3. Phenotypic variances of individual replicates of +3. (c) female data, (d) male data.

occasions the sudden increase in variability lasted only for one generation and was not followed by an accelerated response, it was unlikely to be the result of a new mutation arising within the replication or an unusual cross-over event. The anomalies were probably due to sampling variation or to some changes in the environment to which the females were susceptible. Averaging the four low selection replicate means resulted in removal of much of the generation to generation fluctuations and a definite downward pattern emerged. In fact, the pattern of the Oregon-R low line was remarkably similar to that of the Oregon-R high line, since both showed a consistent but small decline till G7. Like the high line, the low line maintained slightly lower phenotypic variances than the Oregon-R control from as early as G4. Thus, the Oregon-R high and low selection lines showed decline in phenotypic variances in the first half of the selection experiment.

+3 population: Throughout the 14 generations of selection, the +3 high replications showed phenotypic variances which were consistently lower than that of the +3 control. Associated with the low phenotypic variability were the extremely small selection responses and these two features characterised the +3 high selection line. It was difficult to account for the low phenotypic variances of the four high replicates, which occurred right from the start of the selection experiment, particularly when the +3 control, maintained concurrently with the selection line, consistently showed higher variances.

The +3 low replicates showed higher phenotypic variances and greater heterogeneity in variances within a generation than the +3 high replicates. The generation mean of the +3 low line showed a decline which bore a strong resemblance to the trend of the Oregon-R low selection line, with the phenotypic variances declining gradually in the first seven

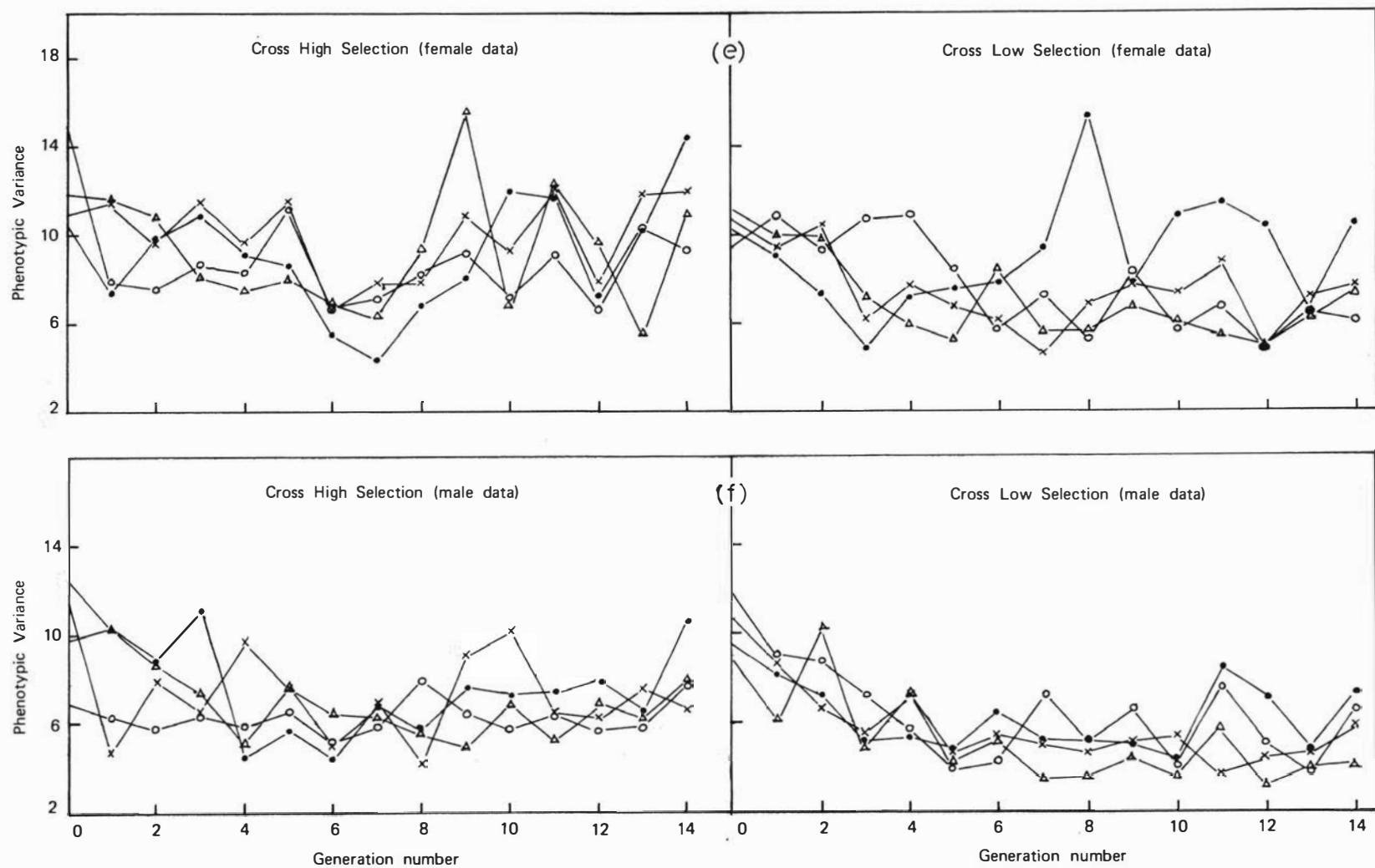


Fig. 3. Phenotypic variances of individual replicates of Cross (e) female data, (f) male data.

selection generations (Period 1) and remaining consistent in the later seven generations (Period 2). This pattern of changes in phenotypic variances corresponded well with the responses in the mean bristle number of the +3 low line (Figs 1(c)-(d) ) where the first seven generations of selection produced greater response than the remaining generations.

Cross population: The  $F_3$  of the hybrid between the Oregon-R and +3 strains formed the base population of the Cross high and low selection lines. The  $F_3$  had a higher phenotypic variance than either of its parental strains. For the Cross high selection, the females of all four high replicates showed a decline in phenotypic variance till G6, and this was followed by an increase to its original level by the ninth generation, which was then maintained till G14. The high replicates showed marked generation to generation fluctuations. The males of the Cross high replicates showed a different pattern from the females in that although a decline occurred in the first half of the selection experiment, there was no subsequent increase as that observed in the females. Since all replicates behaved in a similar way, it indicated that the difference in patterns of phenotypic variance between the males and females of the high replicates was not the result of sampling vagaries but was probably due to different genetic controls for the males and females.

The decline in the Cross low replicates was similar to that of the Oregon-R and +3 low replicates. Once again there was a positive correlation between the trend of the variances and the changes in the mean bristle number of the Cross low replicates.

Controls: The phenotypic variances of the Oregon-R and +3 controls showed no upward or downward trend but fluctuated around their original levels, and there was a definite tendency for higher variances in the Oregon-R control throughout the 14 generations. The Cross control showed a different



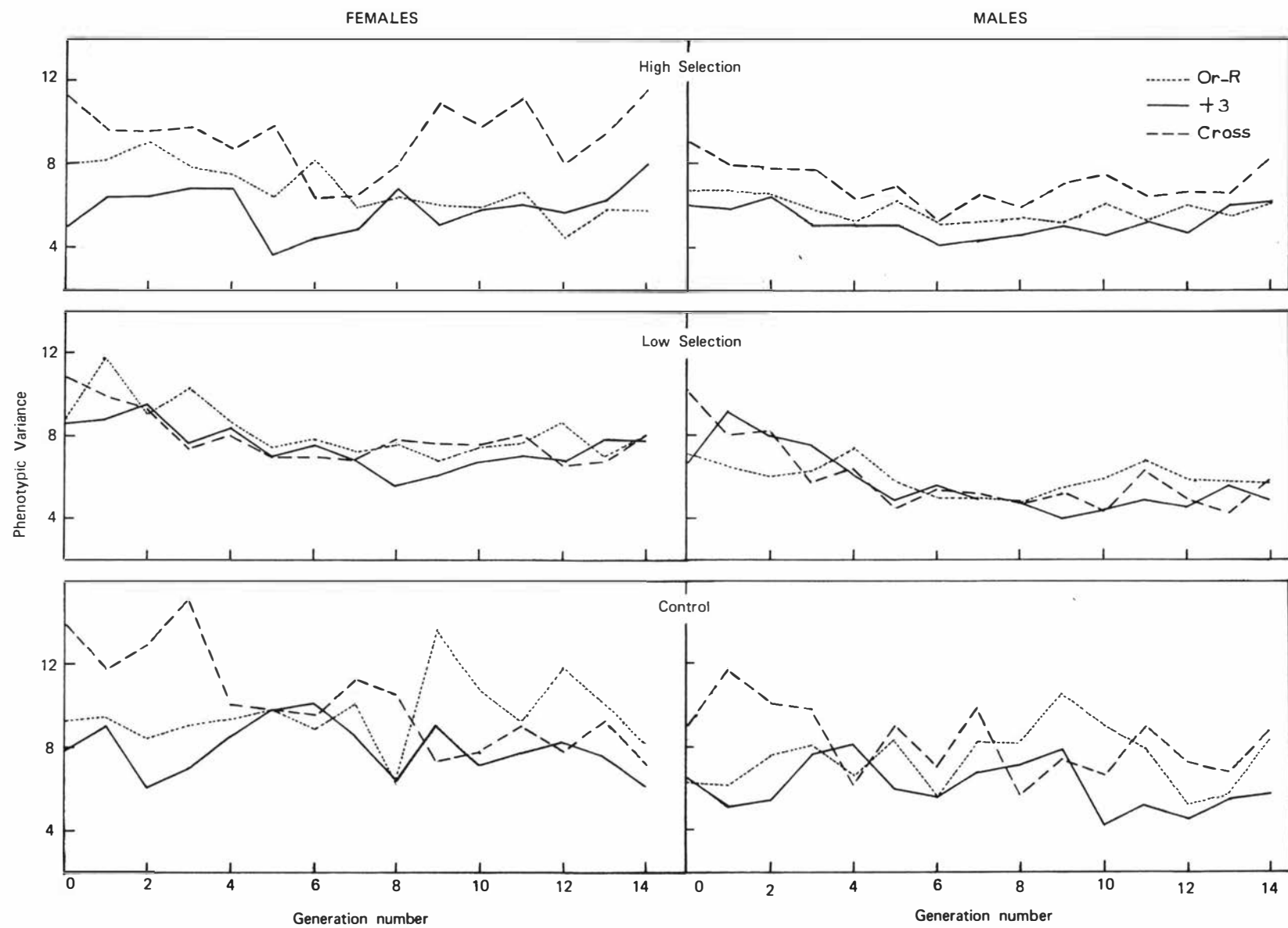


Fig. 4 Comparison of the mean phenotypic variances of high and low selection lines and controls of the Oregon-R , +3 and Cross.

pattern as expected. It should be noted that the  $F_3$  of the Cross formed the base population of the Cross control and selection lines, since Lush (1948) and Kojima and Kelleher (1963) sounded caution against initiating selection from the  $F_1$  or  $F_2$  of a cross. It is worthwhile examining the phenotypic variances of the  $F_1$  and  $F_2$  as well, since this would give some information about the genetic situation in the two original populations (Oregon-R and +3). The  $F_1$  variance, as expected, was comparable to the variances of the two parental populations. However, the variance of the  $F_2$  was almost twice that of the  $F_1$  and this could be the evidence that different alleles were fixed in the +3 and Oregon-R strains. Hence, as a result of segregation and recombination the variance of the  $F_2$  was increased.

Discussion: Except for the +3 high selection line which maintained low phenotypic variability throughout the selection programme and the females of the Cross high line, whose variance fluctuated around that of the  $F_3$ , the Oregon-R high line and all the three low lines showed a decline over the first seven generations of selection. Fig. 4 shows that all the three low lines exhibited a remarkably uniform pattern, which superficially could be taken to reflect the reduction in genetic variability on the underlying scale. But on the other hand, there was a striking similarity between the trend of the phenotypic variance and the corresponding pattern of the changes in mean abdominal bristle number and this could imply that scale effects were present. Falconer (1961) suggested a convenient means of removing scale effects by using another measure of variability - the coefficient of variation - and in the following section, this alternative parameter will be presented and its effectiveness in terms of cancelling scale effects discussed.

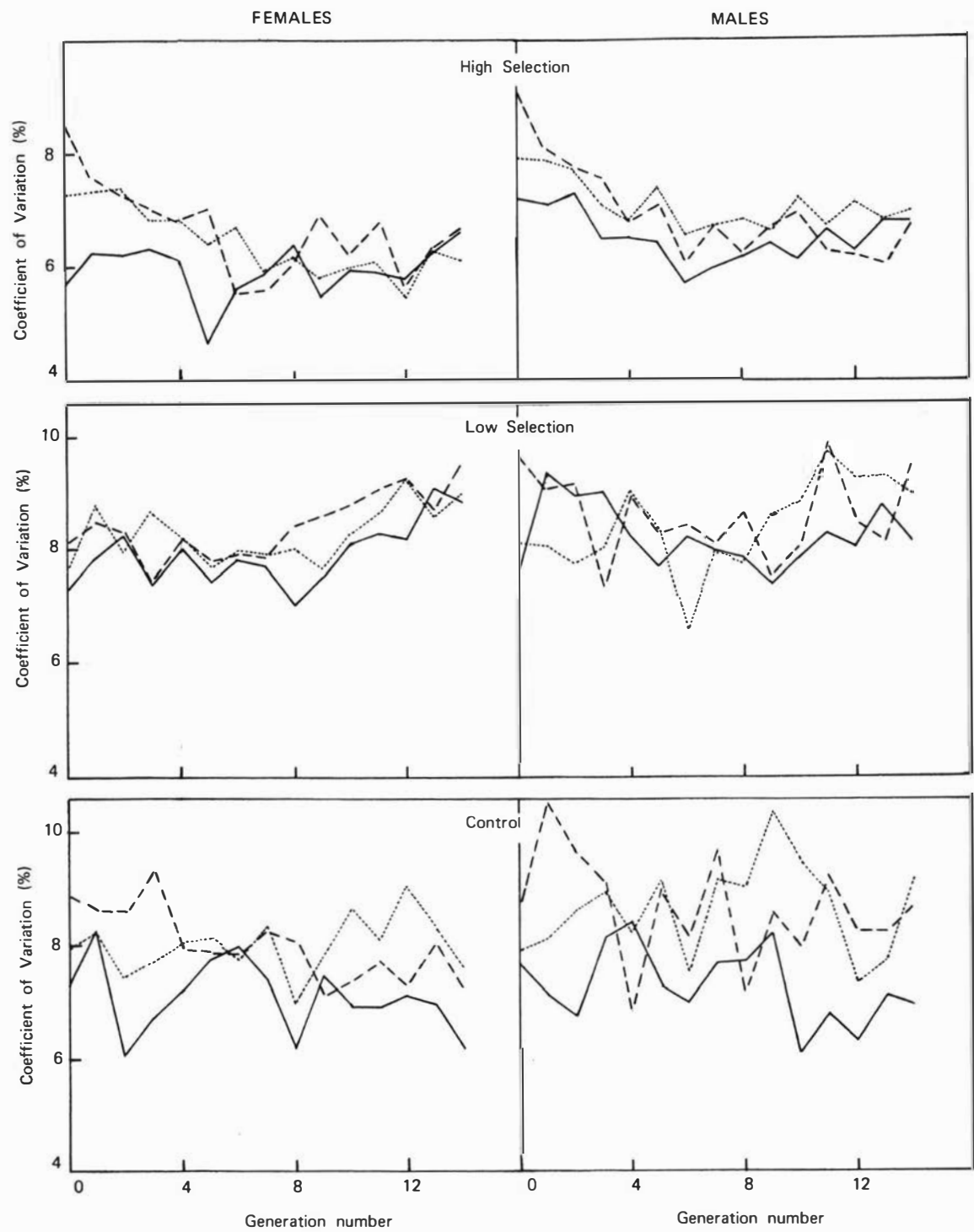


Fig. 5. Comparison of the coefficient of variation of the high and low selection lines and controls of the Oregon-R, +3 and Cross.

(iii) Coefficient of variation

The similarity in trends of the phenotypic variance and the generation mean, particularly in the low selection lines, suggests that these two parameters are not entirely independent but could be related by scale effects. This means that a change in the population mean is accompanied by a change of its variance in the same direction. In an attempt to detect and remove such scale effects, the data is expressed in an alternative form - the coefficient of variation - which takes into account the population mean. This parameter is defined as the standard deviation divided by the population mean ( $s/\bar{x}$ ). If the trend in variability of a line was due to scale effects, its coefficient of variation should then remain fairly constant from generation to generation. Transformation to this parameter would also allow more meaningful comparisons between the two sexes and between the high and low selection lines.

Tables 12(a) and 12(b) present the coefficient of variation for each replication, generation and sex. It is clear that within a generation there are considerable differences in value between the four replications within the lines and also tendencies for inter-generation fluctuations of individual replicates. In order to present a clearer picture, the four replicates within each selection line are averaged for each generation and Fig. 5 shows the changes in coefficient of variation for the high and low selection lines and controls of the three populations. One striking feature which emerges is that the trend of the coefficient of variation appears to be the reverse of that of the phenotypic variation. It means that just as the phenotypic variance is suspected to be positively correlated with the population mean, the coefficient of the variation, on the other hand, is negatively correlated. This conclusion is based on the following observations from the graphs: The males with lower abdominal

Table 12(a): Coefficient of variation (%) of individual selection replicates and controls  
(female data)

| Rep      | High selection |      |      |      |      | Low selection |       |       |       |       | Control |      |
|----------|----------------|------|------|------|------|---------------|-------|-------|-------|-------|---------|------|
|          | 1              | 2    | 3    | 4    | mean | 1             | 2     | 3     | 4     | mean  |         |      |
| OREGON-R |                |      |      |      |      |               |       |       |       |       |         |      |
| Gen 0    | 6.98           | 7.31 | 7.54 | 7.61 | 7.36 | 0             | 7.51  | 6.87  | 8.07  | 8.53  | 7.75    | 7.98 |
| 1        | 7.50           | 7.65 | 7.00 | 7.33 | 7.37 | 1             | 12.87 | 7.89  | 6.79  | 7.66  | 8.80    | 8.29 |
| 2        | 6.60           | 7.56 | 8.68 | 6.80 | 7.41 | 2             | 10.10 | 7.76  | 7.68  | 6.41  | 7.99    | 7.47 |
| 3        | 6.34           | 6.71 | 7.69 | 6.71 | 6.86 | 3             | 8.58  | 9.64  | 9.92  | 6.81  | 8.74    | 7.75 |
| 4        | 5.39           | 6.96 | 7.78 | 7.22 | 6.84 | 4             | 9.37  | 8.71  | 7.10  | 7.76  | 8.24    | 8.09 |
| 5        | 6.48           | 5.78 | 6.42 | 6.25 | 6.23 | 5             | 8.46  | 8.78  | 6.41  | 7.39  | 7.76    | 8.14 |
| 6        | 6.25           | 8.89 | 5.90 | 6.01 | 6.76 | 6             | 7.19  | 9.81  | 7.34  | 7.67  | 8.00    | 7.74 |
| 7        | 6.25           | 6.37 | 5.85 | 5.36 | 5.96 | 7             | 8.33  | 9.02  | 6.27  | 8.08  | 7.93    | 8.35 |
| 8        | 5.50           | 6.01 | 6.53 | 6.76 | 6.20 | 8             | 10.78 | 6.98  | 6.44  | 8.03  | 8.06    | 6.97 |
| 9        | 5.40           | 6.26 | 6.97 | 4.70 | 5.83 | 9             | 7.31  | 9.75  | 7.10  | 6.65  | 7.70    | 9.74 |
| 10       | 5.59           | 5.22 | 7.37 | 5.18 | 5.84 | 10            | 9.55  | 9.14  | 6.83  | 7.74  | 8.32    | 8.67 |
| 11       | 5.82           | 5.60 | 6.72 | 6.50 | 6.16 | 11            | 12.00 | 8.60  | 7.51  | 6.59  | 8.68    | 7.89 |
| 12       | 5.38           | 4.70 | 6.23 | 5.89 | 5.55 | 12            | 15.06 | 8.48  | 6.16  | 7.72  | 9.36    | 9.04 |
| 13       | 5.81           | 6.68 | 6.46 | 5.99 | 6.24 | 13            | 10.30 | 8.90  | 6.63  | 8.63  | 8.62    | 8.35 |
| 14       | 6.86           | 6.02 | 6.47 | 5.24 | 6.15 | 14            | 10.38 | 10.39 | 6.43  | 9.11  | 9.08    | 7.67 |
| +3       |                |      |      |      |      |               |       |       |       |       |         |      |
| Gen 0    | 5.03           | 5.88 | 5.98 | 5.95 | 5.71 | 0             | 6.86  | 7.78  | 7.84  | 6.72  | 7.30    | 7.30 |
| 1        | 6.54           | 5.51 | 6.80 | 6.26 | 6.28 | 1             | 8.89  | 7.14  | 7.58  | 7.73  | 7.84    | 8.30 |
| 2        | 5.10           | 6.91 | 6.00 | 6.82 | 6.21 | 2             | 9.19  | 7.92  | 8.12  | 7.80  | 8.26    | 6.04 |
| 3        | 6.87           | 5.75 | 6.91 | 5.82 | 6.34 | 3             | 6.34  | 7.75  | 8.74  | 6.56  | 7.35    | 6.75 |
| 4        | 6.17           | 5.75 | 6.56 | 6.14 | 6.16 | 4             | 8.30  | 10.34 | 6.04  | 7.22  | 7.98    | 7.21 |
| 5        | 4.12           | 4.75 | 4.50 | 5.12 | 4.62 | 5             | 7.69  | 9.18  | 6.94  | 6.02  | 7.46    | 7.76 |
| 6        | 5.38           | 6.22 | 5.38 | 5.53 | 5.63 | 6             | 6.89  | 9.47  | 6.94  | 8.15  | 7.86    | 7.98 |
| 7        | 6.14           | 6.35 | 4.75 | 6.24 | 5.87 | 7             | 7.36  | 7.28  | 8.81  | 7.34  | 7.70    | 7.39 |
| 8        | 6.34           | 6.56 | 6.41 | 6.25 | 6.39 | 8             | 7.47  | 7.76  | 7.63  | 5.45  | 7.08    | 6.19 |
| 9        | 5.76           | 5.66 | 5.28 | 5.18 | 5.47 | 9             | 7.04  | 8.93  | 8.05  | 6.03  | 7.51    | 7.43 |
| 10       | 5.78           | 6.50 | 5.12 | 6.36 | 5.94 | 10            | 8.12  | 9.25  | 8.39  | 6.89  | 8.16    | 6.90 |
| 11       | 6.49           | 4.91 | 6.53 | 5.72 | 5.91 | 11            | 8.18  | 8.66  | 9.07  | 7.35  | 8.32    | 6.92 |
| 12       | 6.68           | 5.68 | 5.73 | 5.14 | 5.81 | 12            | 7.39  | 10.93 | 8.20  | 6.36  | 8.22    | 7.11 |
| 13       | 6.94           | 5.08 | 6.42 | 5.82 | 6.07 | 13            | 6.95  | 10.74 | 12.26 | 6.55  | 9.13    | 6.95 |
| 14       | 6.82           | 6.71 | 6.04 | 6.91 | 6.62 | 14            | 7.66  | 11.86 | 8.38  | 8.43  | 9.08    | 6.21 |
| CROSS    |                |      |      |      |      |               |       |       |       |       |         |      |
| Gen 0    | 7.05           | 9.95 | 8.93 | 8.17 | 8.53 | 0             | 7.96  | 7.93  | 8.21  | 8.47  | 8.14    | 8.88 |
| 1        | 8.41           | 7.02 | 8.30 | 6.80 | 7.63 | 1             | 8.13  | 8.93  | 8.49  | 8.48  | 8.51    | 8.66 |
| 2        | 7.28           | 6.72 | 7.78 | 7.40 | 7.30 | 2             | 8.94  | 8.20  | 8.47  | 7.68  | 8.32    | 8.58 |
| 3        | 7.48           | 6.73 | 6.71 | 7.33 | 7.06 | 3             | 7.10  | 8.61  | 7.49  | 6.36  | 7.39    | 9.37 |
| 4        | 6.93           | 6.76 | 6.54 | 7.02 | 6.81 | 4             | 8.26  | 9.33  | 7.24  | 8.09  | 8.23    | 7.91 |
| 5        | 7.46           | 7.52 | 6.72 | 6.52 | 7.06 | 5             | 7.99  | 8.25  | 6.74  | 8.33  | 7.83    | 7.87 |
| 6        | 5.74           | 5.64 | 5.86 | 5.09 | 5.58 | 6             | 7.65  | 7.12  | 8.55  | 8.53  | 7.96    | 7.82 |
| 7        | 6.26           | 5.98 | 5.64 | 4.50 | 5.60 | 7             | 6.94  | 8.08  | 7.20  | 9.31  | 7.88    | 8.56 |
| 8        | 6.15           | 6.01 | 6.77 | 5.54 | 6.12 | 8             | 8.50  | 6.78  | 7.13  | 11.37 | 8.45    | 8.15 |
| 9        | 7.14           | 6.18 | 8.55 | 5.85 | 6.93 | 9             | 9.10  | 8.58  | 7.84  | 8.90  | 8.61    | 7.10 |
| 10       | 6.47           | 5.55 | 5.70 | 7.09 | 6.20 | 10            | 9.15  | 7.55  | 7.70  | 10.78 | 8.80    | 7.38 |
| 11       | 7.03           | 6.02 | 7.39 | 6.99 | 6.86 | 11            | 10.19 | 8.02  | 7.33  | 10.88 | 9.11    | 7.70 |
| 12       | 5.58           | 5.13 | 6.51 | 5.27 | 5.62 | 12            | 7.30  | 6.87  | 6.76  | 11.61 | 8.14    | 7.30 |
| 13       | 6.88           | 6.36 | 4.94 | 6.26 | 6.11 | 13            | 9.40  | 8.40  | 8.07  | 9.15  | 8.76    | 8.07 |
| 14       | 6.64           | 5.98 | 6.68 | 7.20 | 6.63 | 14            | 7.73  | 8.04  | 8.79  | 11.70 | 9.57    | 7.26 |

Table 12(b): Coefficient of variation (%) of individual selection replicates and controls  
(male data)

| Rep      | High selection |      |      |      |      | Low selection |       |       |       |       | Control |       |
|----------|----------------|------|------|------|------|---------------|-------|-------|-------|-------|---------|-------|
|          | 1              | 2    | 3    | 4    | mean | 1             | 2     | 3     | 4     | mean  |         |       |
| OREGON-R |                |      |      |      |      |               |       |       |       |       |         |       |
| Gen 0    | 7.38           | 9.28 | 9.02 | 6.01 | 7.92 | 0             | 9.53  | 7.42  | 7.39  | 8.34  | 8.17    | 7.92  |
| 1        | 8.31           | 7.71 | 8.10 | 7.48 | 7.90 | 1             | 8.62  | 8.01  | 7.34  | 8.42  | 8.10    | 8.18  |
| 2        | 8.03           | 7.60 | 8.61 | 6.61 | 7.71 | 2             | 7.69  | 6.74  | 9.34  | 7.34  | 7.78    | 8.62  |
| 3        | 6.11           | 6.99 | 6.71 | 8.66 | 7.12 | 3             | 7.43  | 9.47  | 8.88  | 6.56  | 8.09    | 8.94  |
| 4        | 7.50           | 6.11 | 6.50 | 7.21 | 6.83 | 4             | 7.95  | 9.89  | 9.77  | 9.39  | 9.25    | 8.26  |
| 5        | 7.31           | 8.56 | 7.77 | 5.95 | 7.40 | 5             | 8.58  | 8.36  | 8.30  | 7.88  | 8.28    | 9.15  |
| 6        | 6.22           | 7.86 | 6.07 | 6.08 | 6.56 | 6             | 6.22  | 7.86  | 6.07  | 6.08  | 6.56    | 7.55  |
| 7        | 7.25           | 6.47 | 6.53 | 6.69 | 6.74 | 7             | 8.60  | 8.18  | 6.65  | 8.43  | 7.97    | 9.16  |
| 8        | 7.22           | 7.17 | 6.95 | 6.02 | 6.84 | 8             | 8.73  | 7.71  | 7.64  | 6.93  | 7.75    | 9.02  |
| 9        | 6.14           | 7.23 | 6.97 | 6.14 | 6.62 | 9             | 8.69  | 9.74  | 7.99  | 7.99  | 8.60    | 10.38 |
| 10       | 6.91           | 5.75 | 7.70 | 8.55 | 7.23 | 10            | 9.61  | 9.40  | 7.91  | 8.53  | 8.86    | 9.52  |
| 11       | 6.94           | 6.03 | 6.97 | 7.02 | 6.74 | 11            | 11.05 | 10.00 | 8.20  | 9.65  | 9.73    | 8.97  |
| 12       | 6.76           | 6.10 | 7.95 | 7.90 | 7.18 | 12            | 10.51 | 8.76  | 8.64  | 9.09  | 9.25    | 7.37  |
| 13       | 6.22           | 6.35 | 7.83 | 6.90 | 6.83 | 13            | 13.01 | 8.58  | 7.03  | 8.70  | 9.33    | 7.77  |
| 14       | 6.74           | 6.69 | 6.86 | 7.63 | 6.98 | 14            | 10.63 | 9.20  | 8.22  | 7.83  | 8.97    | 9.25  |
| +3       |                |      |      |      |      |               |       |       |       |       |         |       |
| Gen 0    | 6.84           | 6.51 | 7.95 | 7.47 | 7.19 | 0             | 8.57  | 7.43  | 8.29  | 6.75  | 7.76    | 7.69  |
| 1        | 7.84           | 6.05 | 7.19 | 7.28 | 7.09 | 1             | 9.01  | 8.88  | 10.87 | 8.85  | 9.40    | 7.17  |
| 2        | 7.78           | 6.69 | 7.69 | 7.15 | 7.33 | 2             | 9.58  | 8.89  | 8.11  | 9.19  | 8.94    | 6.76  |
| 3        | 7.39           | 5.81 | 7.29 | 5.45 | 6.49 | 3             | 9.50  | 8.93  | 7.89  | 9.84  | 9.04    | 8.14  |
| 4        | 6.88           | 6.55 | 6.71 | 5.90 | 6.51 | 4             | 9.08  | 8.50  | 6.61  | 8.85  | 8.26    | 8.45  |
| 5        | 6.52           | 6.89 | 6.58 | 5.84 | 6.46 | 5             | 7.56  | 9.04  | 6.98  | 7.37  | 7.74    | 7.32  |
| 6        | 5.86           | 5.22 | 5.45 | 6.28 | 5.70 | 6             | 8.12  | 8.39  | 7.81  | 8.72  | 8.26    | 7.02  |
| 7        | 5.98           | 4.78 | 5.09 | 8.03 | 5.97 | 7             | 7.59  | 6.85  | 8.79  | 8.68  | 7.98    | 7.69  |
| 8        | 6.78           | 6.77 | 4.97 | 6.22 | 6.19 | 8             | 7.16  | 7.98  | 8.21  | 8.13  | 7.87    | 7.76  |
| 9        | 7.23           | 5.87 | 5.99 | 6.61 | 6.43 | 9             | 6.50  | 6.93  | 7.28  | 8.87  | 7.40    | 8.27  |
| 10       | 5.57           | 5.63 | 6.90 | 6.61 | 6.18 | 10            | 7.92  | 7.81  | 8.74  | 7.00  | 7.87    | 6.14  |
| 11       | 6.82           | 5.71 | 7.45 | 6.72 | 6.68 | 11            | 8.21  | 7.86  | 9.82  | 7.51  | 8.35    | 6.82  |
| 12       | 6.67           | 6.71 | 5.70 | 5.80 | 6.22 | 12            | 8.13  | 7.73  | 8.22  | 8.09  | 8.04    | 6.36  |
| 13       | 8.68           | 5.60 | 5.62 | 7.46 | 6.84 | 13            | 6.92  | 8.81  | 9.22  | 10.20 | 8.79    | 7.15  |
| 14       | 7.60           | 6.33 | 7.39 | 5.87 | 6.80 | 14            | 6.47  | 8.27  | 8.20  | 9.59  | 8.13    | 6.96  |
| CROSS    |                |      |      |      |      |               |       |       |       |       |         |       |
| Gen 0    | 10.17          | 8.34 | 8.64 | 9.49 | 9.16 | 0             | 9.61  | 10.58 | 9.00  | 9.49  | 9.67    | 8.71  |
| 1        | 6.34           | 7.61 | 9.41 | 9.18 | 8.16 | 1             | 9.47  | 9.61  | 7.70  | 9.67  | 9.11    | 10.66 |
| 2        | 7.79           | 6.96 | 8.22 | 8.15 | 7.78 | 2             | 8.16  | 9.65  | 10.24 | 8.85  | 9.23    | 9.64  |
| 3        | 6.71           | 7.10 | 7.63 | 8.89 | 7.58 | 3             | 8.29  | 6.09  | 7.13  | 7.96  | 7.37    | 9.14  |
| 4        | 8.28           | 6.80 | 6.39 | 5.83 | 6.83 | 4             | 9.89  | 8.36  | 9.25  | 8.30  | 8.95    | 6.86  |
| 5        | 7.30           | 6.81 | 7.84 | 6.39 | 7.09 | 5             | 8.63  | 7.38  | 8.11  | 9.15  | 8.32    | 8.99  |
| 6        | 5.90           | 5.99 | 7.03 | 5.35 | 6.07 | 6             | 8.60  | 9.90  | 6.74  | 8.43  | 8.42    | 8.16  |
| 7        | 7.17           | 6.42 | 6.69 | 6.74 | 6.76 | 7             | 8.49  | 8.56  | 6.78  | 8.77  | 8.15    | 9.69  |
| 8        | 5.41           | 7.17 | 6.30 | 6.05 | 6.23 | 8             | 8.93  | 9.55  | 7.66  | 8.32  | 8.62    | 7.13  |
| 9        | 7.91           | 6.25 | 5.79 | 6.77 | 6.68 | 9             | 8.21  | 7.04  | 7.04  | 7.94  | 7.56    | 8.58  |
| 10       | 8.14           | 6.09 | 6.98 | 6.59 | 6.95 | 10            | 9.30  | 7.74  | 7.15  | 7.98  | 8.04    | 7.95  |
| 11       | 6.25           | 6.33 | 6.05 | 6.58 | 6.30 | 11            | 7.83  | 10.83 | 9.18  | 11.42 | 9.82    | 9.27  |
| 12       | 5.90           | 5.77 | 6.61 | 6.61 | 6.22 | 12            | 8.39  | 8.69  | 6.68  | 10.24 | 8.50    | 8.30  |
| 13       | 6.00           | 5.80 | 6.40 | 5.94 | 6.04 | 13            | 8.85  | 7.67  | 7.45  | 8.71  | 8.17    | 8.27  |
| 14       | 6.03           | 6.49 | 6.98 | 7.28 | 6.70 | 14            | 9.86  | 9.90  | 7.71  | 10.74 | 9.55    | 8.69  |

bristle number and phenotypic variance than the females tend to have higher coefficient of variation than the females; the inter-generation fluctuations for the males are more marked than for the females and this is particularly noticeable among the three unselected controls; the Oregon-R and Cross high selection lines show a definite decline in coefficient of variation (8% - 6%) for the first six generations and subsequently remain constant till the end of selection. The +3 high selection line, which is characterised by extremely poor response, maintains consistently low coefficient of variation (6%) over the 14 generations; The females of the three low lines show a remarkable similarity in trend, with their coefficients of variation remaining fairly constant over the first eight generations and then gradually increasing (8% - 9%) till G14. In fact the trend of coefficient of variation of the females of the low lines bears some resemblance to the mirror image of the Oregon-R and Cross high lines.

The above observations show that this measure of variability resulted in over-compensation for scale effects, with the population means being negatively correlated with the coefficient of variation. This feature has been reported by Rumball (1966) and was also apparent in the data of Falconer's (1955) large and small lines of mice. The conclusion would be that neither of the parameters, the phenotypic variance nor the coefficient of variation, is entirely satisfactory in portraying the genetic changes in the populations as a result of selection.

#### (iv) Realised heritability

This parameter was first employed by Falconer (1954) and is the ratio of the selection response to the selection differential. Realised heritability is regarded as being superior to the other parameters in

depicting the true genetic response by virtue of the assumption that factors like scale or natural selection which affect the selection response would exert a similar effect on the denominator, the selection differential. This means that the fraction itself will be relatively free of such bias.

The selection response for each generation is calculated according to the formula by Kojima and Kelleher (1963).

$$\Delta \bar{Y}_i = (\bar{Y}_i - \bar{C}_i) - (\bar{Y}_{i-1} - \bar{C}_{i-1})$$

where  $\Delta \bar{Y}_i$  = mean response of replicate at generation i

$\bar{Y}_i$  = mean abdominal bristle number at generation i in  
selection replicate

$\bar{C}_i$  = mean abdominal bristle number at generation i in  
control line

The response each generation obtained is thus corrected for bias due to environmental variations. Like the other parameters, considerable divergences among replicates within the lines are apparent, and for this reason the four replications in each line were averaged to give the line mean. Since the selection responses and selection differentials of the males were proportionately smaller than those of the females, this means that within a selection line, the realised heritabilities of the two sexes would be similar. Thus, for this parameter, it would be valid to combine the data of males and females. Fig. 6 shows the realised heritabilities of the high and low selection lines (sexes combined) for each generation. The trend within each line is quite clear. Among the high selection lines, the Oregon-R, +3 and Cross showed distinctly different patterns. The Cross high line maintained the highest realised heritability throughout the 14 generations although there was a slight decline



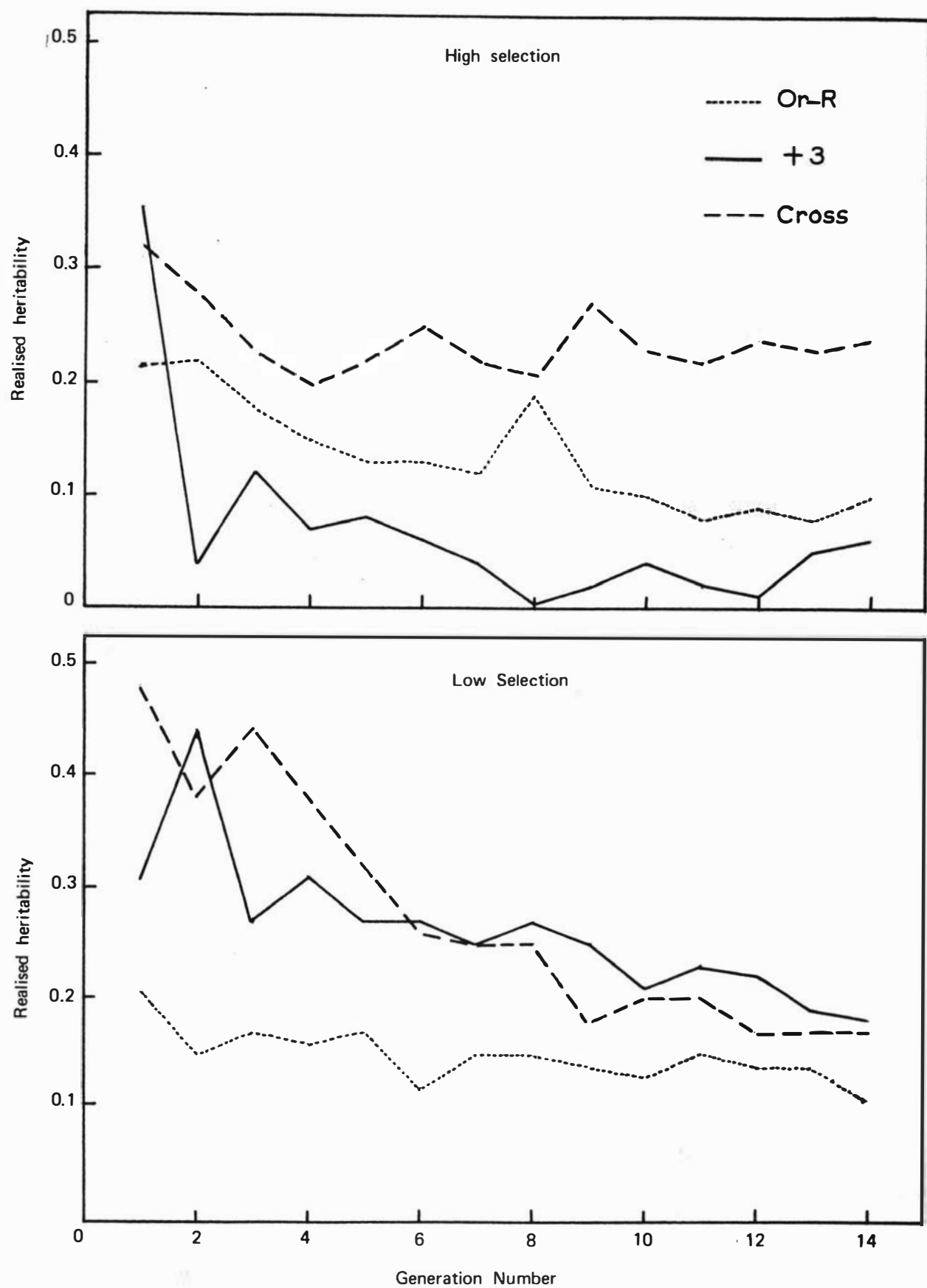


Fig. 6 Combined sexes realised heritability for high and low selection lines of Oregon-R , +3 and Cross.

in the first two generations. The Oregon-R high line on the other hand declined steadily from 0.20 - 0.10 over the 14 generations. The +3 high line declined sharply from 0.35 to 0.05 in the first generation and subsequently continued to maintain this low level.

The Oregon-R low line showed a gradual decline in realised heritability (0.20 - 0.10). The +3 and Cross low lines had higher initial realised heritabilities than that of the Oregon-R but the decline over the 14 generations was rather marked (0.40 - 0.17). The +3 population in particular displayed striking asymmetry in realised heritability in the high and low lines.

The data from the present selection experiment has been presented in four alternative forms in both tables and graphs. To conclude this section it seems fit to examine whether there was any general pattern of changes of these four parameters. One general feature among the selection lines, with the exception of the +3 high line, was the obvious intra-generation variability between replicates within the lines. For this reason the four replicates within each line have been averaged to give the line mean and subsequent observations and discussions were based on the behaviour of the selection lines rather than the individual replicates. It is simpler to follow the patterns of change of the selection lines since they are subjected to less generation to generation fluctuations and the trends over the 14 generations are more apparent to the eye. The trends of the abdominal bristle mean, phenotypic variance and realised heritability bear a qualitative resemblance to each other and present evidence that all selection lines, except the females of the Cross high line declined to varying degrees in the amount of additive genetic variance with the concomitant decrease in the selection response rate. Only the coefficient of variation exhibited qualitatively different trend

| Table 13: Average realised heritabilities of selection lines<br>for each generation (sexes combined) |                |       |       |               |      |       |
|------------------------------------------------------------------------------------------------------|----------------|-------|-------|---------------|------|-------|
| Gen.                                                                                                 | High selection |       |       | Low selection |      |       |
|                                                                                                      | Oregon-R       | +3    | Cross | Oregon-R      | +3   | Cross |
| 1                                                                                                    | 0.22           | 0.36  | 0.32  | 0.21          | 0.31 | 0.48  |
| 2                                                                                                    | 0.22           | 0.04  | 0.28  | 0.15          | 0.44 | 0.38  |
| 3                                                                                                    | 0.18           | 0.12  | 0.23  | 0.17          | 0.27 | 0.44  |
| 4                                                                                                    | 0.15           | 0.07  | 0.20  | 0.16          | 0.31 | 0.38  |
| 5                                                                                                    | 0.13           | 0.08  | 0.22  | 0.17          | 0.27 | 0.32  |
| 6                                                                                                    | 0.13           | 0.06  | 0.25  | 0.12          | 0.27 | 0.26  |
| 7                                                                                                    | 0.12           | 0.04  | 0.22  | 0.15          | 0.25 | 0.25  |
| 8                                                                                                    | 0.19           | -0.01 | 0.21  | 0.15          | 0.27 | 0.25  |
| 9                                                                                                    | 0.11           | 0.02  | 0.27  | 0.14          | 0.25 | 0.18  |
| 10                                                                                                   | 0.10           | 0.04  | 0.23  | 0.13          | 0.21 | 0.20  |
| 11                                                                                                   | 0.08           | 0.02  | 0.22  | 0.15          | 0.23 | 0.20  |
| 12                                                                                                   | 0.09           | 0.01  | 0.24  | 0.14          | 0.22 | 0.17  |
| 13                                                                                                   | 0.08           | 0.05  | 0.23  | 0.14          | 0.19 | 0.17  |
| 14                                                                                                   | 0.10           | 0.06  | 0.24  | 0.11          | 0.18 | 0.17  |

from the other three parameters and is an indication that at least for the abdominal bristle character, this parameter may be the least suitable of the four used in portraying the true genetic responses of selection lines.

The variability between replicates within lines was most noticeable in the Oregon-R low and Cross high lines. The responses from the three high lines were clearly different from each other. What is needed therefore is a detailed analysis of the data to evaluate statistically the significance of the differences both within and between lines. This statistical analysis is presented in the following section.

### C. ANALYSIS OF SELECTION RESPONSE

Presentation and discussion of the basic data (see Part V B) showed that selection responses obtained from the three different Drosophila populations, subjected to identical and simultaneous two-way selection, were variable. Obviously a descriptive account of the differential responses, though useful, is far from adequate in the sense that it does not allow statistically reliable conclusions to be drawn. Consequently, a detailed analysis of the selection responses is attempted. It was difficult to pre-determine the exact course the analysis should take, as the later steps depended to a large extent on the outcome of the earlier analysis. The main purpose of this analysis, however, is clear - to make a direct comparison of the responses both within and between populations. This section is divided into three parts: analysis of the average rate of response per generation, realised heritability and variability between replicates.

#### 1. Average response per generation

The simplest method of estimating the change in population mean brought about by one generation of selection is by division of the total response, obtained by subtraction of the first generation population mean from the last generation mean, by the number of generations of selection. This method has obvious weaknesses; one is that the data from the intermediate generations of selection, which could yield valuable information on the trends and inter-generation fluctuations of response, would not be taken into account. Another disadvantage is that since the generation means of the selection lines are well-known to be subject to inter-generation fluctuations due to causes like

sampling error, random drift and environmental variations, it would mean that if the mean of the first or last selection generation happens to deviate in the high or low direction, the average response obtained would be correspondingly biased upwards or downwards according to the direction and the size of the deviation.

When a suitable unselected control has been incorporated in the experimental design and held concurrently with the selection lines, a slightly different method of estimation could be used. The change in the mean of the selected line for one generation of selection could be evaluated by the formula (Kojima and Kelleher, 1963):

$$\Delta \bar{Y}_i = (\bar{Y}_i - \bar{C}_i) - (\bar{Y}_{i-1} - \bar{C}_{i-1})$$

where  $\Delta \bar{Y}_i$  = mean response at generation i

$\bar{Y}_i$  = mean abdominal bristle number at generation i  
in selection line

$\bar{C}_i$  = mean abdominal bristle number at generation i  
in control line

The average response is found by summing the mean response for each generation and dividing by the number of generations of selection.

Average response/generation:  $\bar{Y} = \sum \Delta \bar{Y}_i / t$

Standard deviation of average response =  $\frac{1}{t-1} (\Delta \bar{Y}_i - \Delta \bar{Y})^2$

This method is superior to the first as it takes into account the mean response for each generation of selection. The second advantage is that the environmental effects are reduced by use of the control (Bray et al., 1962). However, the responses obtained would still be subjected to other sources of bias such as genetic drift, sampling variation, inbreeding and scale effects.

A third commonly used method of estimation is to fit a linear regression line to the population mean plotted against generation number, with the slope of the line yielding an estimate of the average response. The distinct advantage of this method is that the error variance is minimised, thus affording a more precise estimate. Falconer (1953) was one of the earliest workers to employ this method of estimation and has pointed out that unless the two assumptions, absence of non-linearity and correlation between successive generations, inherent in the use of linear regression are realised, the estimate of average response would be in error. This method should theoretically be satisfactory for short-term selection experiments where the trends of change in the population mean are expected to be linear and effects of random drift, in causing correlations between successive generations of selection, are not likely to be important (Falconer, 1953). But on a long-term basis, where selection response rate is expected to decline, linear regression would not suffice. Instead regressions of higher order need to be employed. Attempts to fit more complex curves to selection data have been made. For example, James (1965) fitted three different curves - exponential regression, parabola and straight line - to the data of four selection experiments carried out by earlier workers. The criterion for the goodness-of-fit was based on the size of the sum of squares of the deviations of the actual values from the curve with the smallest deviations giving the best fit. In all four cases, the exponential curve gave the best fit and in two cases the parabola was superior to the straight line. This analysis served to show that the selection responses tended to decline progressively as selection proceeded.

For the present selection experiment, it was decided to evaluate the average response per generation by the use of linear regression method

and by the method used by Kojima and Kelleher (1963).

(1) Regression coefficient

The total response for each generation was found by subtracting the means of the unselected controls from their respective selection line means and this was regressed against generation number.

$$R_i = \bar{Y}_i - \bar{C}_i$$

where  $R_i$  = total response in  $i$ th generation

The responses thus obtained are corrected for effects due to changes in the environment and would reflect the true genetic response to a greater extent than the line means themselves. From the graphs of the changes in mean abdominal bristle number (Fig.1) it would appear that although the observed responses of the three high selection lines over the 14 generations of selection are fairly linear, the low selection lines show an apparent decrease in rate of response during the latter half of the selection experiment. For this reason, all the high and low selection lines would first be tested for linearity of selection responses before computing the regression coefficient of each replicate.

Test for non-linearity: Mather (1949) has given a method for testing the linearity of regression lines using the analysis of variance. All the high and low selection lines are tested for significance of non-linearity. As a numerical example, the analysis for the Oregon-R high and low selection lines are given in Table 14.

From Table 14 it can be seen that for both high and low selection lines of the Oregon-R, the regression component is highly significant. But in the low line, significant deviation from regression indicates that the response is non-linear, thus giving confirmation of earlier suspicions.

Table 14: Analysis of variance. Deviations from linear regression

| Table 14: Analysis of variance. Deviations from linear regression |                    |                |       |       |               |        |        |         |
|-------------------------------------------------------------------|--------------------|----------------|-------|-------|---------------|--------|--------|---------|
| OREGON-R: Gen. 1-14 (female data)                                 |                    |                |       |       |               |        |        |         |
| Source of Variation                                               | d.f.               | High selection |       |       | Low selection |        |        |         |
|                                                                   |                    | M.S.           | F     | Prob. | M.S.          | F      | Prob.  |         |
| Replicates                                                        | 3                  | 4.56           |       |       | 25.96         |        |        |         |
| Generations {                                                     | Regression         | 1              | 33.18 | 94.80 | V.small       | 235.39 | 294.23 | V.small |
|                                                                   | Dev. from<br>regr. | 12             | 7.46  | 1.77  | 0.20          | 1.84   | 2.30   | 0.025   |
| Error                                                             | 39                 | 13.49          |       |       | 0.80          |        |        |         |
|                                                                   | <u>39</u>          |                |       |       |               |        |        |         |
| Total                                                             | 55                 |                |       |       |               |        |        |         |



The +3 and Cross populations, subjected to the same tests for non-linearity, gave very similar results, namely, linearity of the high lines and non-linearity of the low lines over the 14 generations of selection. Thus it would seem that the method of linear regression is inadequate for measuring the rate of changes in bristle number of the three low selection lines. In view of the small numbers of degrees of freedom and also the computational labour involved, it was considered not worthwhile undertaking the process of curve fitting to the non-linear data for this present thesis. Since the trend of response in all three low selection lines seemed to fall into two fairly distinct phases, with the first seven generations of selection yielding good response while the latter seven generations poor or virtually no response, a possible simple way of overcoming this problem was to divide the 14 generations conveniently into two periods. The first seven generations were designated as Period 1 and the latter generations Period 2. Within each period, the responses tended to be fairly linear, so that computations of linear regression coefficients could be made for each replication within each period instead of for the whole period of 14 generations. To prove the validity of the assumption of linearity within each period, tests on non-linearity were again carried out for each period in the three low selection lines (sexes separate). Table 15 shows the test for the significance of deviations from linear regression lines of Period 1 and Period 2 of the Oregon-R low selection line. Division into two separate periods seemed to have successfully eliminated the non-linearity in Period 2 while for Period 1, the probability of non-significant deviations from linearity was increased. Once again very similar results were obtained from tests on non-linearity of regression lines of the separate periods of the +3 and Cross low selection lines.

Table 15: Analysis of variance. Deviations from linear regression

| Table 15: Analysis of variance. Deviations from linear regression |                    |                    |       |        |                     |       |       |      |
|-------------------------------------------------------------------|--------------------|--------------------|-------|--------|---------------------|-------|-------|------|
| OREGON-R: Low selection (female data)                             |                    |                    |       |        |                     |       |       |      |
| Source of Variation                                               | d.f.               | Period 1 (Gen.1-7) |       |        | Period 2 (Gen.8-14) |       |       |      |
|                                                                   |                    | M.S.               | F     | Prob.  | M.S.                | F     | Prob. |      |
| Replicates                                                        | 3                  | 3.95               |       |        | 27.32               |       |       |      |
| Generations                                                       | Regression         | 1                  | 56.66 | 153.14 | V.small             | 18.12 | 1.97  | 0.20 |
|                                                                   | Dev. from<br>regr. | 5                  | 1.60  | 4.32   | 0.05                | 1.64  | 0.18  | -    |
| Error                                                             | 18                 | 0.37               |       |        | 9.19                |       |       |      |
| Total                                                             | 27                 |                    |       |        |                     |       |       |      |

From these results, it was decided to compute the average rate of response of the low selection lines separately for the two periods. On the other hand, a linear regression line was fitted to the 14 generations of selection for each of the high selection lines.

The regression coefficient of each high and low selection replicate was evaluated. Table 16 shows the data of the total response of each generation for individual replicates of the Cross high selection line and included are the regression coefficients of each replicate, which are estimates of the average response rate (bristle number/generation).

| Table 16: Average response rate from the linear regression of response against generation number of the Cross high replicates |       |        |         |        |        |       |
|-------------------------------------------------------------------------------------------------------------------------------|-------|--------|---------|--------|--------|-------|
| Cross: High selection (female data)                                                                                           |       |        |         |        |        |       |
|                                                                                                                               | Rep.I | Rep.II | Rep.III | Rep.IV | Total  | Mean  |
| Gen. 1                                                                                                                        | 0.71  | 0.40   | 1.58    | 0.67   | 3.36   | 0.84  |
| 2                                                                                                                             | 1.99  | 0.41   | 1.68    | 1.70   | 5.78   | 1.45  |
| 3                                                                                                                             | 3.85  | 2.19   | 1.03    | 3.65   | 10.72  | 2.68  |
| 4                                                                                                                             | 4.74  | 2.63   | 1.87    | 2.96   | 12.20  | 3.05  |
| 5                                                                                                                             | 5.60  | 4.56   | 2.38    | 5.27   | 17.81  | 4.45  |
| 6                                                                                                                             | 5.47  | 6.20   | 5.09    | 6.56   | 23.32  | 5.83  |
| 7                                                                                                                             | 5.40  | 5.44   | 5.40    | 7.40   | 23.64  | 5.91  |
| 8                                                                                                                             | 5.73  | 8.00   | 5.62    | 7.40   | 26.75  | 6.69  |
| 9                                                                                                                             | 7.93  | 11.02  | 7.97    | 10.39  | 37.31  | 9.32  |
| 10                                                                                                                            | 9.28  | 10.33  | 8.37    | 11.01  | 38.99  | 9.75  |
| 11                                                                                                                            | 10.17 | 10.89  | 8.06    | 9.87   | 38.99  | 9.75  |
| 12                                                                                                                            | 12.36 | 12.06  | 9.49    | 13.00  | 46.91  | 11.73 |
| 13                                                                                                                            | 12.50 | 12.94  | 10.04   | 13.32  | 48.80  | 12.20 |
| 14                                                                                                                            | 13.66 | 12.97  | 11.28   | 14.41  | 52.32  | 13.08 |
|                                                                                                                               | 99.39 | 100.04 | 79.86   | 107.61 | 386.90 |       |
| Reg. coeff.(b)                                                                                                                | 0.933 | 1.085  | 0.827   | 1.053  |        | 0.974 |

The table shows that the values of the average response of individual replicates of the Cross high line range from 0.827 (XHIII) to 1.085 bristles per generation (XHII). The question which follows is whether the four individual response rates within the Cross high line are homogeneous or not. A test for homogeneity of regression coefficients within selection lines is needed and it would yield valuable information on the repeatability of selection responses within populations.

Test for homogeneity of regression coefficients within selection lines:

An analysis of covariance was employed, with the standard F-test for the homogeneity of the four within-replicate regression coefficients. If the F-ratio does not reach significance, the regression coefficients of the four replicates are regarded as homogeneous and the average regression coefficient, calculated from the pooled data, then gives the best estimate of the average response rate of a particular selection line. The test on homogeneity of regression coefficients of the Cross high line is given as a numerical example (Table 17). The highly significant F-value indicated that the four regression coefficients were heterogeneous and consequently the Cross high replicates were each characterised by their own particular rate of response.

The other selection lines were subjected to similar tests on homogeneity. Table 18 gives a summary of the F-tests for the three high selection lines (sexes separate). The intra-replicate regression coefficients of the Oregon-R and +3 high lines were not significantly different so that the average regression coefficients obtained from the pooled data would give the best description of the rate of response of these two high lines. Finding heterogeneity of regression lines in the Cross and not in the high lines derived from the two original

| Table 17: Test for homogeneity of regression coefficients of the<br>Cross high selection line (female data) |      |                                    |           |            |                  |                |            |                  |
|-------------------------------------------------------------------------------------------------------------|------|------------------------------------|-----------|------------|------------------|----------------|------------|------------------|
| Source of<br>Variation                                                                                      | d.f. | $\sum x^2$                         | $\sum xy$ | $\sum y^2$ | Reg. coeff.<br>b | Errors<br>d.f. | of<br>S.S. | Estimate<br>M.S. |
| Within Reps.                                                                                                |      |                                    |           |            |                  |                |            |                  |
| Rep. I                                                                                                      | 13   | 227.50                             | 212.33    | 207.48     | 0.933            | 12             | 9.31       |                  |
| Rep. II                                                                                                     | 13   | 227.50                             | 246.88    | 277.86     | 1.085            | 12             | 9.95       |                  |
| Rep. III                                                                                                    | 13   | 227.50                             | 188.17    | 163.30     | 0.827            | 12             | 7.66       |                  |
| Rep. IV                                                                                                     | 13   | 227.50                             | 239.57    | 259.27     | 1.053            | 12             | 6.99       |                  |
| Pooled Reps.                                                                                                | 52   | Deviations from indiv. regressions |           |            |                  | 48             | 33.91      | 0.707            |
|                                                                                                             |      | 910.00                             | 886.95    | 907.91     | 0.975            | 51             | 43.43      | 0.852            |
|                                                                                                             |      | Between regression coefficients    |           |            |                  | 3              | 9.52       | 3.173**          |

| Table 18: Test for homogeneity of within-replicate regression coefficients of the high selection lines |      |                    |      |       |      |       |        |
|--------------------------------------------------------------------------------------------------------|------|--------------------|------|-------|------|-------|--------|
| Summary of F-tests                                                                                     |      |                    |      |       |      |       |        |
| HIGH SELECTION LINE<br>(Whole Period)                                                                  |      | Oregon-R           |      | +3    |      | Cross |        |
|                                                                                                        |      | <u>Female data</u> |      |       |      |       |        |
| Source of Variation                                                                                    | d.f. | M.S.               | F    | M.S.  | F    | M.S.  | F      |
| Deviations from<br>aver. regression                                                                    | 51   | 0.411              |      | 1.245 |      | 0.852 |        |
| Between regression<br>coefficients                                                                     | 3    | 0.463              | 1.14 | 0.920 | 0.72 | 3.173 | 4.49** |
| Deviations from<br>indiv. regressions                                                                  | 48   | 0.408              |      | 1.265 |      | 0.707 |        |
|                                                                                                        |      | <u>Male data</u>   |      |       |      |       |        |
| Deviations from<br>aver. regression                                                                    | 51   | 0.255              |      | 0.769 |      | 0.846 |        |
| Between regression<br>coefficients                                                                     | 3    | 0.240              | 0.95 | 0.463 | 0.59 | 3.287 | 4.74** |
| Deviations from<br>indiv. regressions                                                                  | 48   | 0.253              |      | 0.788 |      | 0.693 |        |

laboratory strains was not surprising, since the initial samples of the Cross replicates were drawn from the variable  $F_3$  generation and would therefore tend to be more genetically divergent to start with.

Similar tests for the homogeneity of regression lines were carried out for each period of each of the low selection lines (Table 19). The F-values of the low selection lines do not approach significance on any occasion and consequently it can be concluded that the average response

| Table 19: Test for homogeneity of within-replicate regression coefficients of low selection lines (female data). |      |          |       |                 |       |       |       |
|------------------------------------------------------------------------------------------------------------------|------|----------|-------|-----------------|-------|-------|-------|
| Summary of F-tests                                                                                               |      |          |       |                 |       |       |       |
| LOW SELECTION<br>(female data)                                                                                   |      | Oregon-R |       | +3              |       | Cross |       |
|                                                                                                                  |      |          |       | <u>Period 1</u> |       |       |       |
| Source of Variation                                                                                              | d.f. | M.S.     | F     | M.S.            | F     | M.S.  | F     |
| Deviations from<br>aver. regression                                                                              | 23   | 0.640    |       | 1.963           |       | 0.833 |       |
| Between regression<br>coefficients                                                                               | 3    | 0.273    | 0.393 | 0.537           | 0.246 | 1.487 | 2.024 |
| Deviations from<br>indiv. regressions                                                                            | 20   | 0.695    |       | 2.177           |       | 0.735 |       |
|                                                                                                                  |      |          |       | <u>Period 2</u> |       |       |       |
| Deviations from<br>aver. regression                                                                              | 23   | 0.728    |       | 0.689           |       | 0.572 |       |
| Between regression<br>coefficients                                                                               | 3    | 1.360    | 2.147 | 1.320           | 2.222 | 1.090 | 2.204 |
| Deviations from<br>indiv. regressions                                                                            | 20   | 0.634    |       | 0.594           |       | 0.495 |       |

rates of individual replicates within each period of the three low lines are homogeneous. This then allows the average regression coefficients to be used as the response rates of the low selection lines and these in turn could be tested for heterogeneity of responses between populations.

(ii) Mean response

For each selection line, the generation means of the four replicates were averaged to give the line mean and the actual change in abdominal

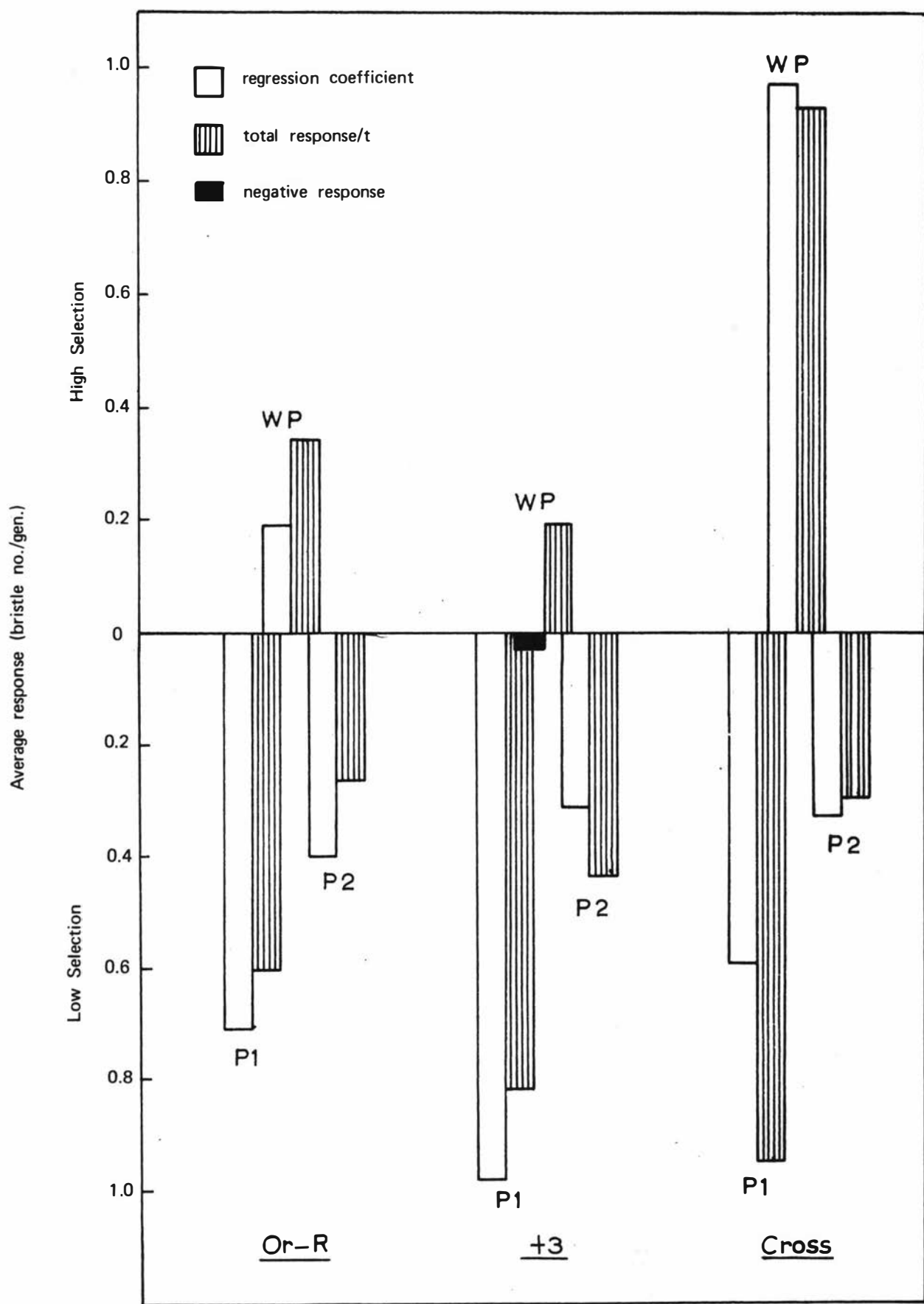


Fig. 7. Comparison of the 2 estimations of average response per generation — regression coefficient and response/t, of Oregon-R, +3 and Cross selection lines (female data).  
Whole Period (WP), Period 1 (P1) and Period 2 (P2).



bristle number in one generation of selection was evaluated by the formula:

$$\Delta \bar{Y}_i = (\bar{Y}_i - \bar{C}_i) - (\bar{Y}_{i-1} - \bar{C}_{i-1})$$

The average responses of the high and low selection lines in each generation are given in Table 20 and included are the mean responses and their standard errors. One noticeable feature of the +3 high selection responses is that six out of the 14 generation responses are negative in value; that is, opposite to the direction of selection so that high selection in this population was virtually ineffective.

Thus, the parameter - average response rate per generation - has been measured using two different methods. It is of interest to compare the two estimates of each selection line to assess the size and also any trends of the discrepancies between the two. To simplify the comparison, the selection line means were used. The average regression coefficients of the selection lines were used, although it must be remembered that for the Cross high selection line this value is strictly not valid since the four replicates were heterogeneous. Fig. 7 illustrates the difference between the two estimates of each selection line. For the high selection lines, the two estimates of the average responses taken over the whole period of 14 generations were compared while for the low lines the two estimates of average responses in Period 1 and Period 2 were compared separately. This diagram also provides a simple way of comparing the average responses between the different selection lines. It can be seen that the average responses of the high selection lines estimated by the first method, the linear regression analysis, are highly variable, with the +3 high line giving negative response. However, the average responses measured by the second method ( $\sum \Delta Y_i / t$ ) are all positive and the

Table 20: Mean response for high and low selection lines

| <u>HIGH SELECTION</u>        |    | Female data |             |             | Male data   |             |             |
|------------------------------|----|-------------|-------------|-------------|-------------|-------------|-------------|
|                              |    | Or-R        | +3          | Cross       | Or-R        | +3          | Cross       |
| Gen.                         | 1  | 0.78        | 1.13        | 0.84        | 0.65        | 1.08        | 1.66        |
|                              | 2  | 0.83        | -0.84       | 0.61        | 0.68        | -0.97       | 1.55        |
|                              | 3  | 0.24        | 1.35        | 1.23        | 0.51        | 0.46        | -0.29       |
|                              | 4  | 0.35        | -0.80       | 0.37        | 0.06        | 0.23        | 0.47        |
|                              | 5  | 0.04        | 0.47        | 1.40        | 0.10        | 0.40        | 0.58        |
|                              | 6  | 0.30        | -0.01       | 1.38        | 0.51        | -0.28       | 1.67        |
|                              | 7  | 0.06        | 0.06        | 0.08        | 0.05        | -0.64       | -0.09       |
|                              | 8  | -0.28       | -1.14       | 0.78        | 0.26        | -0.67       | 0.09        |
|                              | 9  | 1.29        | 0.09        | 2.63        | 0.63        | 0.99        | 2.44        |
|                              | 10 | -0.11       | 1.48        | 0.43        | 0.09        | 0.00        | -0.78       |
|                              | 11 | -0.23       | -0.90       | 0.00        | 0.14        | -0.83       | 0.78        |
|                              | 12 | 0.19        | -0.45       | 1.98        | 0.44        | 0.38        | 1.37        |
|                              | 13 | 0.11        | 1.02        | 0.47        | 0.05        | 1.91        | 0.84        |
|                              | 14 | 1.26        | 1.25        | 0.88        | 0.81        | -0.15       | 0.85        |
| Mean response $\bar{Y}_{WP}$ |    | 0.345       | 0.194       | 0.934       | 0.279       | 0.136       | 0.767       |
| Std. error                   |    | $\pm 0.136$ | $\pm 0.486$ | $\pm 0.196$ | $\pm 0.094$ | $\pm 0.218$ | $\pm 0.234$ |
| <u>LOW SELECTION</u>         |    | Or-R        | +3          | Cross       | Or-R        | +3          | Cross       |
| Gen.                         | 1  | 0.78        | 1.13        | 2.66        | 0.65        | 1.08        | 1.42        |
|                              | 2  | 0.87        | 2.45        | 1.47        | 0.00        | 1.79        | 0.55        |
|                              | 3  | 0.64        | -1.30       | 1.47        | 0.67        | 0.69        | 2.47        |
|                              | 4  | -0.34       | 2.41        | 0.46        | 0.94        | 0.75        | 0.64        |
|                              | 5  | 1.40        | 0.06        | -0.01       | 0.28        | 0.48        | 0.47        |
|                              | 6  | 0.41        | 0.57        | 0.15        | 0.25        | 0.79        | -0.70       |
|                              | 7  | 0.46        | 0.42        | 0.46        | 0.27        | 0.60        | 0.70        |
|                              | 8  | 0.39        | 1.63        | 0.55        | 0.59        | 0.72        | 1.19        |
|                              | 9  | -0.16       | 0.46        | -1.13       | 0.24        | -0.03       | -1.57       |
|                              | 10 | 0.88        | 0.99        | 0.79        | -0.45       | 0.02        | 1.34        |
|                              | 11 | 0.95        | 1.34        | 1.15        | 1.25        | 1.05        | 0.49        |
|                              | 12 | 0.59        | 0.96        | -0.69       | -0.33       | 0.39        | -0.52       |
|                              | 13 | 0.21        | -0.15       | 0.82        | 0.66        | -1.13       | -0.07       |
|                              | 14 | -0.99       | -0.20       | 0.59        | -0.35       | 1.00        | -0.13       |
| Mean response                |    |             |             |             |             |             |             |
| Whole Period $\bar{Y}_{WP}$  |    | 0.435       | 0.628       | 0.624       | 0.334       | 0.586       | 0.449       |
| Std. error                   |    | $\pm 0.125$ | $\pm 0.300$ | $\pm 0.250$ | $\pm 0.134$ | $\pm 0.180$ | $\pm 0.272$ |
| Period 1 $\bar{Y}_{P1}$      |    | 0.603       | 0.820       | 0.951       | 0.437       | 0.883       | 0.793       |
| Std. error                   |    | $\pm 0.200$ | $\pm 0.502$ | $\pm 0.362$ | $\pm 0.123$ | $\pm 0.167$ | $\pm 0.366$ |
| Period 2 $\bar{Y}_{P2}$      |    | 0.267       | 0.436       | 0.297       | 0.230       | 0.289       | 0.104       |
| Std. error                   |    | $\pm 0.255$ | $\pm 0.355$ | $\pm 0.324$ | $\pm 0.242$ | $\pm 0.287$ | $\pm 0.382$ |

Table 21: Comparison of two methods of measuring response rate (bristle number per generation) of the selection lines

|                                            | Female data |        |        | Male data |        |        |
|--------------------------------------------|-------------|--------|--------|-----------|--------|--------|
|                                            | Or-R        | +3     | Cross  | Or-R      | +3     | Cross  |
| <u>HIGH SELECTION</u><br><u>(Gen.1-14)</u> |             |        |        |           |        |        |
| Regression coefficient                     | 0.191       | -0.029 | 0.975  | 0.134     | 0.012  | 0.685  |
| Total response/14                          | 0.345       | 0.194  | 0.934  | 0.279     | 0.136  | 0.767  |
| Difference                                 | -0.144      | -0.223 | 0.041  | -0.065    | -0.124 | -0.082 |
| <u>LOW SELECTION</u><br><u>(Gen.1-14)</u>  |             |        |        |           |        |        |
| Regression coefficient                     | 0.509       | 0.655  | 0.345  | 0.385     | 0.470  | 0.332  |
| Total response/14                          | 0.435       | 0.628  | 0.624  | 0.334     | 0.586  | 0.447  |
| Difference                                 | 0.074       | 0.027  | -0.279 | 0.051     | -0.116 | -0.117 |
| <u>LOW SELECTION</u><br><u>(Gen.1-7)</u>   |             |        |        |           |        |        |
| Regression coefficient                     | 0.711       | 0.980  | 0.592  | 0.645     | 0.916  | 0.687  |
| Total response/7                           | 0.603       | 0.820  | 0.951  | 0.437     | 0.883  | 0.793  |
| Difference                                 | 0.108       | 0.160  | -0.359 | 0.208     | 0.033  | -0.106 |
| <u>LOW SELECTION</u><br><u>(Gen.8-14)</u>  |             |        |        |           |        |        |
| Regression coefficient                     | 0.402       | 0.317  | 0.329  | 0.219     | 0.047  | 0.039  |
| Total response/7                           | 0.267       | 0.436  | 0.297  | 0.230     | 0.289  | 0.104  |
| Difference                                 | 0.135       | -0.199 | 0.032  | -0.011    | -0.242 | -0.065 |

differences between the high lines are less pronounced. The estimates of average response for each high and low line are given in Table 21. The difference between each pair of estimates for each line is also given. The second estimates of all the high selection lines, except for the females of the Cross, are larger than the first estimates (regression coefficients).

In contrast to the high selection lines, differences between the two estimates of the low lines were mostly positive, thus showing that the

first estimates were larger than the second. There is no obvious reason why the first method, the linear regression analysis, should yield larger values of response rate than the second method for the high lines and smaller values than the second method for the low lines. In the following sections where the analyses of differences between the average responses within and between populations are to be carried out, it is necessary to use the values obtained from one method of estimation. As a means of deciding which method of estimation to adopt, the standard errors of the two estimates were compared and the method which gave the smaller standard error was chosen.

The standard error of the first estimate is the square root of the variance of the regression coefficient:-

$$\sigma_b = \sqrt{\frac{\sum y^2 - (\sum xy)^2 / \sum x^2}{(n-2) \sum x^2}}$$

The standard error of the second estimate ( $\sum \Delta \bar{Y}_i / t$ ) is simply the standard deviation of the mean response of the selection line divided by the square root of the number of generations of selection.

$$\text{Standard error} = \sqrt{\frac{\sum (\Delta \bar{Y}_i - \Delta \bar{Y})^2}{(t-1)t}}$$

The standard errors of the two estimates of average response for each selection line are given in Table 22. It is clear that for all high and low selection lines, the regression coefficient is the more precise estimate, with a smaller standard error. The size of the standard errors are represented diagrammatically in Fig. 8 and the differences between the two estimates of standard errors are obvious. Hence,

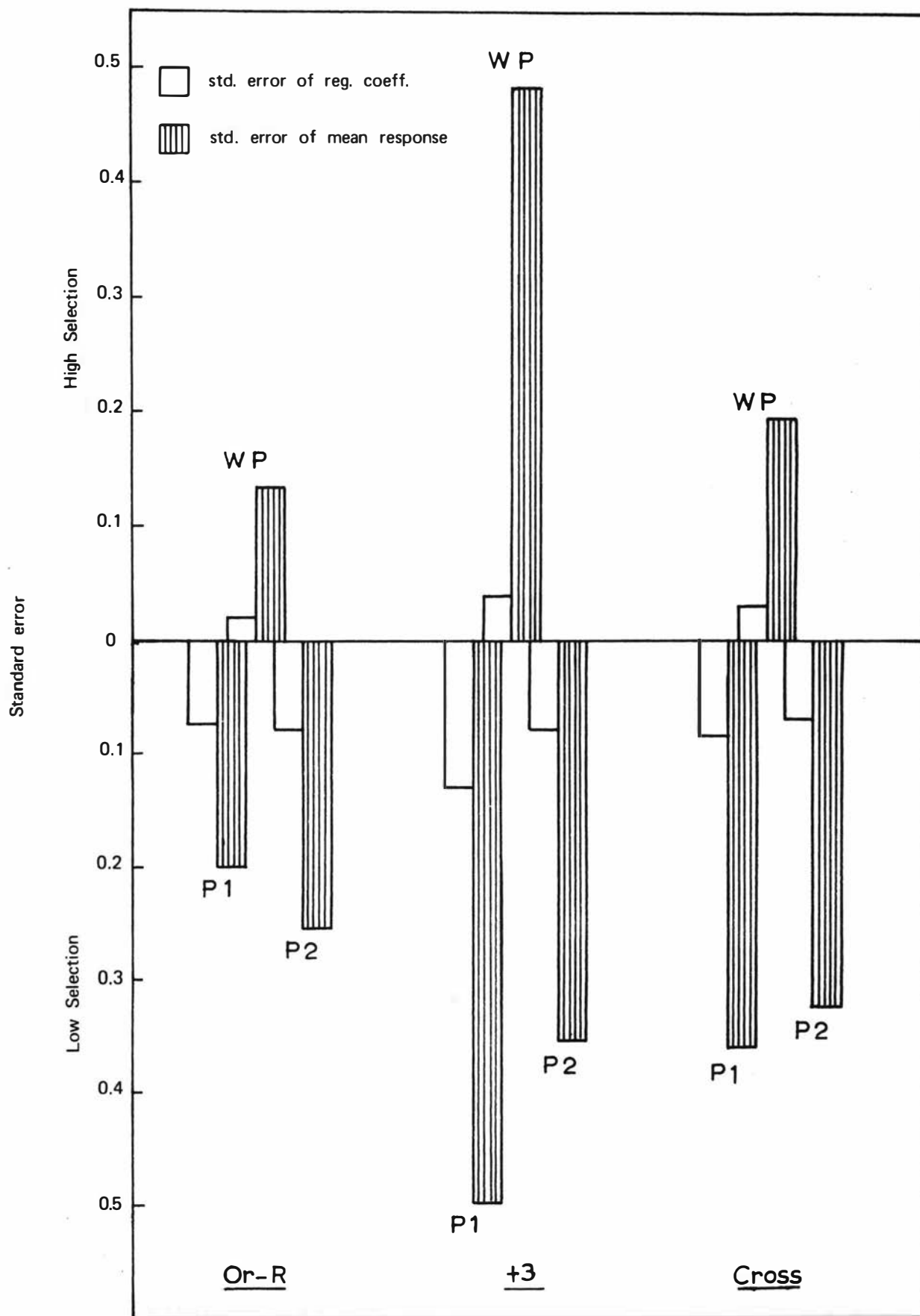


Fig. 8. Comparison of standard errors of average regression coefficient and mean response of the Oregon-R , +3 and Cross selection lines (female data).

Table 22: Comparison of the Standard errors of the two estimates of average selection response

| <u>Standard error</u>               | Female data |       |       | Male data |       |       |
|-------------------------------------|-------------|-------|-------|-----------|-------|-------|
|                                     | Or-R        | +3    | Cross | Or-R      | +3    | Cross |
| <u>HIGH SELECTION</u><br>(Gen.1-14) |             |       |       |           |       |       |
| Regression coefficient              | 0.021       | 0.037 | 0.030 | 0.017     | 0.028 | 0.030 |
| Total response/14                   | 0.136       | 0.486 | 0.196 | 0.094     | 0.218 | 0.234 |
| <u>LOW SELECTION</u><br>(Gen.1-14)  |             |       |       |           |       |       |
| Regression coefficient              | 0.034       | 0.048 | 0.031 | 0.030     | 0.045 | 0.036 |
| Total response/14                   | 0.125       | 0.300 | 0.250 | 0.134     | 0.180 | 0.271 |
| <u>LOW SELECTION</u><br>(Gen.1-7)   |             |       |       |           |       |       |
| Regression coefficient              | 0.076       | 0.132 | 0.086 | 0.071     | 0.075 | 0.098 |
| Total response/7                    | 0.200       | 0.502 | 0.362 | 0.123     | 0.167 | 0.366 |
| <u>LOW SELECTION</u><br>(Gen.8-14)  |             |       |       |           |       |       |
| Regression coefficient              | 0.081       | 0.078 | 0.071 | 0.055     | 0.062 | 0.061 |
| Total response/7                    | 0.255       | 0.355 | 0.324 | 0.242     | 0.287 | 0.382 |

the regression coefficients will be used as a measure of the response rate for all future analyses.

(iii) Intra-line differences in average response

Although the F-tests for the homogeneity of regression coefficients within selection lines revealed that significant differences existed between the replicates in the Cross high selection line, they did not show which replicates were indeed different from each other. A simple method of detecting which specific average responses differ significantly from each other is by direct comparison of their confidence

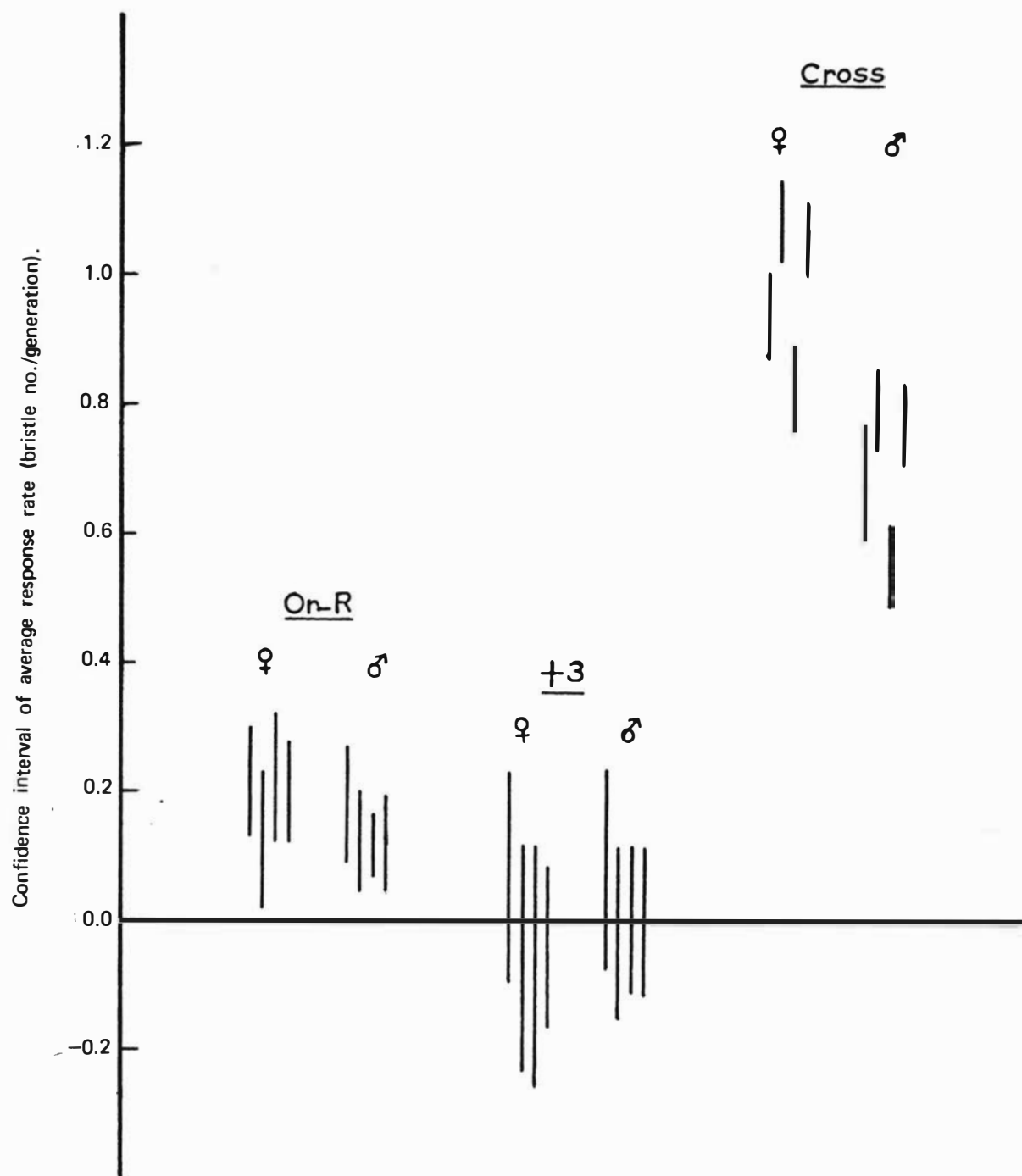


Fig. 9. Confidence intervals of average response rate for individual replicates of high selection lines.

intervals. In this way, the average response rates of any two replicates could be compared and any pairs of regression coefficients which are not enclosed by the confidence intervals of any one replicate are significantly different. The 95% confidence intervals of individual replicates of the high selection lines are given in Table 23. The interval estimates are represented diagrammatically in Fig. 9.

| Table 23: Confidence intervals of average response rates of individual replicates of high selection lines |                   |                     |                   |
|-----------------------------------------------------------------------------------------------------------|-------------------|---------------------|-------------------|
|                                                                                                           | Oregon-R          | +3                  | Cross             |
| <u>Female data</u>                                                                                        |                   |                     |                   |
| Rep. I                                                                                                    | 0.133±0.216±0.299 | -0.094± 0.065±0.224 | 0.873±0.933±0.994 |
| Rep. II                                                                                                   | 0.021±0.125±0.229 | -0.235±-0.063±0.109 | 1.025±1.085±1.145 |
| Rep. III                                                                                                  | 0.123±0.223±0.323 | -0.262±-0.074±0.114 | 0.767±0.827±0.887 |
| Rep. IV                                                                                                   | 0.122±0.200±0.278 | -0.165±-0.042±0.081 | 0.993±1.053±1.113 |
| <u>Male data</u>                                                                                          |                   |                     |                   |
| Rep. I                                                                                                    | 0.093±0.182±0.271 | -0.076± 0.077±0.230 | 0.590±0.650±0.711 |
| Rep. II                                                                                                   | 0.047±0.122±0.197 | -0.153±-0.021±0.111 | 0.730±0.790±0.850 |
| Rep. III                                                                                                  | 0.071±0.116±0.161 | -0.112±-0.001±0.110 | 0.491±0.551±0.611 |
| Rep. IV                                                                                                   | 0.042±0.116±0.190 | -0.133±-0.001±0.111 | 0.709±0.769±0.829 |

From the diagram, the homogeneity of the replicates within the Oregon-R and +3 high selection lines is obvious. For the Cross high line however, it can be seen that the first and third replicates responded at a significantly slower rate than the second and fourth replicates.

For the three low selection lines, the tests of non-linearity of regression lines revealed that the response rates of the first seven



generations of selection were different from those of the latter seven generations. Table 24 provides data on the regression coefficients (average response rates) of individual replicates in Period 1 and Period 2. Within each low selection line, the regression coefficients of the first and second periods were compared. If the two are statistically different, then division into two periods has achieved what it aimed to do. Since the average response rates of the four replicates within each period of the low selection lines were found to be homogeneous (see Part V C.1); consequently, the average regression coefficient of each line was used in the comparison of the two periods within each low line. For the average response of each period, 95% confidence intervals were computed. These interval estimates were employed in the comparisons of response rates of the two periods within each low line. The male data of the three low lines showed no overlapping between the interval estimates of Period 1 and Period 2. Thus, it confirmed the earlier evidence that the response rates in the two periods of the low lines were significantly different. For the Cross and the +3 lines, the Period 2 average responses were not significantly different from zero, showing that these two low lines appeared to have come to a plateau from generation 8 onwards. As a measure of magnitude of the differences between the response rates of Period 1 and Period 2, the ratio, P1 response rate over P2 response rate, for each replicate was computed (Table 24). This ratio was greater than one in all cases, indicating greater response rates in the first period of low selection. Extreme high values of the ratios were found among the +3 and the Cross low replicates, for example, in XLI where the value was 45.75 and this was the result of its response rate in Period 2 being virtually zero.

The females of the low lines showed less extreme differences

Table 24: Regression coefficients of individual replicates of low selection lines  
Interval estimates of average regression coefficients

| FEMALE DATA             |        |         |          |         |                                |
|-------------------------|--------|---------|----------|---------|--------------------------------|
| Regression coefficients |        |         |          |         |                                |
|                         | Rep. I | Rep. II | Rep. III | Rep. IV | Average                        |
| <u>Oregon-R</u>         |        |         |          |         |                                |
| Whole Period (Gen.1-14) | -0.725 | -0.525  | -0.388   | -0.395  | <del>-0.518</del> -0.509-0.576 |
| Period 1 (Gen.1-7)      | -0.678 | -0.855  | -0.628   | -0.685  | <del>-0.555</del> -0.711-0.867 |
| Period 2 (Gen.8-14)     | -0.699 | -0.332  | -0.404   | -0.174  | <del>-0.235</del> -0.402-0.569 |
| Period 1/Period 2       | 0.97   | 2.58    | 1.55     | 3.94    | 1.77                           |
| <u>+3</u>               |        |         |          |         |                                |
| Whole Period            | -0.468 | -0.864  | -0.758   | -0.529  | <del>-0.558</del> -0.655-0.751 |
| Period 1                | -0.785 | -1.023  | -1.002   | -1.110  | <del>-0.706</del> -0.980-1.254 |
| Period 2                | -0.089 | -0.584  | -0.392   | -0.205  | <del>-0.156</del> -0.317-0.479 |
| Period 1/Period 2       | 8.82   | 1.75    | 2.56     | 5.41    | 3.09                           |
| <u>Cross</u>            |        |         |          |         |                                |
| Whole Period            | -0.444 | -0.324  | -0.228   | -0.386  | <del>-0.283</del> -0.345-0.408 |
| Period 1                | -0.902 | -0.562  | -0.556   | -0.346  | <del>-0.414</del> -0.592-0.770 |
| Period 2                | -0.199 | -0.369  | -0.157   | -0.591  | <del>-0.182</del> -0.394-0.477 |
| Period 1/Period 2       | 4.53   | 1.52    | 3.54     | 0.59    | 1.80                           |
| MALE DATA               |        |         |          |         |                                |
|                         | Rep. I | Rep. II | Rep. III | Rep. IV | Average                        |
| <u>Oregon-R</u>         |        |         |          |         |                                |
| Whole Period            | -0.457 | -0.511  | -0.321   | -0.250  | <del>-0.324</del> -0.384-0.445 |
| Period 1                | -0.501 | -1.015  | -0.479   | -0.585  | <del>-0.500</del> -0.645-0.793 |
| Period 2                | -0.403 | -0.151  | -0.249   | -0.074  | <del>-0.106</del> -0.219-0.333 |
| Period 1/Period 2       | 1.24   | 6.72    | 1.92     | 7.91    | 2.95                           |
| <u>+3</u>               |        |         |          |         |                                |
| Whole Period            | -0.389 | -0.523  | -0.536   | -0.463  | <del>-0.381</del> -0.470-0.560 |
| Period 1                | -0.840 | -0.959  | -0.916   | -0.951  | <del>-0.762</del> -0.916-1.071 |
| Period 2                | -0.062 | -0.088  | -0.139   | -0.073  | <del>+0.081</del> -0.047-0.174 |
| Period 1/Period 2       | 13.55  | 10.90   | 6.59     | 13.03   | 19.49                          |
| <u>Cross</u>            |        |         |          |         |                                |
| Whole Period            | -0.386 | -0.302  | -0.320   | -0.274  | <del>-0.260</del> -0.332-0.403 |
| Period 1                | -0.915 | -0.660  | -0.708   | -0.466  | <del>-0.485</del> -0.687-0.890 |
| Period 2                | -0.020 | -0.031  | -0.023   | -0.115  | <del>+0.087</del> -0.039-0.164 |
| Period 1/Period 2       | 45.75  | 21.29   | 30.78    | 4.05    | 17.62                          |

between the two periods. All the replicates were characterised by greater than average response in the first period with two exceptions: in the Or-RLI, where the response rates of the two periods were similar; and the XLIV, where the trend was reversed with the Period 2 giving greater response than Period 1. Comparison of the interval estimates of the average regression coefficients of Period 1 and Period 2 showed slight over-lapping for the Oregon-R and Cross low lines. Although the selection response of the +3 and Cross low selection line males had ceased in Period 2, the females of all three low lines were still responding in the second period, but at a slower rate.

In conclusion, this analysis of low selection lines served to show that it is definitely more meaningful to describe the low responses in two separate phases; Period 1 of good response and Period 2 of poor or virtually zero response. This then completes the results of the trends of response within each high and low selection line of the Oregon-R, +3 and Cross populations. The most logical step to follow would be an analysis of the variability of average responses of the three different populations.

#### (iv) Inter-line differences in average response

The main aim of this analysis is to test for significant differences or similarities between the average responses of the three high and three low selection lines. Earlier analysis of inter-replicate differences within selection lines have shown the average response rates within all lines, except the Cross high line, to be homogeneous. The results from this present analysis would lend evidence to the generality of selection responses, for the same quantitative character, from different populations. The standard F-test was used to test the homogeneity of average regression coefficients of lines selected in the same direction (Table 25). The

**Table 25: F-tests for the homogeneity of average regression coefficients of lines selected in the same direction**

**Summary of F-tests**

| Source of Variation             | d.f. | <u>HIGH SELECTION (Whole Period)</u> |          |           |          |
|---------------------------------|------|--------------------------------------|----------|-----------|----------|
|                                 |      | Female data                          |          | Male data |          |
|                                 |      | M.S.                                 | F        | M.S.      | F        |
| Dev. from average pooled regr.  | 155  | 2.791                                |          | 2.122     |          |
| Dev. from indiv. pooled regrs   | 153  | 0.836                                |          | 0.622     |          |
| Between indiv. pooled regrs     | 2    | 152.330                              | 182.26** | 116.875   | 187.84** |
| <u>LOW SELECTION (Period 1)</u> |      |                                      |          |           |          |
|                                 | d.f. | M.S.                                 | F        | M.S.      | F        |
| Dev. from average pooled regr.  | 71   | 1.238                                |          | 0.803     |          |
| Dev. from indiv. pooled regrs   | 69   | 1.145                                |          | 0.757     |          |
| Between indiv. pooled regrs     | 2    | 4.435                                | 3.87*    | 0.293     | 3.15*    |
| <u>LOW SELECTION (Period 2)</u> |      |                                      |          |           |          |
|                                 | d.f. | M.S.                                 | F        | M.S.      | F        |
| Dev. from average pooled regr.  | 71   | 0.651                                |          | 0.413     |          |
| Dev. from indiv. pooled regrs   | 69   | 0.663                                |          | 0.420     |          |
| Between indiv. pooled regrs     | 2    | 0.235                                | 0.35     | 0.165     | 0.392    |

Table 26: Interval estimates for the average selection responses (bristle number/generation) of high and low selection lines

| Selection line     | High selection      | Low selection        |                      |
|--------------------|---------------------|----------------------|----------------------|
|                    | Whole Period        | Period 1             | Period 2             |
| <u>FEMALE DATA</u> |                     |                      |                      |
| Or-R               | 0.148± 0.191±0.234  | -0.555±-0.711±-0.867 | -0.235±-0.402±-0.569 |
| +3                 | -0.103±-0.029±0.046 | -0.706±-0.980±-1.254 | -0.156±-0.317±-0.479 |
| Cross: Aver.       | 0.915± 0.975±1.035  | -0.414±-0.592±-0.769 | -0.182±-0.329±-0.477 |
| Rep.I              | 0.873± 0.933±0.993  |                      |                      |
| Rep.II             | 1.025± 1.085±1.145  |                      |                      |
| Rep.III            | 0.767± 0.827±0.887  |                      |                      |
| Rep.IV             | 0.993± 1.053±1.113  |                      |                      |
| <u>MALE DATA</u>   |                     |                      |                      |
| Or-R               | 0.099± 0.134±0.169  | -0.500±-0.645±-0.793 | -0.106±-0.219±-0.333 |
| +3                 | -0.044± 0.012±0.069 | -0.762±-0.916±-1.071 | -0.174±-0.047± 0.081 |
| Cross: Aver.       | 0.625± 0.685±0.745  | -0.485±-0.687±-0.890 | -0.164±-0.039± 0.087 |
| Rep.I              | 0.590± 0.650±0.711  |                      |                      |
| Rep.II             | 0.730± 0.790±0.850  |                      |                      |
| Rep.III            | 0.491± 0.551±0.611  |                      |                      |
| Rep.IV             | 0.709± 0.769±0.829  |                      |                      |

heterogeneity of average regression coefficients of the three high lines was found to be highly significant. For low selection, significant heterogeneity of the average responses occurred in the first period only. Here again, comparisons between the selection lines were made using the interval estimates. Table 26 gives the 5% confidence intervals of the average

regression coefficients of the high and low selection lines as well as that of each of the Cross high replicates, since they are heterogeneous. The three high selection lines are clearly different from each other, with the Cross giving the greatest response and the +3 showing negative response although it is not significantly different from zero.

Differences between the low lines in Period 1 are less extreme than those between the high lines and there appears to be a reversal of trends, with the +3 giving the greatest rate of downward response and the Cross the least. The general conclusion from the results of this analysis is that the high selection responses from the three different Drosophila populations are more heterogeneous than the low responses.

#### (v) Patterns of two-directional response

In the earlier section where the basic data of the changes in the mean abdominal bristle number of the selection lines were discussed (see Part V B 2(1) ), different patterns of asymmetrical two-way responses were noted for all three populations. This section will be devoted to the evaluation and comparison of the asymmetry observed in each of the three populations, using the rate of response as the parameter for analysis. To test for the significance of the difference between the high and low response rates of each population, a t-test was employed. Table 27 shows the average response rate for each high and low selection line. For each population, the high selection average response over the whole period is compared in turn with the low response in Period 1 and Period 2. Any change in pattern of asymmetry from Period 1 to Period 2 is due to the change in the low response rate.

The pattern of two-way response of each population in each period will be discussed separately. From Table 27, it was clear that the +3

**Table 27: Asymmetry of selection response. Average regression coefficients of high and low selection lines**

|                                                                                                          | Female Data      |                   |                  | Male data        |                  |                  |
|----------------------------------------------------------------------------------------------------------|------------------|-------------------|------------------|------------------|------------------|------------------|
|                                                                                                          | Or-R             | +3                | Cross            | Or-R             | +3               | Cross            |
| <u>Period 1</u>                                                                                          |                  |                   |                  |                  |                  |                  |
| High selection                                                                                           | 0.191<br>(0.001) | -0.029<br>(0.001) | 0.975<br>(0.001) | 0.134<br>(0.001) | 0.012<br>(0.001) | 0.685<br>(0.9)   |
| Low selection                                                                                            | 0.711            | 0.980             | 0.592            | 0.645            | 0.916            | 0.687            |
| <u>Period 2</u>                                                                                          |                  |                   |                  |                  |                  |                  |
| High selection                                                                                           | 0.191<br>(0.005) | -0.029<br>(0.005) | 0.975<br>(0.001) | 0.134<br>(0.2)   | 0.012<br>(0.7)   | 0.685<br>(0.001) |
| Low selection                                                                                            | 0.402            | 0.317             | 0.329            | 0.219            | 0.047            | 0.039            |
| ( ) Significance probability of the difference between each pair of high and low regression coefficients |                  |                   |                  |                  |                  |                  |

and Oregon-R populations showed a distinctly negative asymmetrical pattern of two-way responses in Period 1 and this negative asymmetry was more marked in the +3. For the Cross population, in Period 1 the two sexes showed differential behaviour with the males giving symmetrical two-directional response while the females, pronounced positive asymmetry. The males of the Cross low line deviated from normal behaviour in giving greater responses than the females, whereas, in all other instances the females with higher mean number of abdominal bristles than the males always gave proportionately greater responses.

In Period 2, the Oregon-R and +3 females continued to show a negative

asymmetry although it was less pronounced due to the decreased low response rates in this period. This decline in response rate of the low lines could be attributed to causes like the depletion of additive genetic variability or natural selection operating against individuals extreme for low bristle number. The response rates of the males of the Oregon-R and +3 low lines declined so considerably in Period 2 that they became similar to their respective high selection response rates. This resulted in symmetry of responses in Period 2 which is in contrast to the negative asymmetry in Period 1. The response rate of the females of the Cross low line declined in Period 2 resulting in positive asymmetry which was more pronounced than that in the first period. For the males of the Cross, in contrast to the symmetry in Period 1, positive asymmetry was observed in Period 2.

In conclusion, the two original laboratory strains (Oregon-R and +3) showed similarity in their selection responses with regard to the negative asymmetrical patterns of two-way responses, although the degree of asymmetry was more extreme in the +3 population. The Cross also demonstrated asymmetry, but in contrast to the two parental strains its high line gave good sustained response over the 14 generations of selection, thus giving rise to positive asymmetry. From observations of responses in the three different populations there is evidence that the genetic systems affecting low bristle number in the two laboratory strains are similar, and this could partly explain the similarity in trends of low selection response over the 14 generations from both original strains and the Cross. On the other hand, the genes or gene complexes responsible for increasing abdominal bristles appear to be different in the two original populations, so that pooling the two together to form the Cross resulted in an increase in genetic variability. This could account



partly for the good response of the Cross high line despite the poor response of the Oregon-R high line and the almost negligible response of the +3 high line.

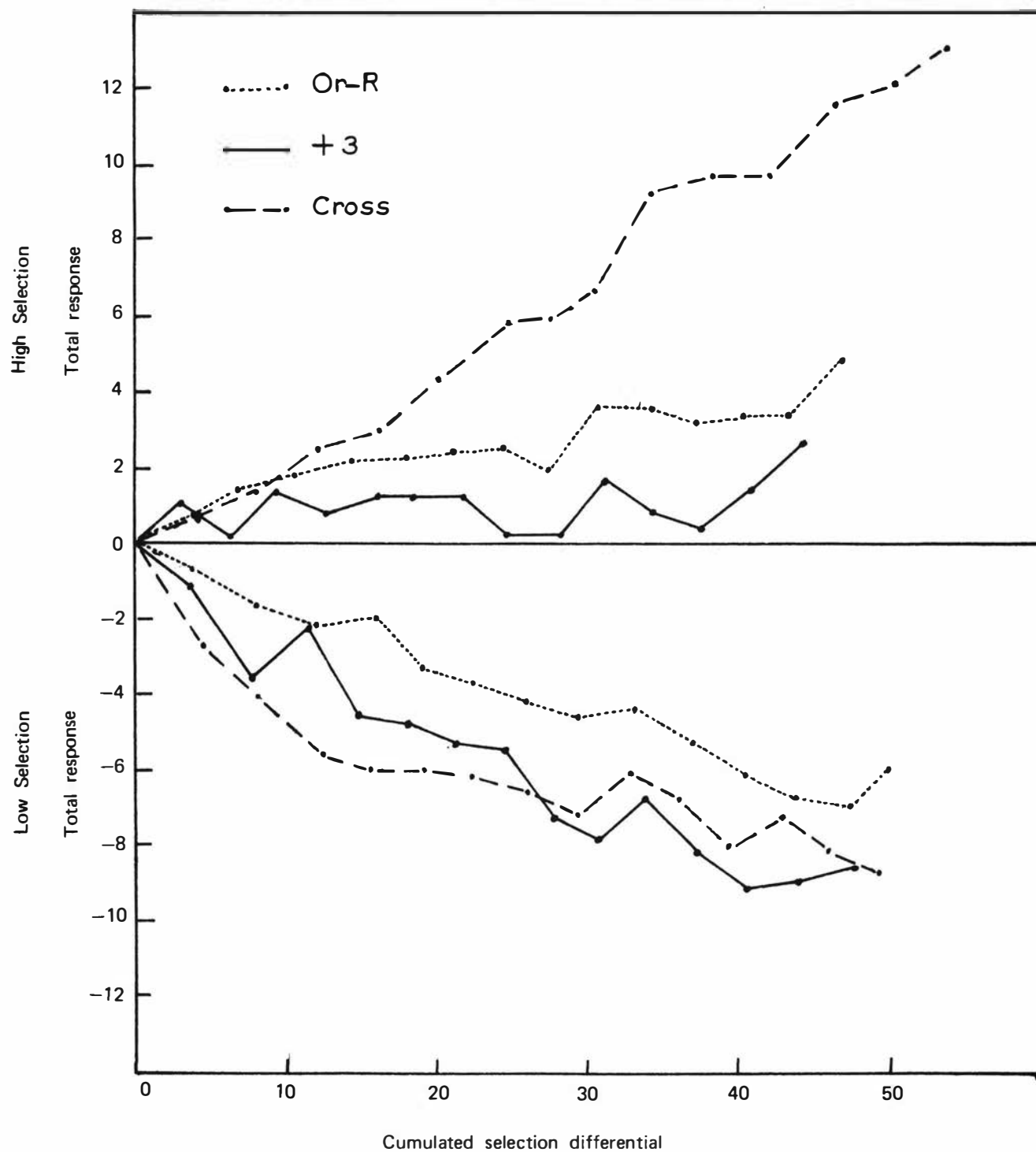


Fig. 10. Total response plotted against cumulated selection differential of high and low selection lines of the Oregon-R , +3 and Cross populations (female data).

## 2. Realised heritabilities

The merits of presenting the data on selection response in the form of realised heritability have been discussed by Falconer (1960). The chief advantage is that the ratio of response over selection differential should be relatively free of bias from effects of scale and natural selection and should thus give a truer representation of the underlying genetic changes in the population as a result of selection rather than other parameters, such as the population mean, phenotypic variance and coefficient of variation. For this reason, a detailed analysis of the realised heritabilities within and between selection lines will be carried out, using similar statistical methods as that used for the analysis of the average response rate.

### (i) Intra-line differences in realised heritability

The average realised heritability of each replicate (sexes considered separately) is obtained by the linear regression of total response each generation against cumulated selection differential. Fig. 10 shows the response plotted against cumulated selection differential for each of the high and low selection lines over the 14 generations. The selection line response and the cumulated selection differential were found by averaging the four intra-line replicates for each generation. All the high and low lines do not appear to depart from linearity and consequently, the test for non-linearity of regression lines was not applied. The realised heritabilities of the high and low selection replicates are given in Table 28. One aberrant feature from the data is the negative values of realised heritabilities of three of the four replicates of the +3 high line. However, they were found to be not significantly different from zero. Variation between replicates within selection lines is quite

| Table 28: Intra-replicate realised heritabilities (regression coefficients) (Sexes separate) |             |        |       |           |        |       |
|----------------------------------------------------------------------------------------------|-------------|--------|-------|-----------|--------|-------|
|                                                                                              | Female data |        |       | Male data |        |       |
|                                                                                              | Or-R        | +3     | Cross | Or-R      | +3     | Cross |
| <u>HIGH SELECTION</u>                                                                        |             |        |       |           |        |       |
| Rep. I                                                                                       | 0.068       | 0.022  | 0.247 | 0.061     | 0.026  | 0.195 |
| Rep. II                                                                                      | 0.038       | -0.019 | 0.296 | 0.038     | -0.008 | 0.265 |
| Rep. III                                                                                     | 0.061       | -0.024 | 0.214 | 0.036     | -0.002 | 0.157 |
| Rep. IV                                                                                      | 0.060       | -0.013 | 0.272 | 0.037     | -0.006 | 0.224 |
| <u>LOW SELECTION</u>                                                                         |             |        |       |           |        |       |
| Rep. I                                                                                       | 0.191       | 0.146  | 0.133 | 0.142     | 0.129  | 0.139 |
| Rep. II                                                                                      | 0.133       | 0.236  | 0.095 | 0.153     | 0.189  | 0.119 |
| Rep. III                                                                                     | 0.119       | 0.234  | 0.075 | 0.108     | 0.199  | 0.120 |
| Rep. IV                                                                                      | 0.116       | 0.175  | 0.121 | 0.080     | 0.154  | 0.090 |

apparent from the data in Table 28. Consequently, all the selection lines were tested for homogeneity of intra-replicate realised heritabilities using the standard F-test. A summary of the F-test is presented in Tables 29(a) and 29(b). Significant heterogeneity was detected in the Cross high line and the Oregon-R low line for both males and females while only the females of the +3 low line showed heterogeneity. The behaviour of the low selection lines was contrary to expectation, with the two original strains - Oregon-R and +3 - showing greater differences between replicates than the hybrid population. The behaviour of the high lines was more in accordance with expectations, with the Cross showing greater heterogeneity than the Oregon-R and +3 high lines.

The 95% confidence intervals were computed for each of the intra-

Table 29(a): Test for homogeneity of intra-replicate regression coefficients (realised heritabilities) of high selection lines

Summary of F-tests

| <u>HIGH SELECTION</u>         |      | Oregon-R |      | +3                 |      | Cross |        |
|-------------------------------|------|----------|------|--------------------|------|-------|--------|
| Source of Variation           | d.f. |          |      | <u>Female data</u> |      |       |        |
|                               |      | M.S.     | F    | M.S.               | F    | M.S.  | F      |
| Dev. from aver. regression    | 51   | 0.418    |      | 1.245              |      | 0.949 |        |
| Betw. regression coefficients | 3    | 0.427    | 1.02 | 0.937              | 0.74 | 4.053 | 5.37** |
| Dev. from indiv. regressions  | 48   | 0.418    |      | 1.264              |      | 0.755 |        |
| <u>Male data</u>              |      |          |      |                    |      |       |        |
| Dev. from aver. regression    | 51   | 0.255    |      | 0.770              |      | 0.831 |        |
| Betw. regression coefficients | 3    | 0.290    | 1.15 | 0.493              | 0.63 | 3.747 | 5.58** |
| Dev. from indiv. regressions  | 48   | 0.253    |      | 0.788              |      | 0.648 |        |

Table 29(b): Test for homogeneity of intra-replicate regression coefficients (realised heritabilities) of low selection lines

Summary of F-tests

| <u>LOW SELECTION</u>          |      | Oregon-R |        | +3                 |       | Cross |      |
|-------------------------------|------|----------|--------|--------------------|-------|-------|------|
|                               |      |          |        | <u>Female data</u> |       |       |      |
| Source of Variation           | d.f. | M.S.     | F      | M.S.               | F     | M.S.  | F    |
| Dev. from aver. regression    | 51   | 0.929    |        | 1.854              |       | 0.815 |      |
| Betw. regression coefficients | 3    | 3.727    | 4.94** | 4.963              | 2.99* | 1.393 | 1.79 |
| Dev. from indiv. regressions  | 48   | 0.754    |        | 1.659              |       | 0.779 |      |
|                               |      |          |        | <u>Male data</u>   |       |       |      |
| Dev. from aver. regression    | 51   | 0.743    |        | 1.266              |       | 1.074 |      |
| Betw. regression coefficients | 3    | 0.632    | 3.99** | 1.224              | 1.58  | 1.090 | 0.76 |
| Dev. from indiv. regressions  | 48   | 2.520    |        | 1.933              |       | 0.827 |      |

**Table 30: The 95% confidence intervals of realised heritabilities of individual replicates (in percentage)**

|                       |          | Female data (%) | Male data (%) |
|-----------------------|----------|-----------------|---------------|
| <u>HIGH SELECTION</u> |          |                 |               |
| Oregon-R              | Rep. I   | 4.2 - 9.4       | 3.2 - 9.0     |
|                       | Rep. II  | 0.7 - 6.9       | 1.3 - 6.2     |
|                       | Rep. III | 3.2 - 11.8      | 2.2 - 5.1     |
|                       | Rep. IV  | 3.5 - 8.5       | 1.3 - 6.1     |
| +3                    | Rep. I   | -2.9 - 7.4      | -2.7 - 7.9    |
|                       | Rep. II  | -7.1 - 3.4      | -5.8 - 4.1    |
|                       | Rep. III | -8.5 - 3.8      | -4.1 - 3.7    |
|                       | Rep. IV  | -5.2 - 2.5      | -4.4 - 3.3    |
| Cross                 | Rep. I   | 21.5 - 27.9     | 15.8 - 23.2   |
|                       | Rep. II  | 26.0 - 33.3     | 23.5 - 29.5   |
|                       | Rep. III | 18.1 - 24.7     | 12.0 - 19.4   |
|                       | Rep. IV  | 24.2 - 30.3     | 19.0 - 25.7   |
| <u>LOW SELECTION</u>  |          |                 |               |
| Oregon-R              | Rep. I   | 15.5 - 22.7     | 10.9 - 17.5   |
|                       | Rep. II  | 9.6 - 16.9      | 10.8 - 19.8   |
|                       | Rep. III | 9.2 - 14.6      | 8.5 - 13.1    |
|                       | Rep. IV  | 8.0 - 15.3      | 4.4 - 11.7    |
| +3                    | Rep. I   | 9.1 - 20.1      | 7.7 - 18.0    |
|                       | Rep. II  | 19.0 - 28.2     | 12.9 - 25.0   |
|                       | Rep. III | 17.1 - 29.7     | 14.1 - 25.8   |
|                       | Rep. IV  | 11.3 - 23.7     | 10.2 - 20.6   |
| Cross                 | Rep. I   | 8.3 - 18.3      | 7.0 - 20.8    |
|                       | Rep. II  | 7.0 - 16.9      | 7.3 - 16.4    |
|                       | Rep. III | 3.2 - 11.8      | 7.2 - 16.9    |
|                       | Rep. IV  | 9.3 - 14.9      | 5.0 - 13.0    |

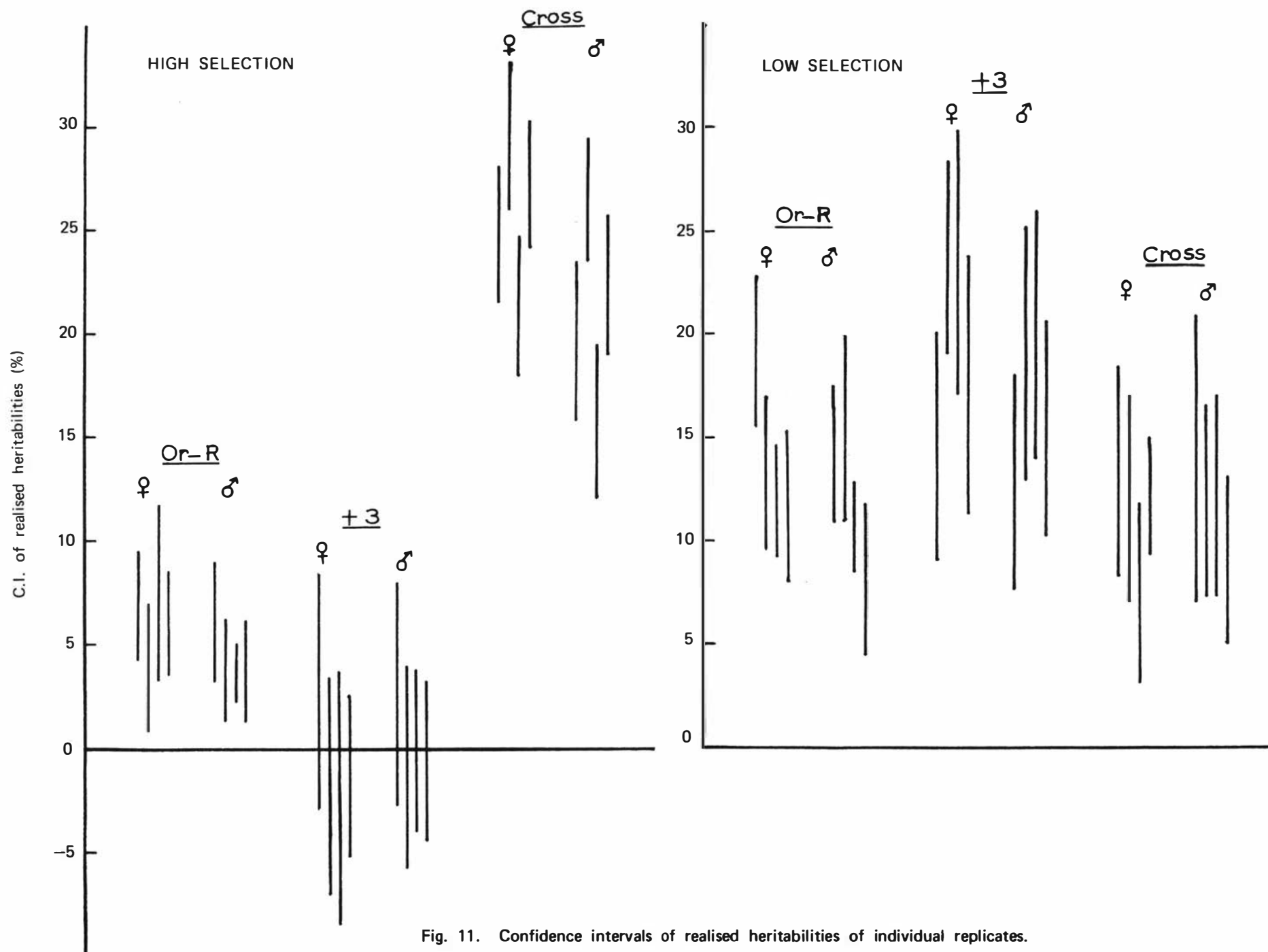


Fig. 11. Confidence intervals of realised heritabilities of individual replicates.



replicate realised heritabilities, and for the heterogeneous selection lines they were used as a means of determining which of the four replicates within the lines differed significantly from each other. All the values are given in percentages for ease of reference (Table 30). One feature is clear, that is, the large interval estimates of individual replicates indicating considerable sampling variation of the estimates of realised heritability, and gives warning against using simply the estimates themselves when discussing differences between replicates. The confidence intervals are represented diagrammatically in Fig. 11. Each vertical line represents the confidence interval of a single replicate and for each selection line the values for replicate I to IV are always given from left to right. It is clear from the diagram that the Oregon-R and +3 high selection replicates have low realised heritabilities and that all four +3 replicates are not significantly different from zero. The replicates within these two high lines are clearly homogeneous. The Cross high replicates are different from that of the Oregon-R and +3, in having high realised heritabilities. It can be seen clearly that XHII is significantly greater than XHIV and this difference is more pronounced for the males.

For the females of the Oregon-R low line, the realised heritabilities of Or-RLIII and Or-RLIV are apparently significantly smaller than that of Or-RLI. The +3 low line showed differences between the females of the first and second replicates. The homogeneity of the Cross low replicates, despite the heterogeneity among the Oregon-R and +3 low lines, was surprising and for the present the question as to the cause or causes of this deviation from the expectation of greater variability within the hybrid selection line must be left open.

(ii) Inter-line differences in realised heritability

From Fig. 11 it is apparent that among the high selection lines, the realised heritability of the Cross is considerably greater than the Oregon-R and +3. The +3 high line could be considered to have virtually zero realised heritability. However, the trend appears to be reversed among the low lines, with the +3 having the highest values and the Cross the lowest, although the differences between the low lines are less obvious than between the high lines. The differences between the realised

Table 31: F-tests for homogeneity of average realised heritabilities of lines selected in the same direction. Summary of F-tests

| Source of Variation                                              | d.f. | <u>High selection</u> |          |           |          |
|------------------------------------------------------------------|------|-----------------------|----------|-----------|----------|
|                                                                  |      | Female data           |          | Male data |          |
|                                                                  |      | M.S.                  | F        | M.S.      | F        |
| Dev. from aver. pooled regression                                | 155  | 3.670                 |          | 1.953     |          |
| Dev. from indiv. pooled regressions                              | 153  | 0.871                 |          | 0.619     |          |
| Between indiv. pooled regressions                                | 2    | 217.800               | 250.11** | 104.040   | 168.17** |
|                                                                  |      | <u>Low selection</u>  |          |           |          |
|                                                                  |      |                       |          |           |          |
|                                                                  |      |                       |          |           |          |
|                                                                  |      |                       |          |           |          |
| Dev. from aver. pooled regression                                | 155  | 1.512                 |          | 1.089     |          |
| Dev. from indiv. pooled regressions                              | 153  | 1.199                 |          | 1.028     |          |
| Between indiv. pooled regressions                                | 2    | 25.510                | 21.27**  | 5.800     | 5.64*    |
| F <sub>0.05</sub> = 3.91, F <sub>0.01</sub> = 6.81 (2, 153 d.f.) |      |                       |          |           |          |

heritabilities of lines selected in the same direction were tested for significance using the F-test. The average realised heritabilities of the lines were used for these tests on homogeneity, although it must be remembered that this average is strictly not valid for the Cross high line and the Oregon-R low line. These tests were nevertheless carried out as it is felt that the average of the replicates within a line would give a more reliable estimate of the response of a population than any single replicate itself, since by pooling together the data, variations due to sampling, random drift and environmental effects would be expected to be cancelled to some extent. Table 31 shows that the high selection lines and the females of the low lines were heterogeneous. The usual confidence intervals were used to determine approximately which of the lines were

| Table 32: Confidence intervals of average realised heritabilities (%) of high and low selection lines |                       |                   |
|-------------------------------------------------------------------------------------------------------|-----------------------|-------------------|
|                                                                                                       | Female data (%)       | Male data (%)     |
|                                                                                                       | <u>High selection</u> |                   |
| Oregon-R                                                                                              | 4.39± 5.67± 6.95      | 3.20± 4.28± 5.36  |
| +3                                                                                                    | -3.24±-0.89± 1.46     | -1.76± 0.31± 2.38 |
| Cross                                                                                                 | 23.93±25.64±27.35     | 18.65±20.46±22.27 |
|                                                                                                       | <u>Low selection</u>  |                   |
| Oregon-R                                                                                              | 12.47±14.24±16.01     | 10.47±12.28±14.09 |
| +3                                                                                                    | 17.34±20.07±22.80     | 14.04±16.64±19.24 |
| Cross                                                                                                 | 8.44±10.19±11.94      | 9.23±11.60±13.97  |



heritabilities of high and low selection lines is extremely low ( $P < 0.001$ ). Thus, it shows that the asymmetry present in the three different populations was not due to scale effects, nor differential effects of natural selection on high and low selection lines. The extreme negative asymmetry encountered in the +3 population, right from the very early generations of selection, presents a particularly puzzling case and none of the possible known causes of asymmetry seem to be able to cater for its behaviour.

### 3. Variability between replicates within selection lines

#### (1) Introduction

Variability between replicates derived from the same base population and raised under reasonably constant environmental conditions had been reported by different workers (Sismanidis, 1942; Marien, 1958; Frankham et al., 1968) but few have attempted to statistically analyse this variability. Clayton et al. (1957) were among the first who attempted to partition the variability between selection replicates into the component due to genetic drift and that due to the differential effects of artificial selection. Their results from the data of the 5th selection generation indicated that theoretical genetic drift could account for the divergences between the low replicates but not for those between the high replicates.

De Fries and Touchberry (1961) specifically set out to investigate the variability of response to selection for increasing and decreasing body weight in D. affinis at two intensities of selection and with ten replicates within each selection line. They computed the between replicates and within replicates variance components and used them to construct confidence intervals for the means of the replicates. The range of the confidence intervals indicated the considerable variability of responses both within and between replicates. This was expected since the effects of random drift would be maximum for the minimum population size of two, in each of their replications.

This section will be devoted to the analysis of the variation between the means of the four replicates within each selection line. The author regrets that more replicates could not be carried for each line in this present selection experiment. However the results from this analysis, it is hoped, would provide additional evidence on this important aspect

of selection.

(ii) Methods of analysis and results

In the previous section on the analysis of selection response (see Part V C 1(i) ), the significance of divergences between replicates was evaluated from the test for heterogeneity of average response rate and of realised heritability of individual replicates within each selection line. Heterogeneity was found to be significant in some lines but not in others. As mentioned, De Fries and Touchberry (1961) showed another meaningful way of looking into this question using the analysis of variance where they isolated the between replicates ( $V_B$ ) and within replicates ( $V_W$ ) variance components. The author decided to adopt this same method to evaluate the  $V_B$  and  $V_W$  for each generation of each selection line. Theoretically, the variance component between replicates is expected to increase as selection proceeds. The reasons for this increase are: (a) random drift can cause replicates to diverge and this effect is decreased with an increase in the number of parents used per generation for each replicate; (b) secondly, if the quantitative character is controlled by relatively few genes which are present at low initial frequencies, then the initial samples from the base population could be genetically different if favourable genes are included in some replicates and not in others. Artificial selection could have differential effects on these genetically different replicates, causing them to diverge in their selection response and (c) lastly, environmental variation could perhaps be important in long-term selection experiments if the replicates have become genetically divergent so as to react differently to environmental shifts.

Variance component between replicates: Before carrying out the analysis of variance, an inspection of the graphs of the changes of phenotypic

variance of individual replicates (Fig. 3) revealed considerable intra-generation differences within selection lines on some occasions, which suggested that heterogeneity of variances may have occurred. If the basic assumption of homogeneity of variances is violated, the analysis of variance and the subsequent F-test would yield erroneous results (Snedecor, 1967). For this reason, it was decided first to test the null hypothesis of homogeneity ( $\sigma_1^2 = \sigma_2^2 = \sigma_3^2 = \sigma_4^2 = \sigma^2$ ) using Bartlett's test. It consists of calculating:

$$E = \frac{2.3026}{C} \left\{ (\sum f_i) \log \bar{s}^2 - \sum f_i \log s_i^2 \right\}$$

where C (correction factor) =  $1 + \frac{1}{3(a-1)} \left\{ \sum \frac{1}{f_i} - \frac{1}{\sum f_i} \right\}$

2.3026 = constant ( $\log_e 10$ )

a = number of replications within line (4)

$n_i$  = number of observations in ith replicate

$f_i = n_i - 1$

$\bar{s}^2 = (\sum f_i s_i^2 / \sum f_i)$

$s_i^2$  = variance of ith replicate

E is distributed approximated as  $\chi^2$  with (a-1) degrees of freedom. For each selection line, 120 separate computations of E were involved. Significant heterogeneity was detected on nine occasions for the Oregon-R population, five for the +3 and three for the Cross. Considering the number of tests involved, it appears likely that the heterogeneity detected is not greatly different from what would be expected under the null hypothesis. Consequently, the analyses of variance were carried out and the between ( $V_B$ ) and within ( $V_W$ ) replicates components resolved. The F-ratio is also evaluated and it provides a test for the heterogeneity of mean abdominal bristle numbers of intra-generation replicates.



Table 34(b): Variance components between and within replicates of low selection lines

| Gen      | Female data |         |                |         |    | Male data |         |                |         |
|----------|-------------|---------|----------------|---------|----|-----------|---------|----------------|---------|
|          | Within MS   | Betw.MS | V <sub>B</sub> | F-ratio |    | Within MS | Betw.MS | V <sub>B</sub> | F-ratio |
| OREGON-R |             |         |                |         |    |           |         |                |         |
| 0        | 8.80        | 26.48   | 0.393          | 3.01    | 0  | 7.12      | 12.52   | 0.120          | 1.76    |
| 1        | 11.65       | 20.51   | 0.197          | 1.76    | 1  | 6.52      | 58.01   | 1.114          | 8.90    |
| 2        | 8.97        | 21.56   | 0.280          | 2.40    | 2  | 6.00      | 45.49   | 0.878          | 7.58    |
| 3        | 10.40       | 69.01   | 1.302          | 6.64    | 3  | 6.40      | 34.03   | 0.675          | 5.32    |
| 4        | 8.56        | 68.89   | 1.102          | 8.05    | 4  | 7.40      | 50.79   | 0.895          | 6.86    |
| 5        | 7.39        | 42.97   | 0.593          | 5.81    | 5  | 5.75      | 3.66    | -0.035         | 0.64    |
| 6        | 7.77        | 60.55   | 0.880          | 7.79    | 6  | 5.56      | 11.23   | 0.095          | 2.02    |
| 7        | 7.22        | 56.83   | 0.827          | 7.87    | 7  | 5.05      | 18.30   | 0.221          | 3.62    |
| 8        | 7.60        | 112.38  | 1.746          | 14.79   | 8  | 4.69      | 48.26   | 0.726          | 10.29   |
| 9        | 6.79        | 133.59  | 2.113          | 19.67   | 9  | 5.50      | 57.64   | 0.869          | 10.48   |
| 10       | 7.44        | 207.65  | 3.337          | 27.91   | 10 | 5.87      | 67.93   | 1.034          | 11.57   |
| 11       | 7.65        | 332.67  | 5.417          | 43.49   | 11 | 6.76      | 96.45   | 1.495          | 14.27   |
| 12       | 8.65        | 424.69  | 6.934          | 49.10   | 12 | 5.93      | 136.85  | 2.182          | 23.08   |
| 13       | 7.05        | 239.56  | 3.875          | 33.98   | 13 | 5.86      | 215.14  | 3.488          | 36.71   |
| 14       | 8.03        | 233.29  | 5.006          | 29.05   | 14 | 5.68      | 64.60   | 1.309          | 11.37   |
| +3       |             |         |                |         |    |           |         |                |         |
| 0        | 6.98        | 16.48   | 0.211          | 2.36    | 0  | 6.53      | 35.22   | 0.638          | 5.39    |
| 1        | 8.93        | 28.78   | 0.441          | 3.22    | 1  | 9.21      | 36.49   | 0.606          | 3.96    |
| 2        | 9.46        | 21.94   | 0.277          | 2.32    | 2  | 7.97      | 14.67   | 0.149          | 1.84    |
| 3        | 7.54        | 22.17   | 0.325          | 2.94    | 3  | 7.48      | 21.91   | 0.321          | 2.93    |
| 4        | 8.38        | 9.83    | 0.032          | 1.17    | 4  | 6.05      | 45.93   | 0.886          | 7.59    |
| 5        | 7.06        | 5.06    | -0.044         | 0.72    | 5  | 4.99      | 10.98   | 0.133          | 2.20    |
| 6        | 7.45        | 4.65    | -0.062         | 0.62    | 6  | 5.51      | 22.38   | 0.375          | 4.06    |
| 7        | 6.73        | 0.92    | -0.126         | 0.14    | 7  | 4.93      | 11.43   | 0.141          | 2.32    |
| 8        | 5.60        | 34.96   | 0.619          | 6.24    | 8  | 4.69      | 32.60   | 0.588          | 6.95    |
| 9        | 6.01        | 41.29   | 0.641          | 6.87    | 9  | 4.05      | 28.08   | 0.437          | 6.93    |
| 10       | 6.73        | 67.24   | 1.009          | 9.99    | 10 | 4.42      | 60.15   | 0.949          | 13.61   |
| 11       | 7.06        | 135.13  | 2.135          | 19.14   | 11 | 4.89      | 116.86  | 1.866          | 23.90   |
| 12       | 6.69        | 193.74  | 3.118          | 28.96   | 12 | 4.55      | 52.50   | 0.799          | 11.54   |
| 13       | 7.88        | 280.14  | 4.538          | 35.55   | 13 | 5.53      | 53.74   | 0.804          | 9.72    |
| 14       | 7.88        | 172.36  | 3.655          | 21.87   | 14 | 4.88      | 11.39   | 0.145          | 2.33    |
| CROSS    |             |         |                |         |    |           |         |                |         |
| 0        | 10.37       | 118.60  | 2.405          | 11.44   | 0  | 10.23     | 23.62   | 0.297          | 2.30    |
| 1        | 9.84        | 34.80   | 0.554          | 3.54    | 1  | 7.95      | 51.76   | 0.973          | 6.51    |
| 2        | 9.26        | 33.64   | 0.541          | 3.63    | 2  | 8.20      | 11.54   | 0.074          | 1.41    |
| 3        | 7.24        | 106.17  | 2.198          | 14.66   | 3  | 5.75      | 70.82   | 1.446          | 12.32   |
| 4        | 7.99        | 34.18   | 0.582          | 4.28    | 4  | 6.32      | 40.46   | 0.637          | 6.40    |
| 5        | 7.06        | 68.23   | 1.227          | 9.66    | 5  | 4.43      | 99.95   | 1.592          | 22.56   |
| 6        | 7.00        | 33.40   | 0.493          | 4.77    | 6  | 5.35      | 13.01   | 0.127          | 2.43    |
| 7        | 6.79        | 59.53   | 0.939          | 8.77    | 7  | 5.22      | 47.64   | 0.707          | 9.13    |
| 8        | 7.79        | 108.35  | 1.676          | 13.91   | 8  | 4.70      | 64.25   | 1.014          | 13.67   |
| 9        | 7.64        | 138.28  | 2.177          | 18.10   | 9  | 5.28      | 45.91   | 0.677          | 8.69    |
| 10       | 7.49        | 63.33   | 0.930          | 8.45    | 10 | 4.31      | 23.42   | 0.318          | 5.43    |
| 11       | 8.09        | 130.67  | 2.043          | 16.15   | 11 | 6.35      | 26.96   | 0.343          | 4.25    |
| 12       | 6.45        | 137.35  | 2.181          | 21.29   | 12 | 4.91      | 22.07   | 0.286          | 4.51    |
| 13       | 6.65        | 142.27  | 2.260          | 21.39   | 13 | 4.19      | 45.72   | 0.692          | 10.91   |
| 14       | 7.97        | 139.35  | 2.919          | 17.48   | 14 | 5.86      | 70.88   | 1.444          | 12.10   |

Table 34(a): Variance components between and within replicates of high selection lines

| Gen      | Female data |          |                |         |    | Male data |          |                |         |
|----------|-------------|----------|----------------|---------|----|-----------|----------|----------------|---------|
|          | Within MS   | Betw. MS | V <sub>B</sub> | F-ratio |    | Within MS | Betw. MS | V <sub>B</sub> | F-ratio |
| OREGON-R |             |          |                |         |    |           |          |                |         |
| 0        | 8.04        | 36.02    | 0.622          | 4.48    | 0  | 6.73      | 14.71    | 0.177          | 2.19    |
| 1        | 8.29        | 18.55    | 0.228          | 2.24    | 1  | 6.69      | 18.14    | 0.254          | 2.71    |
| 2        | 9.09        | 64.27    | 1.226          | 7.07    | 2  | 6.62      | 47.79    | 0.915          | 7.22    |
| 3        | 7.65        | 50.51    | 0.952          | 6.60    | 3  | 6.17      | 18.44    | 0.273          | 3.00    |
| 4        | 7.54        | 41.15    | 0.585          | 5.46    | 4  | 5.22      | 15.55    | 0.198          | 2.98    |
| 5        | 6.39        | 58.24    | 0.903          | 9.11    | 5  | 6.17      | 35.11    | 0.504          | 5.69    |
| 6        | 8.10        | 65.46    | 0.956          | 8.08    | 6  | 5.06      | 44.23    | 0.653          | 8.74    |
| 7        | 5.91        | 60.08    | 0.903          | 10.17   | 7  | 5.79      | 51.64    | 0.764          | 8.92    |
| 8        | 6.44        | 24.27    | 0.297          | 3.77    | 8  | 5.38      | 23.72    | 0.306          | 4.41    |
| 9        | 5.93        | 31.04    | 0.419          | 5.24    | 9  | 5.13      | 7.93     | 0.047          | 1.55    |
| 10       | 5.93        | 15.20    | 0.155          | 2.56    | 10 | 6.06      | 22.69    | 0.277          | 3.74    |
| 11       | 6.67        | 27.28    | 0.344          | 4.09    | 11 | 5.28      | 15.61    | 0.172          | 2.96    |
| 12       | 5.36        | 8.70     | 0.056          | 1.62    | 12 | 6.04      | 14.89    | 0.148          | 2.47    |
| 13       | 6.73        | 8.40     | 0.028          | 1.25    | 13 | 5.41      | 8.36     | 0.051          | 1.55    |
| 14       | 6.70        | 18.08    | 0.190          | 2.70    | 14 | 6.04      | 41.76    | 0.794          | 6.91    |
| ±3       |             |          |                |         |    |           |          |                |         |
| 0        | 5.02        | 21.84    | 0.374          | 4.35    | 0  | 5.97      | 13.46    | 0.166          | 2.25    |
| 1        | 6.40        | 23.39    | 0.378          | 3.65    | 1  | 5.80      | 8.45     | 0.059          | 1.46    |
| 2        | 6.37        | 6.92     | 0.012          | 1.09    | 2  | 6.40      | 6.33     | -0.002         | 0.99    |
| 3        | 6.78        | 10.81    | 0.090          | 1.59    | 3  | 4.99      | 24.05    | 0.424          | 4.82    |
| 4        | 6.40        | 20.06    | 0.304          | 3.13    | 4  | 5.07      | 9.81     | 0.105          | 1.93    |
| 5        | 3.69        | 7.30     | 0.080          | 1.98    | 5  | 5.09      | 2.61     | -0.055         | 0.51    |
| 6        | 5.36        | 8.03     | 0.059          | 1.50    | 6  | 3.98      | 9.80     | 0.129          | 2.46    |
| 7        | 5.78        | 0.91     | -0.108         | 0.16    | 7  | 4.35      | 11.78    | 0.165          | 2.71    |
| 8        | 6.78        | 10.70    | 0.087          | 1.58    | 8  | 4.48      | 4.66     | 0.004          | 1.04    |
| 9        | 4.94        | 21.92    | 0.358          | 4.44    | 9  | 4.92      | 13.56    | 0.178          | 2.76    |
| 10       | 5.84        | 13.68    | 0.157          | 2.34    | 10 | 4.50      | 23.33    | 0.378          | 5.18    |
| 11       | 6.00        | 2.24     | -0.072         | 0.37    | 11 | 5.27      | 5.38     | 0.002          | 1.02    |
| 12       | 5.68        | 17.55    | 0.216          | 3.09    | 12 | 4.59      | 0.35     | -0.074         | 0.08    |
| 13       | 6.25        | 9.88     | 0.066          | 1.58    | 13 | 5.95      | 19.76    | 0.251          | 3.32    |
| 14       | 7.58        | 17.80    | 0.227          | 2.35    | 14 | 6.13      | 5.35     | -0.017         | 0.87    |
| CROSS    |             |          |                |         |    |           |          |                |         |
| 0        | 11.32       | 20.01    | 0.193          | 1.77    | 0  | 8.99      | 24.60    | 0.347          | 2.74    |
| 1        | 9.62        | 11.77    | 0.048          | 1.22    | 1  | 7.86      | 22.86    | 0.333          | 2.91    |
| 2        | 9.46        | 22.26    | 0.284          | 2.35    | 2  | 7.78      | 28.02    | 0.450          | 3.60    |
| 3        | 10.46       | 79.30    | 1.530          | 7.58    | 3  | 7.84      | 72.60    | 1.439          | 9.26    |
| 4        | 8.68        | 66.38    | 1.282          | 7.65    | 4  | 6.33      | 32.71    | 0.586          | 5.17    |
| 5        | 9.83        | 94.42    | 1.880          | 9.61    | 5  | 6.87      | 69.15    | 1.384          | 10.07   |
| 6        | 6.38        | 20.17    | 0.306          | 3.16    | 6  | 5.25      | 91.66    | 1.920          | 17.46   |
| 7        | 6.43        | 44.36    | 0.843          | 8.90    | 7  | 6.46      | 33.61    | 0.603          | 5.20    |
| 8        | 8.36        | 64.10    | 1.239          | 7.67    | 8  | 5.86      | 52.26    | 1.004          | 8.92    |
| 9        | 10.82       | 137.94   | 2.423          | 12.75   | 9  | 6.96      | 111.78   | 1.998          | 16.06   |
| 10       | 8.84        | 74.16    | 1.188          | 8.39    | 10 | 7.48      | 103.40   | 1.744          | 13.82   |
| 11       | 11.29       | 85.01    | 1.255          | 7.53    | 11 | 6.40      | 115.47   | 1.818          | 18.04   |
| 12       | 7.89        | 142.09   | 2.237          | 18.01   | 12 | 6.64      | 107.03   | 1.673          | 16.12   |
| 13       | 9.51        | 131.38   | 2.031          | 13.81   | 13 | 6.23      | 160.87   | 2.577          | 25.82   |
| 14       | 11.66       | 80.46    | 1.529          | 6.90    | 14 | 8.18      | 138.85   | 2.904          | 16.97   |

Tables 34(a) and 34(b) present the  $V_W$ ,  $V_B$  and F-ratio for each generation, sex and selection line. To depict visually the changes of variability of response within lines over the 14 generations,  $V_B$  for each generation is plotted against generation number (Fig. 12). The question is, how much of this difference between replications is due to sampling variation? Wright (1921) has given a simple formula for evaluating the variance due to genetic drift:

$$V_B = 2FV_A$$

where  $F$  = inbreeding level of the population

$V_A$  = additive genetic variance of the base population

It must be stressed that this is a rough method of assessing the size of the genetic drift variance since both the terms, inbreeding level and additive genetic variance of the population, are estimated with large errors.

The first term  $F$  can be calculated from the rate of inbreeding which is dependent on the number of parents used in each generation for each replicate ( $F = \frac{1}{2N}$ ). Falconer (1960a) has pointed out that the effective population size ( $N_e$ ) is invariably smaller than the actual population size ( $N$ ) due to causes like non-random mating among the parents, unequal contribution of each parent to the offsprings of the next generation and prevalence of differential natural selection. From his study with Drosophila, Crow (1954) reported differential fecundity among the females and mating ability among the males. This inevitably means that some parents would leave more progeny than others leading to a higher degree of inbreeding. Morley (1954) pointed out that particularly where heritability is high, the selected parents tend to be more closely related than expected from inbreeding theory, again resulting in higher inbreeding rates.

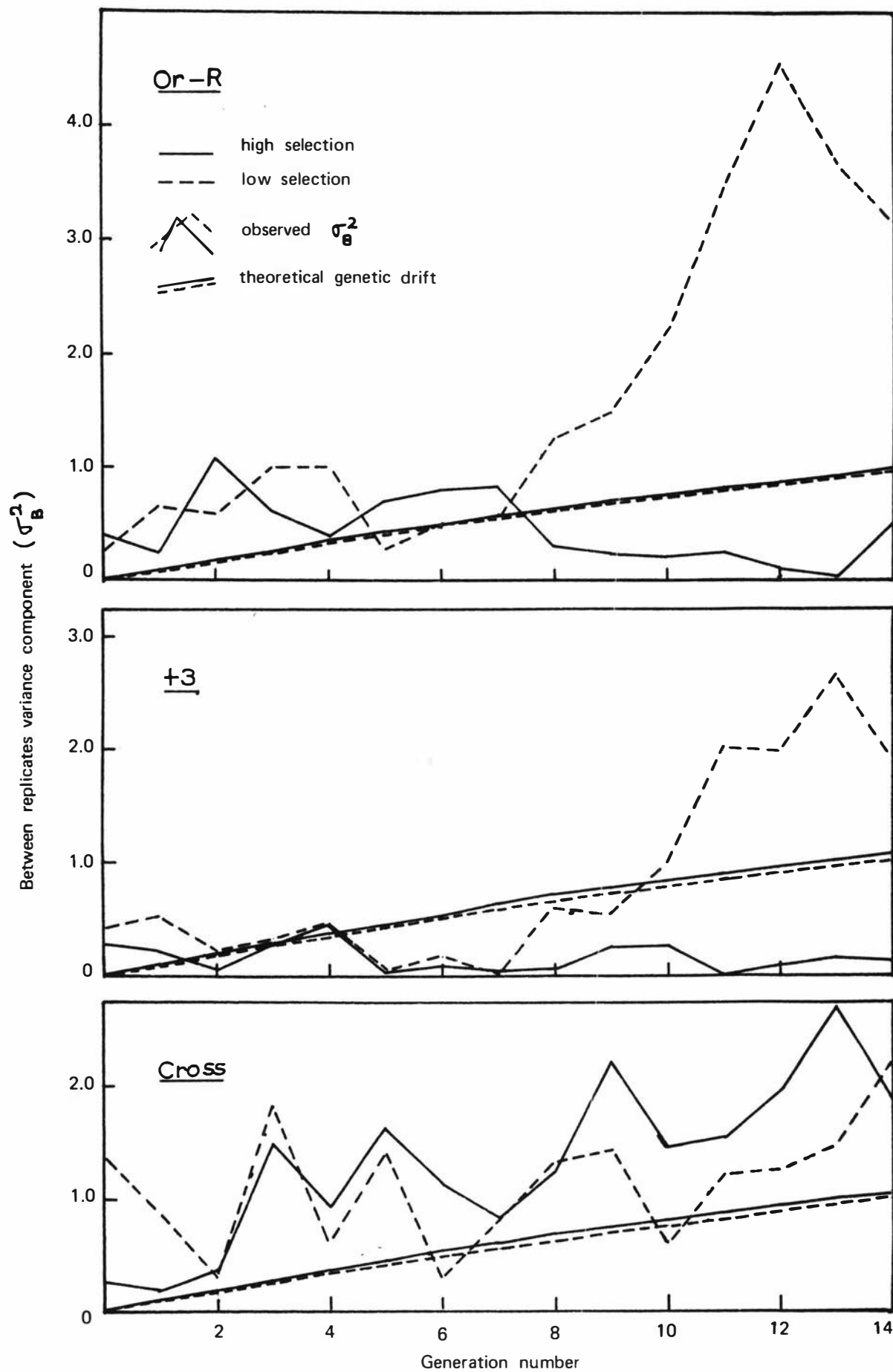


Fig.12. Comparison of observed between replicates variance with expected genetic drift variance (sexes combined).

Thus, it is difficult to get any accurate estimate of the effective population size. Crow (1954) derived a formula for calculating the effective population size relative to the actual population size from the parameter, the variance of family size. He found the ratio of the effective population size to the actual population size ( $N_e/N$ ) in Drosophila to be 0.73 for the females and 0.42 for the males. Using these ratios, the effective number of males and females in each replicate of this present selection experiment were evaluated. The rate of inbreeding per generation within a replicate is found by the formula (Wright 1931):

$$F = \frac{1}{8N_m} + \frac{1}{8N_f}$$

where  $N_m$  = effective number of males

$N_f$  = effective number of females

| Table 35: Rate of increase in inbreeding<br>per generation<br><br>( $F = \frac{1}{8N_m} + \frac{1}{8N_f}$ ) |                |               |
|-------------------------------------------------------------------------------------------------------------|----------------|---------------|
|                                                                                                             | High selection | Low selection |
| Oregon-R                                                                                                    | 4.33%          | 4.33%         |
| +3                                                                                                          | 4.97%          | 4.97%         |
| Cross                                                                                                       | 4.83%          | 4.48%         |

The inbreeding level of each line for every generation is calculated by

the formula (Falconer, 1960a):

$$F_t = F + (1 + \Delta F)F_{t-1}$$

The second term necessary for the evaluation of the theoretical genetic drift variance is the additive genetic variance of the base population ( $V_A$ ). This is obtained from the sire and dam component in the diallel analysis of the +3 and Oregon-R base populations (see Part IV C). The data of the males and females were analysed separately and provided separate estimates of  $V_A$  which were then averaged to give the value for the base population.

|                       |               |                 |
|-----------------------|---------------|-----------------|
| Oregon-R: female data | $V_A = 0.935$ |                 |
| male data             | $V_A = 1.205$ | Average = 1.070 |
| +3: female data       | $V_A = 0.331$ |                 |
| male data             | $V_A = 1.734$ | Average = 1.033 |

Since the realised heritability of the Cross was comparable to those of the +3 and Oregon-R in the first generation of selection, the additive variance used for the Cross was taken as the average of the two parental base populations.

$$\text{Cross: } V_A = (1.020 + 1.033) / 2 = 1.052$$

The inbreeding level and the random drift variance for each generation and selection line is given in Table 36. The genetic drift variances are plotted on the same graph as the observed between replicate variances (Fig. 12) as this enables visual comparison between the two values.

The trends of changes of between replicate variance turned out to be very interesting with the Oregon-R and the +3 behaving in a very similar manner. It is found that the genetic drift could account for the

Table 36: Inbreeding level (F) of selection lines and replicate differences due to genetic drift ( $V_B$ ) (Sexes combined)

| Generation | <u>High selection</u> |       |       |       |       |       |
|------------|-----------------------|-------|-------|-------|-------|-------|
|            | Oregon-R              |       | +3    |       | Cross |       |
|            | F                     | $V_B$ | F     | $V_B$ | F     | $V_B$ |
| 0          | 0.000                 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 1          | 0.043                 | 0.093 | 0.050 | 0.103 | 0.048 | 0.102 |
| 2          | 0.085                 | 0.181 | 0.097 | 0.200 | 0.094 | 0.198 |
| 3          | 0.124                 | 0.266 | 0.142 | 0.293 | 0.138 | 0.290 |
| 4          | 0.162                 | 0.347 | 0.184 | 0.381 | 0.180 | 0.378 |
| 5          | 0.199                 | 0.425 | 0.225 | 0.465 | 0.219 | 0.461 |
| 6          | 0.233                 | 0.499 | 0.263 | 0.544 | 0.257 | 0.540 |
| 7          | 0.266                 | 0.570 | 0.313 | 0.647 | 0.293 | 0.616 |
| 8          | 0.298                 | 0.638 | 0.347 | 0.717 | 0.327 | 0.688 |
| 9          | 0.329                 | 0.703 | 0.380 | 0.784 | 0.359 | 0.756 |
| 10         | 0.358                 | 0.766 | 0.410 | 0.848 | 0.390 | 0.821 |
| 11         | 0.385                 | 0.825 | 0.440 | 0.908 | 0.420 | 0.883 |
| 12         | 0.412                 | 0.881 | 0.468 | 0.966 | 0.448 | 0.942 |
| 13         | 0.437                 | 0.936 | 0.494 | 1.021 | 0.474 | 0.998 |
| 14         | 0.462                 | 0.988 | 0.519 | 1.073 | 0.500 | 1.052 |

| Generation | <u>Low selection</u> |       |       |       |       |       |
|------------|----------------------|-------|-------|-------|-------|-------|
|            | F                    |       | $V_B$ |       | F     |       |
|            | F                    | $V_B$ | F     | $V_B$ | F     | $V_B$ |
| 0          | 0.000                | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| 1          | 0.043                | 0.093 | 0.047 | 0.098 | 0.045 | 0.094 |
| 2          | 0.085                | 0.181 | 0.092 | 0.191 | 0.088 | 0.184 |
| 3          | 0.124                | 0.266 | 0.135 | 0.280 | 0.129 | 0.270 |
| 4          | 0.162                | 0.347 | 0.176 | 0.364 | 0.168 | 0.352 |
| 5          | 0.199                | 0.425 | 0.215 | 0.445 | 0.201 | 0.423 |
| 6          | 0.233                | 0.499 | 0.252 | 0.521 | 0.237 | 0.498 |
| 7          | 0.266                | 0.570 | 0.288 | 0.594 | 0.271 | 0.570 |
| 8          | 0.298                | 0.638 | 0.321 | 0.664 | 0.304 | 0.639 |
| 9          | 0.329                | 0.703 | 0.354 | 0.730 | 0.335 | 0.704 |
| 10         | 0.358                | 0.766 | 0.384 | 0.794 | 0.365 | 0.767 |
| 11         | 0.386                | 0.825 | 0.413 | 0.854 | 0.393 | 0.827 |
| 12         | 0.412                | 0.881 | 0.441 | 0.910 | 0.420 | 0.884 |
| 13         | 0.437                | 0.936 | 0.467 | 0.965 | 0.446 | 0.939 |
| 14         | 0.462                | 0.988 | 0.493 | 1.018 | 0.471 | 0.991 |

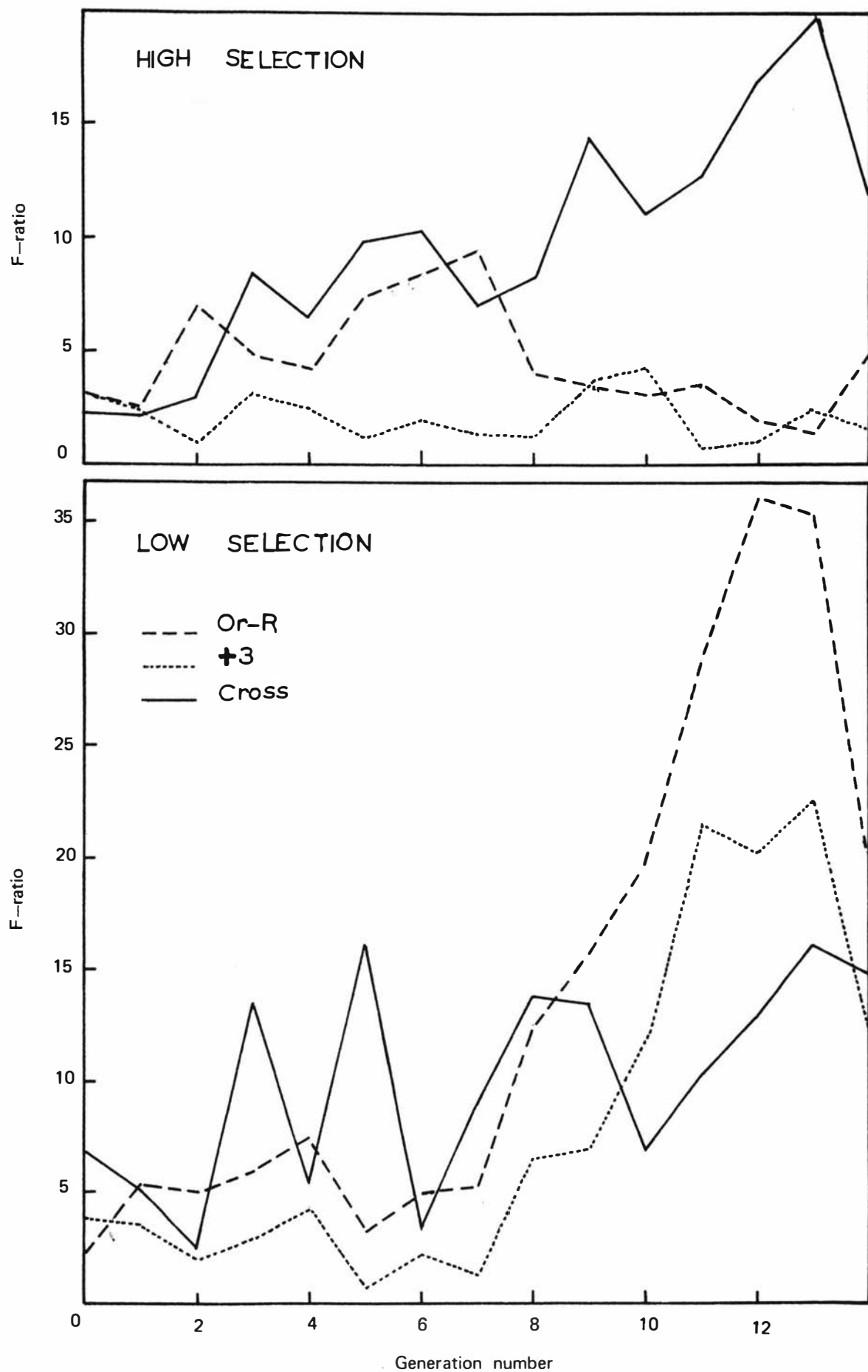


Fig. 13. F-ratio of selection lines (sexes combined).



divergences between the replicates within the Oregon-R and the +3 high selection lines. In fact for the latter part of the selection programme, the observed variability was actually smaller than the predicted. For these two low selection lines, the random drift could be responsible for the variability between low replicates for the first eight or nine generations of selection, from then on there was a sudden sharp increase in variability within these two low lines. The Cross high and low selection lines were characterised by violent fluctuations of  $V_B$  from generation to generation right from the onset of selection. There was a slight rise in  $V_B$  over the 14 generations but this upward trend was masked to a large extent by the strong inter-generation fluctuations. This erratic behaviour of the Cross selection lines was not unexpected since this hybrid population contained greater genetic variability than either of the parental strains.

F-ratio: Using the between replicates variance component can be misleading if there is some reason to suspect scale effects; i.e., if, for example, a positive correlation exists between  $V_B$  and  $V_W$ . A way to overcome this problem is to look at the change in the variance ratio (between replicates mean square divided by within replicates mean square) where some of the bias due to scale would be cancelled. The larger the value of the F-ratio, the greater are the differences between replicates. The F-ratios, calculated for each selection line in every generation, were plotted against generation numbers (Fig.13). The trends of the F-ratio are very similar to those of the between replicate variance components shown in Fig. 12. Two features are shown clearly in this diagram; the steady increase in divergences between the Cross high selection replicates and the great variability in response in the Oregon-R low selection line in the later generations of selection.

#### 4. Discussion

Results from the analysis of high and low selection responses from the Oregon-R, +3 and Cross populations were by no means simple and clear-cut. Some results were in accordance with expectations while others were in direct contradiction.

Among the high selection lines, high repeatability of response was observed from replicates within the Oregon-R and +3 high lines. On the other hand, significant heterogeneity of response was detected among the four replicates of the Cross high line and this is in accordance to the expectations that greater variability would be present in the hybrid base population. The Cross high line gave significantly greater response than the Oregon-R and +3 high lines which meant that selection within the Cross population was able to exploit the greater genetic variation generated by combining the two laboratory strains. The Oregon-R high line gave weak response over the 14 generations of selection. After the first two to three generations of selection, the +3 high line unexpectedly stopped responding altogether to high selection and even showed a very slight negative response despite continued upward selection. The aberrant behaviour of all four +3 high replicates could be due to the following causes; depletion of additive genetic variance through gene fixation, prevalence of loci with dominance in the direction of high abdominal bristles and the accumulation of subvital factors which prevented further upward response. In an attempt to elucidate the real cause of the extreme negative asymmetry of the +3 population, the following subsidiary tests were carried out at the end of the selection experiment; heritability estimations, crossing between the +3 high and low selection lines and lethal tests.

From the commercial breeder's point of view of improving some

economic trait by artificial selection, the results from this present experiment give evidence that it is clearly advantageous to cross original strains together and practise selection on the hybrid base population. Variability between replicates derived from the Cross base population is expected and in order to minimise this heterogeneity Kojima and Kelleher (1963) suggested that, "It is preferable therefore to advance hybrid populations by random mating for several generations prior to selection in order to reduce drastic effects of linkage-epistasis complexes ...". Frankham et al. (1968) advocated using replicates with larger population sizes to increase repeatability of responses.

Responses from the three low selection lines could be considered to be almost in direct contrast to high selection responses. Contrary to expectations, the responses from the Cross low line were more homogeneous and also smaller in size when compared with those of the Oregon-R and +3 low lines. Unlike the high selection lines, the low lines bore a striking similarity to each other in pattern of response, with the first seven generations of the selection experiment giving good downward response and the latter seven generations poor response. The conclusion from the low selection responses from these three different populations is that responses from the "purebred" laboratory strains are comparable to responses from the hybrid strain. Another feature which emerges from these studies is that divergence between replicates within selection lines seems to be the usual observation in replicated Drosophila selection experiments.

#### D. PREDICTION OF SELECTION RESPONSE

This section will be concerned with comparing the responses predicted for the base populations with the observed selection responses. To date, results from various selection experiments have produced controversial evidence on the reliability of the simple additive prediction theory. There is evidence that where the population size is not too small, the agreement between predicted and observed responses for short-term selection experiment (five generations or so) is reasonably good (Clayton et al., 1957; Dawson, 1965; Wong and Boylan, 1970). But Sheldon (1963) and Frankham et al. (1968) have found that the predictions are not borne out even on short-term basis.

Heritability estimates of abdominal bristles in the Oregon-R and +3 base populations were obtained by parent-offspring regression and diallel analysis. The usefulness of each method of estimation is assessed by comparing the estimated heritability with the realised heritability obtained from the slope of the linear regression line fitted to the points on the graph of response plotted against cumulated selection differential. The method which yields an estimate which is closer to the realised heritability would be considered to be the more reliable.

##### 1. Heritability

The heritabilities predicted from the Oregon-R and +3 base populations were compared with the average realised heritability of their respective selection lines. Since strictly speaking the prediction holds for only one generation of selection the estimated heritabilities will be first compared with the first generation realised heritabilities and then

with the average realised heritabilities over the 14 generations to see how far the predictions are carried out. Within each population, the first generation (G1) realised heritabilities for high and low selection are similar so that the asymmetry has not as yet appeared. The average G1 realised heritabilities for the Oregon-R and +3 are 0.21 and 0.33 respectively (Table 37). The parent-offspring regressions by far over-estimate the G1 realised heritabilities even when their large sampling errors are taken into account. The inflation of the regression coefficients could be caused by sampling variance and possibly by sex-linked effects in the Oregon-R and non-additive genetic variance in the +3.

The noticeable weakness of the diallel analysis is the apparent large discrepancies between the four estimates from each analysis. The values ranged from 0.16 to 0.42 for the Oregon-R and -0.06 to 0.66 for the +3. This weakness, the author admits, is due mainly to insufficient replications of the present experiment where only 31 block matings were successfully completed for the Oregon-R and 43 for the +3. Two main reasons accounted for this low replication of these diallel tests; lack of facilities, and low viability and fertility of the stocks particularly the Oregon-R. The discrepancies between the individual estimates are likely to be due to accidents of sampling from various sources. Kojima and Kelleher (1963) also obtained highly variable heritability estimates including some negative values. They attributed the inconsistency to sampling errors, resulting in some values being over-estimated while others under-estimated. Consequently, they accepted the negative values to be valid even though they were contrary to the additive gene theory. They found that by averaging the individual estimates the sampling variations were cancelled to a large degree, leaving a mean which accorded well with the observed. Taking the same attitude as Kojima and Kelleher, the

Table 37: Summary of realised and predicted heritabilities ( $h^2$ ) of Oregon-R and +3 populations

|                               | Oregon-R         |                  | +3                |                  |
|-------------------------------|------------------|------------------|-------------------|------------------|
|                               | Female           | Male             | Female            | Male             |
| <u>Predicted Heritability</u> |                  |                  |                   |                  |
| Regression:                   |                  |                  |                   |                  |
| Sire-son                      | 0.34             | 0.10             | 0.52              | 0.10             |
| Dam-son                       | 0.42             | 0.13             | 0.49              | 0.13             |
| Sire-daughter                 | 0.45             | 0.14             | 0.16              | 0.13             |
| Dam-daughter                  | 0.40             | 0.11             | 0.44              | 0.11             |
| Diallel Analysis $h^2_{S^2}$  | 0.32 $\pm$ 0.12  | 0.27 $\pm$ 0.12  | -0.06 $\pm$ 0.05  | 0.24 $\pm$ 0.09  |
| $h^2_D$                       | 0.16 $\pm$ 0.10  | 0.42 $\pm$ 0.13  | 0.16 $\pm$ 0.08   | 0.66 $\pm$ 0.13  |
| Weighted average              | 0.32             | 0.11             | 0.37              | 0.11             |
| <u>Realised heritability</u>  |                  |                  |                   |                  |
| Gen.1: High selection         | 0.24             | 0.20             | 0.37              | 0.31             |
| Low selection                 | 0.19             | 0.21             | 0.34              | 0.30             |
| Average: High selection       | 0.06 $\pm$ 0.006 | 0.04 $\pm$ 0.005 | -0.01 $\pm$ 0.012 | 0.00 $\pm$ 0.010 |
| (Gen.1-14) Low selection      | 0.14 $\pm$ 0.009 | 0.12 $\pm$ 0.009 | 0.20 $\pm$ 0.014  | 0.17 $\pm$ 0.013 |
| Average of high and low       | 0.10             | 0.07             | 0.10              | 0.09             |

present author averaged the four estimates within each diallel analysis and obtained average values of 0.29 for the Oregon-R and 0.25 for the +3. When compared with their respective G1 realised heritabilities, the diallel method gave an over-estimate of the Oregon-R first generation response and an under-estimate of the +3 response.

In summing up, a simple way to show how well estimates of heritability by the two different designs corresponded with the observed heritability of the first generation of selection was to examine the size of the deviation of the average heritability estimates from each method from the average first generation realised heritabilities (Table 38).

| Table 38: Deviation of the estimated heritability from the realised heritability of the first selection generation |                       |                                                     |                       |                                                     |
|--------------------------------------------------------------------------------------------------------------------|-----------------------|-----------------------------------------------------|-----------------------|-----------------------------------------------------|
| Method of estimation                                                                                               | Oregon-R              |                                                     | +3                    |                                                     |
|                                                                                                                    | Aver. estimated $h^2$ | Deviation from observed = $\text{est. } h^2 - 0.21$ | Aver. estimated $h^2$ | Deviation from observed = $\text{est. } h^2 - 0.33$ |
| Parent-offspring regression                                                                                        | 0.40                  | 0.19                                                | 0.40                  | 0.07                                                |
| Diallel analysis                                                                                                   | 0.29                  | 0.08                                                | 0.25                  | -0.08                                               |
| Combined weighted est.                                                                                             | 0.32                  | 0.11                                                | 0.37                  | 0.04                                                |

It is apparent that for the Oregon-R population, both methods provided over-estimates of the first generation realised heritabilities of the high and low selection lines. The average regression heritability estimate was less reliable than the average diallel heritability estimate

since the deviation from the observed was larger. On the other hand for the +3, the regression analysis provided an over-estimate and the diallel analysis an under-estimate of the first generation realised heritability but the combined weighted heritability estimate accorded well with the observed.

As expected, there was even greater discrepancy between the estimated heritabilities and the average realised heritabilities over the 14 generations of selection (Table 37). The average realised heritabilities in all cases were lower than their respective first-generation realised heritabilities. This decline was more marked in the high selection lines than in the low lines thus indicating the asymmetrical pattern of two-way responses in both the Oregon-R and +3 populations. Falconer (1953, 1955), Martin and Bell (1960) and Wong and Boylan (1970) found that where asymmetrical two-way responses occurred, the estimated base population heritabilities were more in line with the realised heritabilities of the average divergence between high and low selection lines than with the realised heritabilities of either the high or low selection lines. However, in the present experiment the discrepancy between the expected and the observed heritabilities could not be remedied by averaging the values of the high and low selection lines within a population since the base population heritability was an over-estimation of the realised heritabilities of both the high and low selection lines.

The general conclusion from this comparative study of estimated with the realised heritabilities is not very encouraging. The only reasonable agreement was between the estimated +3 base population heritability and the first generation realised heritability of the +3 selection lines. It is clear from this discussion that to use these estimated base population heritabilities to evaluate the responses to be expected from artificial



selection would definitely yield over-estimates of both upward and downward responses. Sheldon (1963) and Dawson (1965) suggested that the first-generation selection responses may be more reliable estimators of subsequent generation responses than the estimated heritabilities. Hence, the author decided to check the usefulness of this recommendation. This will be carried out in the following section.

## 2. Average response rate

The standard prediction equation for obtaining the expected response from one generation of selection is simply the heritability multiplied by the standardised selection differential for selection intensity of  $9/45$  (from Falconer 1960a) and the phenotypic standard deviation of the base population. The heritability values used will not be the estimated values from the base populations but the average realised heritabilities of the selection lines in the first selection generation. The average realised heritabilities are obtained by dividing the average response of the four replicates within a line by the average selection differential. The phenotypic deviations employed are those of the G1 unselected controls and the Cross was found to have the highest value which was not unexpected since it was the  $F_3$  generation where segregation and recombination with the resulting increase in variability were still occurring. The predicted responses as well as the genetic parameters needed for evaluating them are presented in Table 39. It was mainly because of its high phenotypic standard deviation that the expected response for the Cross was the highest. Except for the males of the Oregon-R population, greater upward responses are expected from all three populations. The greatest response is expected from the Cross population and the least from the Oregon-R. The

Table 39: Response per generation predicted from first generation realised heritabilities

| Parameter                              | Oregon-R |       | +3      |       | Cross   |       |
|----------------------------------------|----------|-------|---------|-------|---------|-------|
|                                        | Females  | Males | Females | Males | Females | Males |
| <u>HIGH SELECTION</u>                  |          |       |         |       |         |       |
| Phenotypic standard deviation          | 3.03     | 2.50  | 2.81    | 2.58  | 3.73    | 2.98  |
| Standardised selection differential    | 1.40     | 1.40  | 1.40    | 1.40  | 1.40    | 1.40  |
| Predicted selection differential       | 4.24     | 3.50  | 3.93    | 3.61  | 5.22    | 4.17  |
| Observed selection differential        | 3.26     | 3.45  | 3.04    | 3.20  | 4.26    | 3.87  |
| First generation realised heritability | 0.24     | 0.20  | 0.37    | 0.31  | 0.41    | 0.41  |
| Predicted high selection response rate | 1.02     | 0.70  | 1.45    | 1.12  | 2.14    | 1.67  |
| <u>LOW SELECTION</u>                   |          |       |         |       |         |       |
| Predicted selection differential       | 4.24     | 3.50  | 3.93    | 3.61  | 5.22    | 4.17  |
| Observed selection differential        | 3.92     | 3.08  | 3.70    | 3.58  | 4.29    | 4.22  |
| First generation realised heritability | 0.19     | 0.21  | 0.34    | 0.30  | 0.40    | 0.36  |
| Predicted low selection response rate  | 0.81     | 0.73  | 1.34    | 1.08  | 2.09    | 1.50  |

reliability of these predictions is tested by comparison with the observed average response rate over 14 selection generations obtained from the linear regression method and from the total response divided by the number of selection generations (Table 40). The relative sizes of the predicted and observed response rates are represented diagrammatically in

Table 40: Comparison of observed with predicted response (bristle number/generation)  
(t = number of generations of selection)

|                                  | Females            |                   |                     | Males              |                   |                     |
|----------------------------------|--------------------|-------------------|---------------------|--------------------|-------------------|---------------------|
|                                  | Predicted response | Observed response |                     | Predicted response | Observed response |                     |
|                                  |                    | Reg. coeff.       | Total/ <sub>t</sub> |                    | Reg. coeff.       | Total/ <sub>t</sub> |
| <u>HIGH SELECTION (Gen.1-14)</u> |                    |                   |                     |                    |                   |                     |
| Oregon-R                         | 1.02               | 0.19              | 0.34                | 0.70               | 0.13              | 0.28                |
| +3                               | 1.45               | -0.03             | 0.19                | 1.12               | 0.01              | 0.14                |
| Cross                            | 2.14               | 0.97              | 0.93                | 1.67               | 0.68              | 0.77                |
| <u>LOW SELECTION (Gen.1-7)</u>   |                    |                   |                     |                    |                   |                     |
| Oregon-R                         | 0.81               | 0.71              | 0.60                | 0.73               | 0.64              | 0.44                |
| +3                               | 1.34               | 0.98              | 0.82                | 1.08               | 0.92              | 0.88                |
| Cross                            | 2.09               | 0.59              | 0.95                | 1.50               | 0.69              | 0.79                |
| <u>LOW SELECTION (Gen.1-14)</u>  |                    |                   |                     |                    |                   |                     |
| Oregon-R                         | 0.81               | 0.51              | 0.43                | 0.73               | 0.38              | 0.33                |
| +3                               | 1.34               | 0.65              | 0.63                | 1.08               | 0.47              | 0.58                |
| Cross                            | 2.09               | 0.34              | 0.62                | 1.50               | 0.33              | 0.45                |

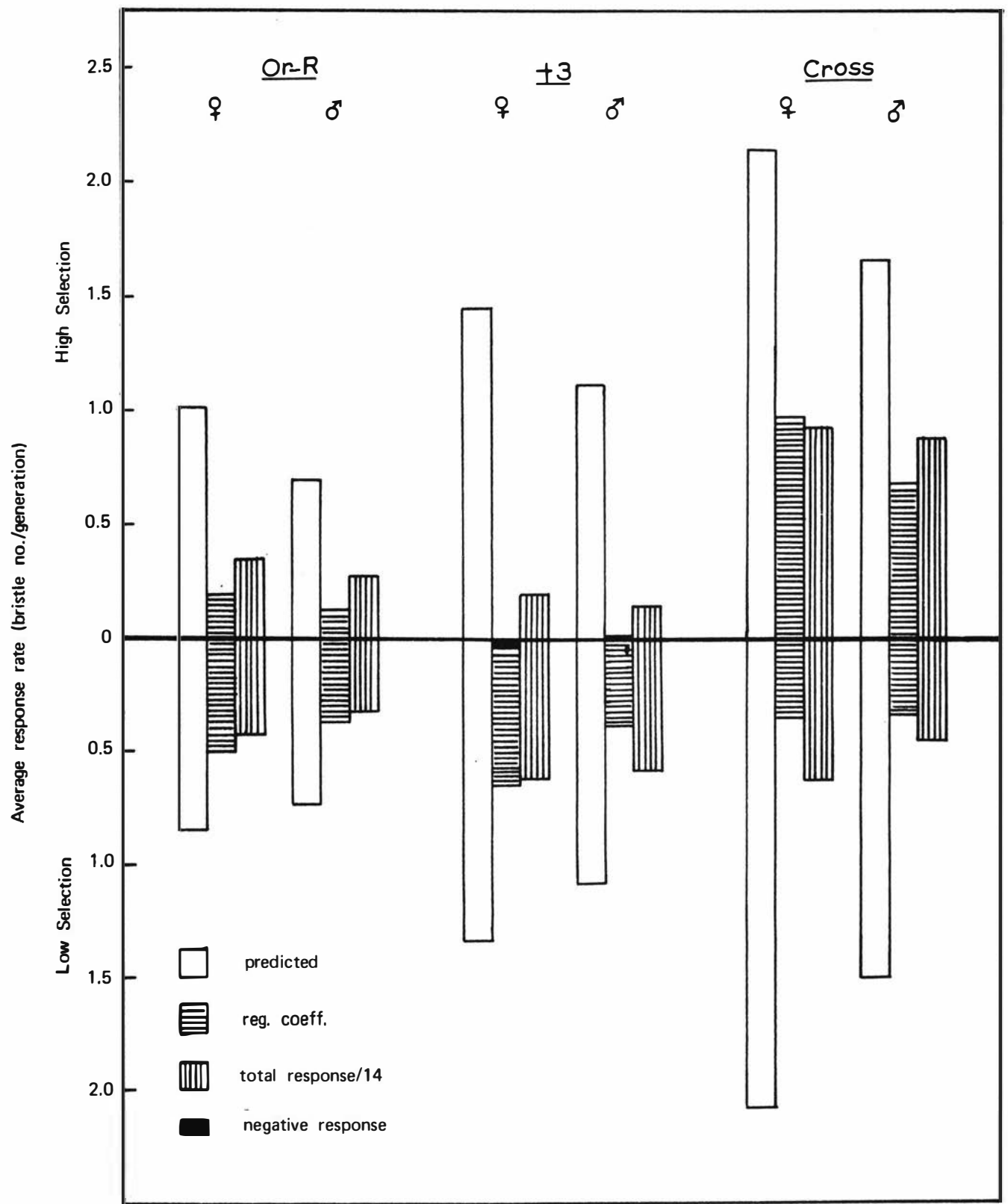


Fig. 14. Comparison of predicted responses with observed average response over fourteen selection generations

Fig.14 and it shows clearly that the predictions from the first-generation selection responses on every occasion considerably exceed the observed average responses over 14 generations. One cause of this discrepancy between the predicted and observed responses was that the expected selection differentials used in the equation for obtaining expected responses were found to be greater than the realised selection differential in the first selection generation. It has been shown earlier that the average response of the low selection lines declined significantly after the first seven generations or so of selection (see Part V C 1(iii) ), so that the average observed response over the 14 generations is smaller than the average response of the first seven generations. For this reason, the predicted low selection responses are also compared with the average response in Period 1 (G1-7). The results of this comparison are slightly more promising, for at least there is reasonably good agreement between the observed response rate over the first seven generations and the predicted responses for the Oregon-R low selection line and the males of the +3 low line.

The pattern of two-way selection response predicted from the first generation was for slight positive asymmetry or for symmetry. Only the observed pattern of response from the Cross accorded with the prediction. Contrary to expectations, negative asymmetry was observed from the Oregon-R and +3 populations. With regards to the actual size of the response per generation among the three high selection lines, the Cross gave the largest response as predicted but the +3 response was the lowest instead of the Oregon-R. For the low selection, responses from the three lines were similar but contrary to expectations response from the Cross was lower than the +3 response. These results show that in general, the predictions of both the sizes and the trends of the selection response from the

first-generation responses were inadequate in this present experiment.

### 3. Discussion

The main conclusion which stands out from the study of the prediction of selection responses is one of poor reliability of the estimates of heritabilities of the unselected base populations by the standard methods. Theoretically, the prediction is expected to hold at least for the first generation of selection. But actual comparisons revealed that the average estimated heritabilities exceeded the realised heritabilities of even the first generation of selection in both the Oregon-R and +3 populations. As expected, the discrepancies between the estimated and the average realised heritabilities of the 14 generations were even greater. The immediate question which follows is what are the causes of this poor predictability. The highly variable values of the individual heritability estimates made it difficult to elucidate the possible sources of upward bias which may have contributed to the discrepancy. There is slight evidence that the estimated heritability of the Oregon-R base population could be biased upwards by sex-linked effects and that of the +3 population by epistatic variance. Sheldon (1963) reported some evidence of sex-linked effects but negligible epistatic effects in his base population. Sheridan et al. (1968) found moderate amounts of sex-linkage and additive x additive variance. The discrepancies between individual heritability estimates within and between different methods seem to suggest that the high overall values could be the result of sampling errors. It stresses the necessity to improve on the experimental design utilised in this present experiment from the point of view of increasing the number of two sires and two dams block matings and perhaps also increasing the number of animals scored from each mating in

order to increase the precision of the estimates.

Another method of prediction tried in this thesis was to extrapolate from the responses observed in the first generation, the trends of response in the subsequent generations of short-term selection. Here the realised heritabilities of the first generation of high and low selection lines were used in the prediction equation to evaluate the expected responses. These were then compared with the observed responses of the selection lines. It was hoped that any asymmetry might be predicted by this method. All the predictions for the three high and three low selection lines exceeded the observed average response over 14 generations. The only reasonable agreements were found between the predicted and the observed responses over the first seven generations for the Oregon-R low selection line and the males of the +3 low line. The asymmetrical patterns of two-way response observed from the females of the Oregon-R and the +3 population were actually in the opposite direction to the predicted.

Using first-generation realised heritabilities instead of the estimated heritabilities of the base populations did not appear to have improved to any large extent the reliability of the predictions since the discrepancies were still obvious. It had been suggested by Griffing (1960) that heritabilities from the first-generation responses tend to be over-estimated if additive x additive genetic variance was an important source of variation as its contribution to responses declined very rapidly in a few generations. The interaction variance which includes dominance and epistatic deviations was estimated to be negligible in the base populations and if this conclusion is valid, the discrepancies could not be attributed to this source of bias. Another possible cause of discrepancy was the large standard errors of both the observed and predicted responses, the latter due to the inaccuracy in estimation of the genetic parameters

( $\bar{l}$ ,  $\sigma_p$  and  $h^2$ ) used in its evaluation. The results from computer simulation studies of Gill (1965) showed that for small population sizes the effects of random drift and artificial selection could cause the genetic parameters of the selection line to deviate considerably from that of the base population in a few generations, thus resulting in poor agreement between the predicted and observed responses.



## VI. GENETIC ANALYSES OF SELECTED LINES

## VI. GENETIC ANALYSES OF SELECTED LINES

### A. ANALYSES OF +3 HIGH SELECTION LINE

The cessation of response from all four replicates of the +3 high selection line after the first few generations of response, despite continued selection for increased bristles, was quite unexpected. Particularly, since heritability was estimated to be about 37% in the +3 base population. In an attempt to elucidate the genetic situation responsible for this aberrant behaviour, two subsidiary experiments were carried out on the +3 high selection line after completion of the 14 generations of selection. The first experiment was designed to estimate heritability. The second experiment, crossing between +3 high and low selection lines was undertaken to attempt to elucidate directional dominance.

#### 1. Heritability estimations of the +3 high selection line

##### (1) Materials and methods

The two sires and two dams restricted diallel cross employed in the heritability estimates of the Oregon-R and +3 base populations was similarly used here. From each of the +3 high replicates in generation 14, equal numbers of bottle cultures were set up from flies selected at random from each of the replicates. Progeny emerging from these cultures were used in the diallel cross. It was pointed out earlier that the diallel crosses of the Oregon-R and +3 base populations suffered from the disadvantage of insufficient replications. For this present diallel cross, efforts were taken to set up as many single-pair matings as facilities allowed. For

Each replicate, at least 40 single pair matings were made. Both first and second matings for the diallel cross were made strictly between males and females of the same replicate.

#### (11) Results and discussion

Since the four +3 high replicates were found to have homogeneous means and phenotypic variances, data from the four replicates were pooled before carrying out the analyses for heritabilities. Altogether 68 blocks yielded complete data for the diallel analysis. As before, the results were analysed by parent-offspring regression and diallel analysis. Results of the analyses from these two methods are summarised in Table 41.

The results from the parent-offspring regression analysis give evidence that a fair proportion of the remaining additive genetic variance in the +3 high selection line, after 14 generations of selection, could be due to additive sex-linked effects. This is indicated by the dam-son and dam-daughter heritability estimates being considerably higher than the sire-son heritability estimate. However, the sire-daughter estimate, which is similarly biased by sex-linked effects and is therefore expected to be comparable to the dam-son and dam-daughter heritability estimates, is similar to the sire-son estimate instead. Thus it offers contrary evidence to the prevalence of sex-linkage.

Estimates of heritability from the diallel analysis varied considerably (from -0.14 to 0.47), despite the larger number of degrees of freedom (68) in this present diallel analysis when compared with the diallel analysis of the +3 base population which involved only 43 degrees of freedom. There is no evidence of sex-linkage from this analysis. The size of the interaction term is of the same order of magnitude as that obtained from the +3 base population. The average of the four estimates from the diallel analysis (0.12) is remarkably

**Table 41: Heritability estimates of the +3 high selection line (Gen.14)**

Regression analysis

|               |   |       |   |                  |
|---------------|---|-------|---|------------------|
| Sire-son      | : | $h^2$ | = | $-0.04 \pm 0.11$ |
| Dam-son       | : | $h^2$ | = | $0.23 \pm 0.08$  |
| Sire-daughter | : | $h^2$ | = | $0.02 \pm 0.13$  |
| Dam-daughter  | : | $h^2$ | = | $0.35 \pm 0.09$  |
| Average       |   | $h^2$ | = | 0.14             |

Diallel analysis

| Source of Variation                       | d.f. | Mean squares     |                 |
|-------------------------------------------|------|------------------|-----------------|
|                                           |      | Females          | Males           |
| Between sires within blocks               | 68   | 9.14             | 7.04            |
| Between dams within blocks                | 68   | 12.48            | 13.59           |
| Sire x dam interaction                    | 68   | 11.40            | 5.46            |
| Residual                                  | 1088 | 7.38             | 5.97            |
| $h_S^2$                                   |      | $-0.14 \pm 0.07$ | $0.10 \pm 0.06$ |
| $h_D^2$                                   |      | $0.05 \pm 0.08$  | $0.47 \pm 0.13$ |
| Average                                   |      | = 0.12           |                 |
| Interaction ( $\sigma_I^2 / \sigma_P^2$ ) |      | 0.12             | 0.02            |

|                                | <u>Female</u> | <u>Male</u> |
|--------------------------------|---------------|-------------|
| Realised heritability (Gen.14) | 0.06          | 0.05        |

similar to the average of the estimates from the regression analysis (0.14). The overall weighted average heritability of the +3 high selection line was found to be  $0.10 \pm 0.08$ .

There are two ways of looking at the estimated components of variation of the +3 high selection line. The first is to compare with the components of variation estimated in the original +3 base population. The second is to compare the estimated heritability with the realised heritability of the +3 high selection line in the 14th selection generation.

Comparison with the +3 base population: Theoretically, the genetic composition of the selection line is expected to deviate from the original base population as a result of selection, random drift or natural selection. The additive genetic variance is expected to decline while the non-additive component of genetic variance to increase. The components of variation of the +3 base population and +3 high line at the end of selection are given below:

|                      | <u>+3 base pop.</u> | <u>+3 high selection</u> |
|----------------------|---------------------|--------------------------|
| Additive genetic     | 0.35-0.40           | 0.10-0.15                |
| Non-additive genetic | 0.05-0.10           | 0.05-0.10                |
| Developmental error  | 0.25                | 0.25-0.35                |
| True environmental   | 0.30-0.40           | 0.50-0.60                |

The decline in additive genetic variance is evident but it is not accompanied by any apparent increase in non-additive genetic variance. Sheldon (1963) reported increase in non-additive genetic variance and decrease in additive genetic variance in his selection lines by the thirteenth selection generation, although he also found that the interaction variance declined with further selection. Both the developmental error and the

true environmental variance appeared to have increased with decrease in additive genetic variance and this could be indication of the weaker buffering ability of the more homozygous +3 high selection line when compared with the +3 base population. The average heritability of  $0.10 \pm 0.08$  estimated in the +3 high selection line leads to the expectation of further response being possible with continued selection. This estimated heritability will be compared with the realised heritability of the last selection generation in the following section.

Comparison with the realised heritability of the 14th selection generation:

From Fig. 5 it is clear that the average realised heritability of the +3 high selection line had declined drastically from 0.35 in G1 to 0.05 in G2 and subsequently remained at this low level till the end of the selection experiment. Thus, although the estimated heritability of the +3 high line ( $0.10 \pm 0.08$ ) showed a decline in additive genetic variance, it did not predict cessation of selection response. There is some evidence that the discrepancy between the estimated and the realised heritability could be due to sex-linked effects, although there was no evidence of sex-linkage in the unselected +3 base population.

2. Crossing between +3 high and low selection lines

There are two reasons for suspecting the prevalence of directional dominance for high bristle number in the +3 population. The first is the marked negative asymmetry of two-directional response. The second is the much greater decline in reproductive fitness of the +3 low selection line than in the high selection line. A means of testing this hypothesis for the prevalence of directional dominance is to make crosses between the high and low selection lines and observe the mean bristle score of the  $F_1$  progeny.

Table 42: Reciprocal crosses between +3 high selection line  
and +3 low selection replicates

|                             | Mean abdominal bristle number |         |
|-----------------------------|-------------------------------|---------|
|                             | Males                         | Females |
| Mid-parent value            | 30.30                         | 36.84   |
| Reciprocal ( ♂+3H x ♀+3LI   | 29.94                         | 37.74   |
| Progeny ( ♀+3H x ♂+3LI      | 29.94                         | 37.22   |
| Mid-parent value            | 30.99                         | 36.45   |
| Reciprocal ( ♂+3H x ♀+3LII  | 30.46                         | 36.28   |
| Progeny ( ♀+3H x ♂+3LII     | 30.84                         | 36.62   |
| Mid-parent value            | 30.28                         | 37.45   |
| Reciprocal ( ♂+3H x ♀+3LIII | 31.14                         | 37.58   |
| Progeny ( ♀+3H x ♂+3LIII    | 30.10                         | 38.08   |
| Mid-parent value            | 30.81                         | 36.56   |
| Reciprocal ( ♂+3H x ♀+3LIV  | 30.58                         | 36.20   |
| Progeny ( ♀+3H x ♂+3LIV     | 31.66                         | 37.62   |

The crosses were carried out after the selected lines had been relaxed for five generations. Equal numbers of males and virgin females were collected from each of the +3 high replicates. Since the four high replicates were shown to be homogeneous, it was decided to pool the flies from these replicates. Reciprocal crosses were then made between the +3 high selection line and each of the +3 low replicates separately. This was because the +3 low replicates were more variable. Values of the reciprocal crosses would give an indication of the effects of the sex chromosomes. From each of the crosses, 50 male and 50 female progeny

were scored for abdominal bristle and their means were given in Table 42.

If the hypothesis was true, the means of the  $F_1$  progeny would exceed the mid-parent means. In all cases, the  $F_1$  means were comparable to the mid-parent values. Thus it gives evidence that directional dominance was not responsible for the asymmetry observed in the +3 population. Also, the similarity between the pairs of reciprocal crosses in the males indicated the absence of sex-linked effects.

The conclusion from the above two tests is that the lack of response in the +3 high line was largely due to the decline in additive genetic variance, although the estimated heritability was greater than the realised heritability at the end of the selection. Since there was no evidence of directional dominance, an alternative hypothesis is needed to account for the asymmetry. It is possible that a few additive genes with large effects are responsible for high bristle number. Fixation of these genes in the early generations of selection could account for the ineffectiveness of further high selection and also the observed decline in both the phenotypic and additive genetic variance.



## B. RELAXATION OF SELECTION LINES

The main purpose in relaxing selection was to observe the magnitude of the forces of natural selection opposing artificial selection and to see whether there was any differential action of natural selection contributing to the observed asymmetry of responses from the three populations.

All the high and low replicates were relaxed for nine generations after the 14 generations of selection. The relaxed replicates were cultured under identical conditions as the selection replicates, with three bottles maintained for each replicate. The only difference was that for each relaxed generation, five pairs of randomly selected parents were used in each culture bottle instead of the three pairs used in the selection lines. This was used in attempt to maximise any action of natural selection and also to reduce random drift.

The changes of the mean abdominal bristle number over the nine generations of relaxation of individual replicates were graphed in Fig. 1. The general picture which emerged from the graphs was that there was little tendency for the selected replicates to regress to the unselected population means. To bring out the trends of regression on relaxation more clearly, Fig. 15 shows the deviation of the mean of the relaxed selection line from that of the unselected control line for each generation of relaxation for the females. The males showed very similar trends. Generation 0 in the figure corresponded to the 14th selection generation.

The Cross high line showed no tendency to return to its original population means over the nine relaxed generations. A gradual decline of about two bristles over the nine generations was observed in the Oregon-R high line. At first it would appear that the +3 high line quickly returned to its control population means within two generations

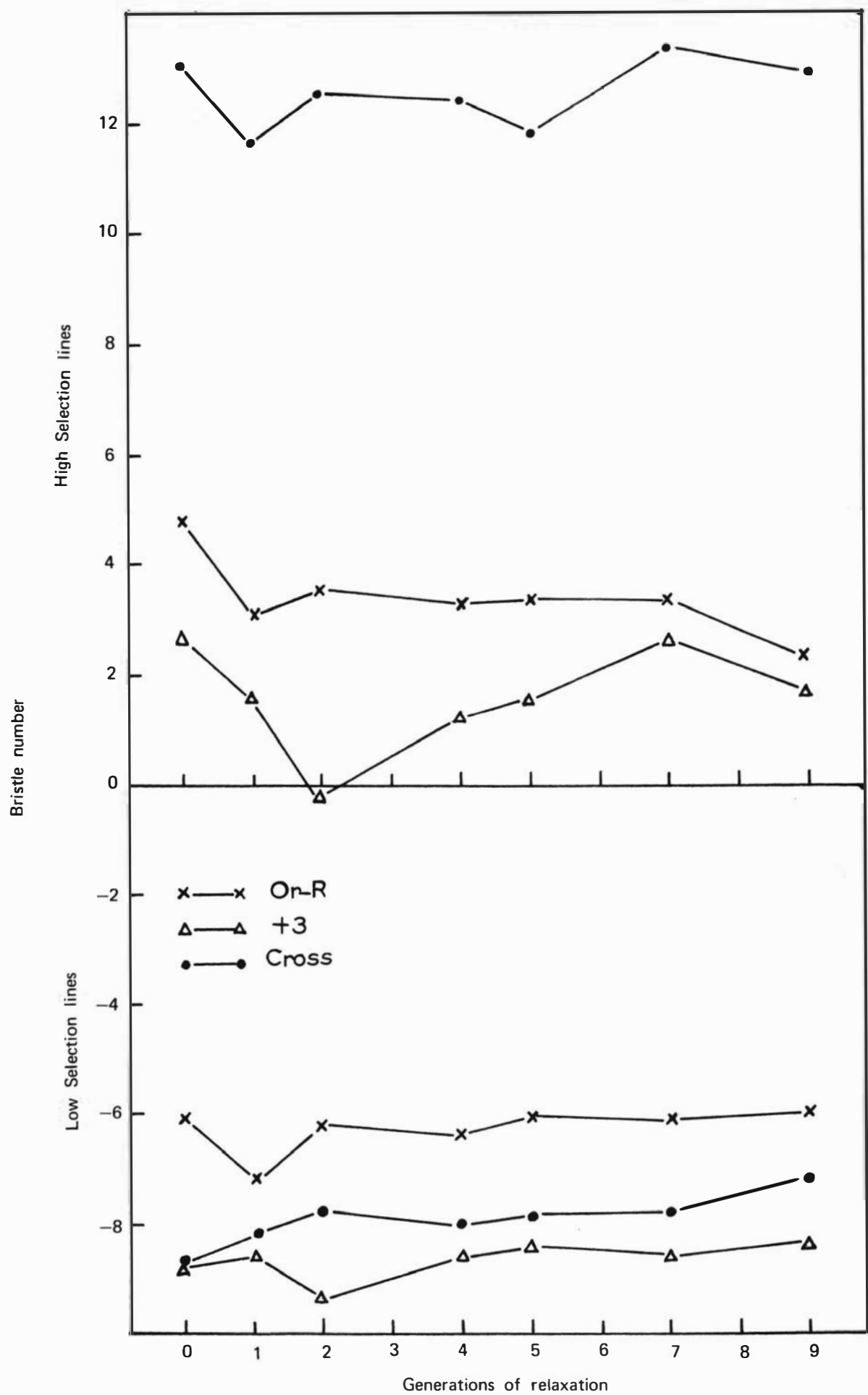


Fig. 15. Effects of relaxing selection. Deviations of selected line from the control line.

of relaxation, but it rose back to its original selection means after further relaxation, thus indicating that the regression was probably due to sampling variation. The +3 and the Oregon-R low lines showed no apparent regression while the Cross low line declined about one bristle over the whole period of relaxation.

The behaviour of the relaxed high and low selected lines indicated that the forces of natural selection were not strong in moving gene frequencies back to their original levels. It seems probable that the slight decline observed in the Oregon-R high line and the Cross low line could be due to the break-down of favourable epistatic combinations. The final conclusion is that the observed asymmetry in the three different populations is not caused by natural selection opposing artificial selection in any one direction.

## C. CHROMOSOME ANALYSIS

Simple tests to determine the relative effects of different chromosomes on the quantitative character in selection lines have been used extensively by Thoday and his associates (1959, 1964, 1966). Such tests consist essentially of substituting different chromosomes from the selection lines into an unselected tester stock, which is homozygous for recessive marker genes, on the chromosomes where the effect on the selected character is desired to be assessed. This test will be used in the present experiment as a means of giving information on the location of the genes controlling the selection response for high and low abdominal bristle numbers in the selection replicates of the Oregon-R, +3 and Cross populations.

### 1. Materials and methods

The tester stock employed for these chromosome assays was unselected for abdominal bristle score. It was homozygous for a second chromosome recessive vg (vestigial) and a third chromosome recessive se (sepia) and was consequently designated the vg se stock. Both these recessive mutants have no apparent effects on abdominal bristle number (Bridges and Brehme, 1944).

To limit the amount of work, it was decided to assay two replicates from each selection line. The two replicates within each selection line chosen were those which gave the greatest and least selection response. These same replicates were tested later for the presence of recessive lethals as this may reveal whether there was any association between the

size of the effect of the chromosome on bristle character and the presence of lethals.

It was not possible to assay all 12 replicates at the same time due to lack of facilities and difficulties of obtaining sufficient numbers of virgin female vg se flies needed for the matings. Consequently, the tests were spread out from the 12th generation of selection to the third relaxed generation. The mating scheme used in the substitution of second and third (II and III) chromosomes from the selection replicates to the vg se genetic background is shown in Table 43. The first generation matings (P) consisted of reciprocal crosses between flies randomly picked from the selection replicate and the vg se stock. For each reciprocal cross, five females and three males were used. In generation two ( $F_1$ ), male progeny from the reciprocal crosses were randomly selected and mated to virgin vg se females. Five cultures were set up for each reciprocal test cross and similarly three males and five or six vg se females were used for each culture bottle. In the  $F_2$ , four different marker type progeny were segregating. The four types were:

- (a) wild-type flies which were heterozygous for the second and third chromosomes
- (b) se flies which were heterozygous for the second chromosome
- (c) vg flies, heterozygous for the third chromosome
- (d) vg se flies, homozygous for vg and se.

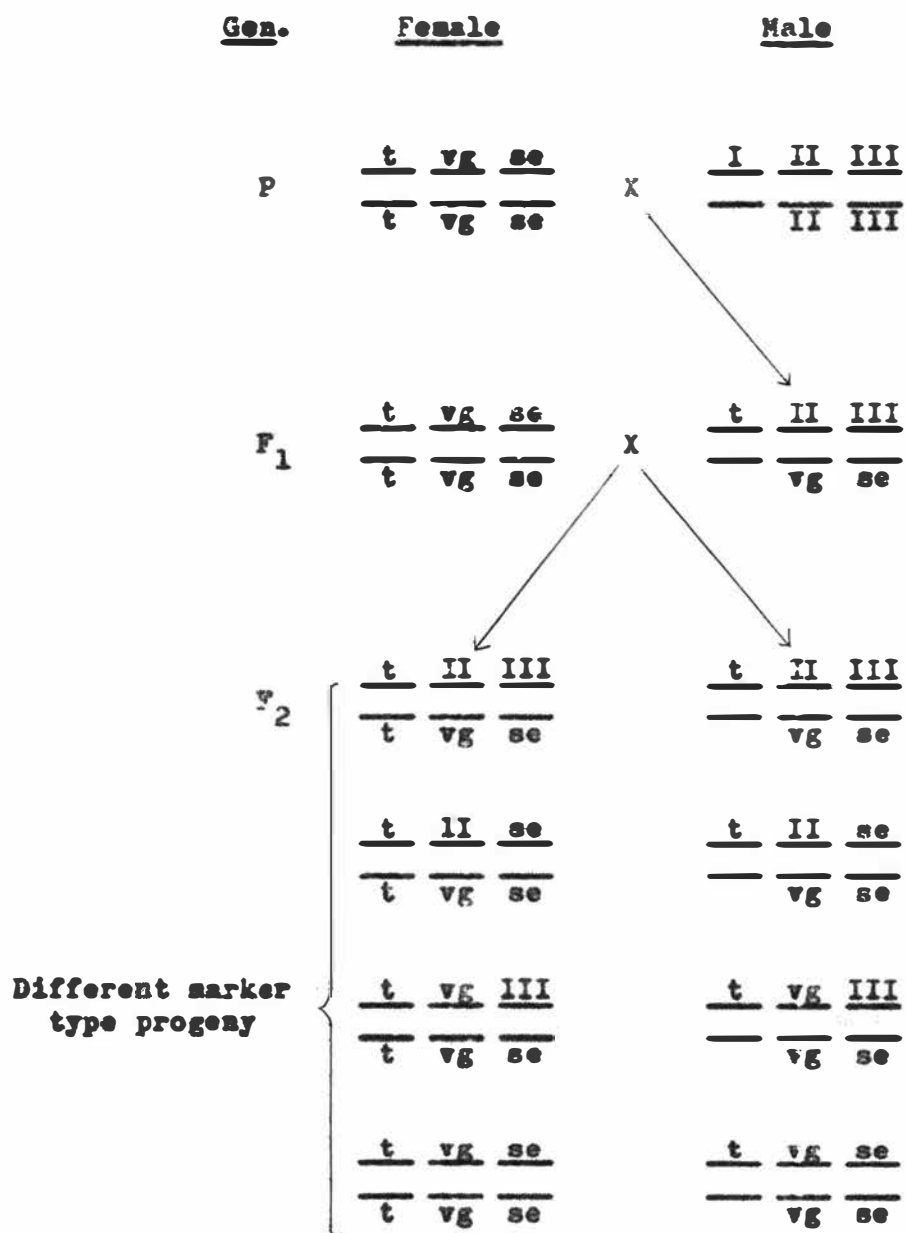
From each culture, five males and five females for each of the marker type progeny were scored for abdominal bristle number.

## 2. Observations and results

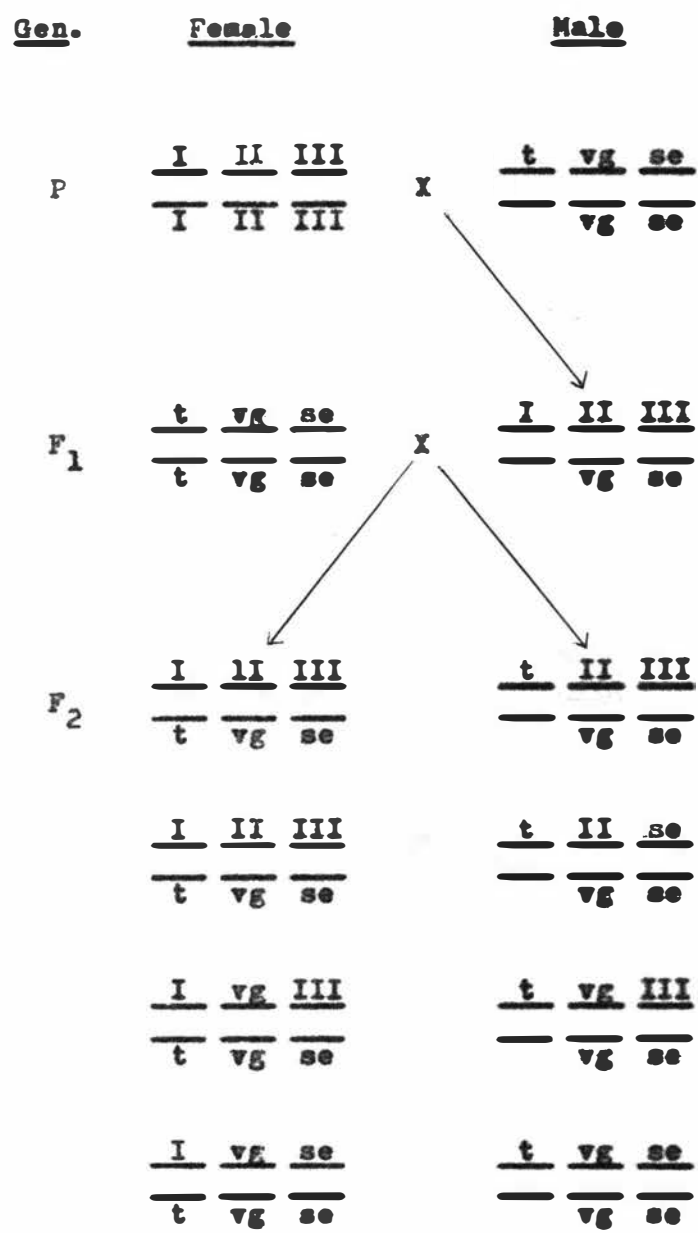
Before the results of the chromosome assays are presented it is

Table 43: Mating scheme for chromosome assays of selection replicates against vg se tester stock

(I, II and III refer to X chromosome, second and third chromosome of the selected replicate respectively. t is the X chromosome of the vg se stock)



Females of the F<sub>2</sub> progeny derive both X chromosomes from the vg se stock.



Females of the F<sub>2</sub> progeny are heterozygous for an X chromosome from the vg se stock and the other from the selected replicate.

worthwhile commenting on the vg se stock. It proved to be a difficult stock to handle because of the low viability of the adults and low hatchability of the pupae. The male vestigial wing flies in particular tended to get trapped and subsequently killed on the moist food surface. Thus, among the  $F_2$  progeny, the survival rate of the vg + and vg se flies was low compared with their relatives with normal wings and this was particularly noticeable when the cultures were crowded. In attempt to reduce the mortality rate of the vestigial flies, every effort was taken to make prompt and regular counts of the  $F_2$  flies as soon as they emerged. However, in spite of this precaution, the male data in most cases were incomplete. Among the five cultures set up for each reciprocal cross, invariably one of them failed to give the full quota of progeny so that final analysis involved only four cultures for each test-cross.

A full analysis of variance was carried out for the female data only. The significance of the chromosome effects and the interaction was tested by the standard F-test. The statistical model used for the analysis is as follows :-

$$Y_{ijkl} = \mu + a_i + b_{ij} + c_k + ac_{ik} + bc_{ijk} + e_{ijkl}$$

where  $Y_{ijkl}$  = lth observation on bristle number within the smallest subclass

$\mu$  = grand mean common to all observations

$a_i$  = effect of the ith cross

$b_{ij}$  = effect of the jth culture within the ith cross

$c_k$  = effect of the kth genotype

$ac_{ik}$  = interaction between ith cross and kth genotype

$bc_{ijk}$  = interaction between the jth culture within the ith cross and the kth genotype

$e_{ijkl}$  = random error peculiar to ijklth observation

(These errors are assumed to have zero mean, constant variance and to be normally and independently distributed.)

The results of the analysis of variance for each selection replicate assayed against the vg se stock are summarised in Table 44. Among the high selection replicates, all except the two +3 high replicates have chromosome II with significantly larger high abdominal bristle effect than the vg second chromosome. The chromosome III effects were significant for all six high replicates. Interactions between the second and third high selection chromosomes were significant in the Oregon-R and Cross high replicates. Effects of all other sources of variation were shown to be negligible.

The results from analysis of the low selection replicates were not so clear-cut and simple as from the high replicates. On most occasions, the third chromosomes of the low replicates had significantly higher instead of lower bristle effects than the se third chromosome. This analysis however, does show in a qualitative sense that the second chromosomes have larger effects on low abdominal bristles than the third chromosomes. Significant genotype by cross interactions were present in the two Oregon-R low replicates but their mean squares were small when compared with the effects of the second and third chromosomes.

Having shown by these F-tests that the effects of chromosomes II and III and the interactions between them are significant in most cases, the next step is to make a comparative study of the actual size of effects on high and low bristle character of the different chromosomes from different selection replicates. Results from this comparative study would show whether there is any regularity of the relative effects of chromosomes II and III on the selected character from replicates within populations and from different populations.

The mean abdominal bristle number of each marker type progeny of each selection replicate is given in Table 45. The effects of chromosomes



Table 44: Analysis of variance of female abdominal bristle number from chromosome assays

| Source of Variation                    | df  | Mean Squares          |          |           |          |          |          |
|----------------------------------------|-----|-----------------------|----------|-----------|----------|----------|----------|
|                                        |     | <u>HIGH SELECTION</u> |          |           |          |          |          |
|                                        |     | Or-RHII               | Or-RHIII | +3HI      | +3HIII   | XHIII    | XHIV     |
| Chrom. II: II se                       | 1   | 191.41**              | 378.23** | 24.03*    | 7.66     | 275.63** | 483.03** |
| Chrom.III: vg III                      | 1   | 57.76*                | 148.23** | 1254.40** | 596.76** | 902.50** | 113.23** |
| Interaction                            | 1   | 29.76*                | 25.60*   | 0.00      | 1.41     | 18.23*   | 40.00*   |
| Between Crosses                        | 1   | 1.40                  | 25.60    | 1.22      | 31.50    | 27.23    | 0.03     |
| Cultures within crosses                | 6   | 8.80                  | 3.47     | 11.76     | 9.72     | 10.90    | 9.01     |
| Genotypes x crosses                    | 3   | 10.52                 | 1.64     | 4.34      | 9.27     | 10.04    | 43.67*   |
| Genotypes x cultures<br>within crosses | 18  | 6.40                  | 8.51     | 5.34      | 4.17     | 15.27    | 6.35     |
| Within genotype,<br>culture and cross  | 128 | 6.64                  | 6.34     | 5.60      | 6.74     | 6.39     | 5.94     |
| <u>LOW SELECTION</u>                   |     |                       |          |           |          |          |          |
|                                        |     | Or-RLI                | Or-RLIII | +3LII     | +3LIV    | XLI      | XLIII    |
| Chrom. II: II se                       | 1   | 148.23**              | 30.63*   | 41.01*    | 170.16** | 61.26*   | 138.76** |
| Chrom.III: vg III                      | 1   | 40.00                 | 52.90**  | 131.41**  | 51.76*   | 0.76     | 218.56** |
| Interaction                            | 1   | 10.00                 | 8.10     | 51.76**   | 2.26     | 10.51    | 2.76     |
| Between crosses                        | 1   | 2.50                  | 0.02     | 0.15      | 0.30     | 17.55    | 5.25     |
| Cultures within crosses                | 6   | 13.08                 | 8.39     | 5.10      | 34.82*   | 9.92     | 9.50     |
| Genotypes x crosses                    | 3   | 56.12**               | 14.31*   | 1.36      | 1.19     | 10.32    | 8.84     |
| Genotypes x cultures<br>within crosses | 18  | 4.77                  | 3.58     | 5.44      | 7.33     | 5.29     | 4.68     |
| Within genotype,<br>culture and cross  | 128 | 4.62                  | 5.61     | 6.16      | 5.36     | 5.70     | 4.17     |

\* P = 0.05    \*\* P ≤ 0.01

II and III and the size of the interaction between II and III in the vg se genetic background are found by orthogonal comparisons. The effects of the X chromosome can be assessed by comparing the females of the reciprocal  $F_2$  offspring. It can be seen from Table 43 that in one reciprocal cross, both X chromosomes of the females were derived from the vg se stock (t/t) while the females of the other reciprocal cross were heterozygous for a X chromosome from the vg se stock and the other from the selected replicate (I/t). Thus, the effect of the X chromosome (chromosome I) can be assessed by subtracting the former from the latter within each of the four classes of genotypes. The value of the effect of the X chromosome within each replicate, given in Table 45, is the average of the effects of the X chromosomes in the four different classes of genotypes.

From Table 45, it can be seen that the X chromosome of both the high and low selection replicates has small effects when compared with chromosomes II and III. Frankham (1970) reported larger effects of X chromosomes in two of his high abdominal bristle selection lines. Results of effects of chromosomes II and III on high bristle number proved to be very interesting. One noticeable feature of the three high selection lines is that there are clear similarities between replicates within the same high line and strong differences between the replicates from different high lines. For the two Oregon-R high replicates, both chromosomes II and III have significant effects, although it is evident that the effect of the former is larger. The +3 high replicates show different results. There is strong evidence that nearly all the genes controlling high selection response were located in chromosome III and the chromosome II on the other hand had lower bristle effects than the vg second chromosome. For the Cross, both chromosomes II and III have sizable high bristle effects. It

Table 45: Chromosome assays of selection replicates against vg se atock (female data)

|                       |        | Mean abdominal bristle no.<br>(test cross progeny) |       |       |        | Chromosome effect |         |         | Interaction<br>between<br>II and III |
|-----------------------|--------|----------------------------------------------------|-------|-------|--------|-------------------|---------|---------|--------------------------------------|
|                       |        |                                                    |       |       |        | X                 | II      | III     |                                      |
|                       |        | II                                                 | III   | II se | vg III | vg se             |         |         |                                      |
| <u>HIGH SELECTION</u> |        |                                                    |       |       |        |                   |         |         |                                      |
| Or-RHII               | (t/t   | 40.35                                              | 39.00 | 38.15 | 36.80  |                   |         |         |                                      |
|                       | (I/t   | 39.45                                              | 40.25 | 39.00 | 36.35  |                   |         |         |                                      |
|                       | (Aver. | 39.90                                              | 39.63 | 38.58 | 36.58  | 0.19              | 4.37**  | 2.27**  | -1.73*                               |
| Or-RHIII              | (t/t   | 39.60                                              | 38.45 | 36.95 | 34.60  |                   |         |         |                                      |
|                       | (I/t   | 40.20                                              | 39.10 | 38.30 | 35.20  |                   |         |         |                                      |
|                       | (Aver. | 39.90                                              | 38.78 | 37.63 | 34.90  | 0.80              | 6.15**  | 3.85**  | -1.61*                               |
| +3HI                  | (t/t   | 40.05                                              | 34.75 | 41.45 | 35.95  |                   |         |         |                                      |
|                       | (I/t   | 41.05                                              | 35.15 | 41.20 | 35.50  |                   |         |         |                                      |
|                       | (Aver. | 40.55                                              | 34.95 | 41.33 | 35.73  | 0.19              | -1.56*  | 11.20** | 0.00                                 |
| +3HIII                | (t/t   | 40.60                                              | 36.20 | 40.15 | 37.60  |                   |         |         |                                      |
|                       | (I/t   | 39.40                                              | 35.70 | 40.35 | 35.55  |                   |         |         |                                      |
|                       | (Aver. | 40.00                                              | 35.95 | 40.05 | 36.58  | -0.89             | -0.68   | 7.52**  | 0.58                                 |
| XHIII                 | (t/t   | 41.65                                              | 38.65 | 39.75 | 34.80  |                   |         |         |                                      |
|                       | (I/t   | 43.30                                              | 38.15 | 41.30 | 35.40  |                   |         |         |                                      |
|                       | (Aver. | 42.48                                              | 38.40 | 40.53 | 35.10  | 0.83              | 5.25**  | 9.51**  | -1.35                                |
| XHIV                  | (t/t   | 45.00                                              | 41.55 | 41.30 | 34.90  |                   |         |         |                                      |
|                       | (I/t   | 44.15                                              | 38.95 | 42.90 | 36.65  |                   |         |         |                                      |
|                       | (Aver. | 44.58                                              | 40.25 | 42.10 | 35.78  | 0.00              | 6.95**  | 10.65** | -1.99*                               |
| <u>LOW SELECTION</u>  |        |                                                    |       |       |        |                   |         |         |                                      |
| Or-RLI                | (t/t   | 36.35                                              | 35.90 | 36.70 | 35.30  |                   |         |         |                                      |
|                       | (I/t   | 34.10                                              | 33.55 | 38.60 | 37.00  |                   |         |         |                                      |
|                       | (Aver. | 35.23                                              | 34.73 | 37.65 | 36.15  | 0.25              | -3.84** | 2.00**  | -1.00                                |
| Or-RLIII              | (t/t   | 37.95                                              | 36.60 | 36.35 | 34.80  |                   |         |         |                                      |
|                       | (I/t   | 37.40                                              | 35.55 | 36.35 | 36.50  |                   |         |         |                                      |
|                       | (Aver. | 37.68                                              | 36.08 | 36.35 | 35.65  | 0.00              | 1.76*   | 2.30**  | 0.90                                 |
| +3LII                 | (t/t   | 34.05                                              | 33.70 | 36.15 | 33.50  |                   |         |         |                                      |
|                       | (I/t   | 34.25                                              | 33.25 | 36.45 | 33.20  |                   |         |         |                                      |
|                       | (Aver. | 34.15                                              | 33.48 | 36.30 | 33.35  | -0.06             | -2.02** | 3.62**  | -2.28*                               |
| +3LIV                 | (t/t   | 34.60                                              | 33.70 | 37.05 | 35.90  |                   |         |         |                                      |
|                       | (I/t   | 34.95                                              | 34.05 | 37.10 | 35.50  |                   |         |         |                                      |
|                       | (Aver. | 34.78                                              | 33.88 | 37.08 | 35.70  | 0.11              | -4.12** | 2.28*   | -0.48                                |
| XLI                   | (t/t   | 35.90                                              | 34.60 | 36.40 | 36.25  |                   |         |         |                                      |
|                       | (I/t   | 34.15                                              | 34.70 | 35.10 | 36.55  |                   |         |         |                                      |
|                       | (Aver. | 35.03                                              | 34.65 | 35.75 | 36.40  | -0.69             | -2.47*  | -0.27   | 1.03                                 |
| XLIII                 | (t/t   | 35.65                                              | 32.60 | 37.50 | 34.30  |                   |         |         |                                      |
|                       | (I/t   | 34.95                                              | 33.85 | 37.35 | 35.35  |                   |         |         |                                      |
|                       | (Aver. | 35.30                                              | 33.23 | 37.43 | 34.83  | 0.36              | -3.73** | 4.67**  | -0.53                                |

\* P = 0.05

\*\* P ≤ 0.01

could be inferred that the high chaetae factors of the Cross chromosome II were derived from the Oregon-R parental strain and those of chromosome III from the +3 parental strain. No interaction between chromosomes II and III of the +3 high replicates was apparent. Significant negative interactions were detected in the Oregon-R and Cross high replicates, implying that the two chromosomes reacted with each other to depress the bristle score instead of increasing it. However, these interactions were small when compared with the effects of the chromosomes themselves.

Among all the six low replicates, there is evidence that the loci responsible for low abdominal bristles were located mainly in the second chromosome. The third chromosomes of all the low replicates, except XLI, have significantly higher bristle effects than the se third chromosome. The +3LII showed the interesting phenomenon of interaction, with chromosomes II and III reacting with each other in the positive direction to cause further reduction in bristle number. Positive interaction has also been observed by Thoday et al. (1966) between the second chromosome and a located "gene" in the third chromosome of a high sternopleural selection line.

### 3. Discussion

It must be mentioned that these simple chromosome assays are limited in their uses since they cannot detect the effects of any recessive genes which may affect the selected quantitative character. However, the results from the chromosome analyses tie in remarkably well with the observed two-way responses of the three populations and provide further supporting evidence for the hypothesis proposed earlier to cater for the observed responses. Comparative genetic analyses of the high selection

replicates revealed strong similarity between replicates within selection lines and apparent differences between the Oregon-R, +3 and Cross high lines. For the Oregon-R, more of the loci controlling high bristles were located in chromosome II while in the +3, such loci were located almost entirely in the third chromosome. Both chromosomes II and III of the Cross high replicates have considerable abdominal bristle effects. Such evidence indicates that the two original strains, Oregon-R and +3, have different array of genes affecting high bristles and that by amalgamating the two populations to form the Cross, the factors responsible for increase in abdominal bristles, situated predominantly in chromosome II of the Oregon-R and chromosome III of the +3, are brought together and subsequently selected for in the Cross. This could account for the strong high response observed in the Cross despite the poor response upwards from the two parental strains.

The chromosome assays reveal that the third chromosomes of the +3 high replicates have considerable effects on high bristles. The third chromosomes of +3HI and +3HIII exceeded the se third chromosome by 11.20 and 7.52 bristles respectively. This deviates considerably from the observed response of one to two bristles in the +3 high replicates after 14 generations of selection. The observation seems to give some support to the hypothesis of inter-allelic epistatic interactions proposed by Clarke et al. (1961), to explain asymmetrical response. It would seem that the +3 genetic background acted as a "barrier" inhibiting the expression of the alleles for high bristles. But when these alleles were transferred to a different genetic background such as that of the vg se or the "Cross", the phenotypic expression of the +3 alleles for increased bristles was no longer inhibited. This genetic situation could partly account for the extremely poor upward response of the +3 high replicates.

The loci responsible for low bristle number appeared to be located on the second chromosome in both the Oregon-R and +3. The homogeneity of selection responses and also the similarity in chromosome effects, not only of the Oregon-R and +3 but also of the Cross low line, gave further evidence that the loci responsible for low bristles in the two parental strains were similar, thus resulting in no apparent increase in genetic variability or selection response in the Cross low replicates.

## D. LETHAL TEST

In Drosophila, the availability of special stocks carrying marked-inversions affords a unique technique for determining the frequencies of deleterious genes in a population. Such lethal tests have been used extensively by Dobzhansky and his associates to study the hidden genetic variability of natural populations of Drosophila (Dobzhansky and Spassky, 1953; Dobzhansky, Spassky and Tidwell, 1963; Dobzhansky, 1964). In later years, it has been adopted by other workers to analyse the genetic situation underlying the response in selection lines. Reeve and Robertson (1953) tested for the presence of second and third chromosome recessive lethals in lines of D. melanogaster selected for long and short wings for 58 generations. Results from these tests showed that the recessive lethals were confined to the third chromosomes in both long and short-winged flies. The overall viability of the short-winged flies was about 5% higher than that of their long-winged counterparts. A similar test was conducted by Brown and Bell (1961) to assess the importance of lethal and other detrimental factors in a population of D. melanogaster which had completely ceased responding to selection for high fecundity. Their results showed that neither sex-linked or autosomal lethals or other subvital factors were responsible for retarding response to selection as their frequencies were no higher than those reported for natural populations which were in equilibrium.

Clayton et al. (1957), using similar techniques, found an appreciable frequency of lethals on the second chromosomes in some high and low abdominal bristle selection replicates and on the third chromosomes in other replicates. Evidence indicated that these recessive lethals were maintained at high frequencies in the selection lines because of lethal heterozygote

superiority for extreme bristle number. They were responsible for the high genetic variability persisting in the selection lines despite cessation of response.

Two high and two low abdominal bristle lines were tested by Latter and Robertson (1962) at the tenth generation of selection. Frequency of third chromosome lethals, which is near its theoretical maximum of 33%, was detected in one of the low selection lines.

Frankham et al. (1968) analysed 27 high abdominal bristle selection lines. Most of the lines had low frequencies of second and third chromosome lethals. However, two lines showed a high frequency of lethals and, because both lines regressed considerably on relaxation of selection, it was clear that these lethals had large effects on bristle score.

The prevalence of recessive lethals appear to be a common phenomenon in both natural and selected populations. The deleterious factors may be maintained in high frequencies in selection lines for the following reasons: (a) The lethals are favoured by artificial selection because of large effects of the lethal heterozygote on the selected trait; (b) Natural selection may favour lethals because of their heterozygote superiority for fitness; and (c) Lethal recessives may be linked with genes affecting the selection character.

Lethal tests were carried out on the selection replicates of the present experiment to detect whether the presence of lethals was limiting the response to selection, particularly in the Oregon-R and +3 high selection lines. The tests were extended to evaluate the effects of second and third chromosome homozygotes on viability and also the effects of epistatic interactions between second and third chromosome homozygotes.



# 1. Materials and methods

The two replicates from each high and low selection line, which had been assayed earlier for effects on bristle number, were subjected to lethal tests. This would afford the opportunity to examine whether there is any direct correlation between chromosome effect and frequency of lethals in the selection lines. The tests were made between the 12th selection generation and the second relaxed generation.

The method employed was a modification of the technique used by Brown and Bell (1961). The tester stock carried the dominant mutants Curly (Cy) and Flum (Pm) on the second chromosomes and Dichaete (D) and Stubble (Sb) on the third chromosomes. These dominant lethal marker genes are associated with multiple inversions which suppress virtually all crossing-over in the heterozygote, so that the chromosomes segregate as whole units. The second and third chromosomes from the selection replicate were tested for the presence of recessive lethals or subvital factors by transferring the chromosomes into the genetic background of the tester-stock and rendering them homozygous by a series of controlled crosses. The mating scheme used is shown in Table 46 and it involves three crosses:-

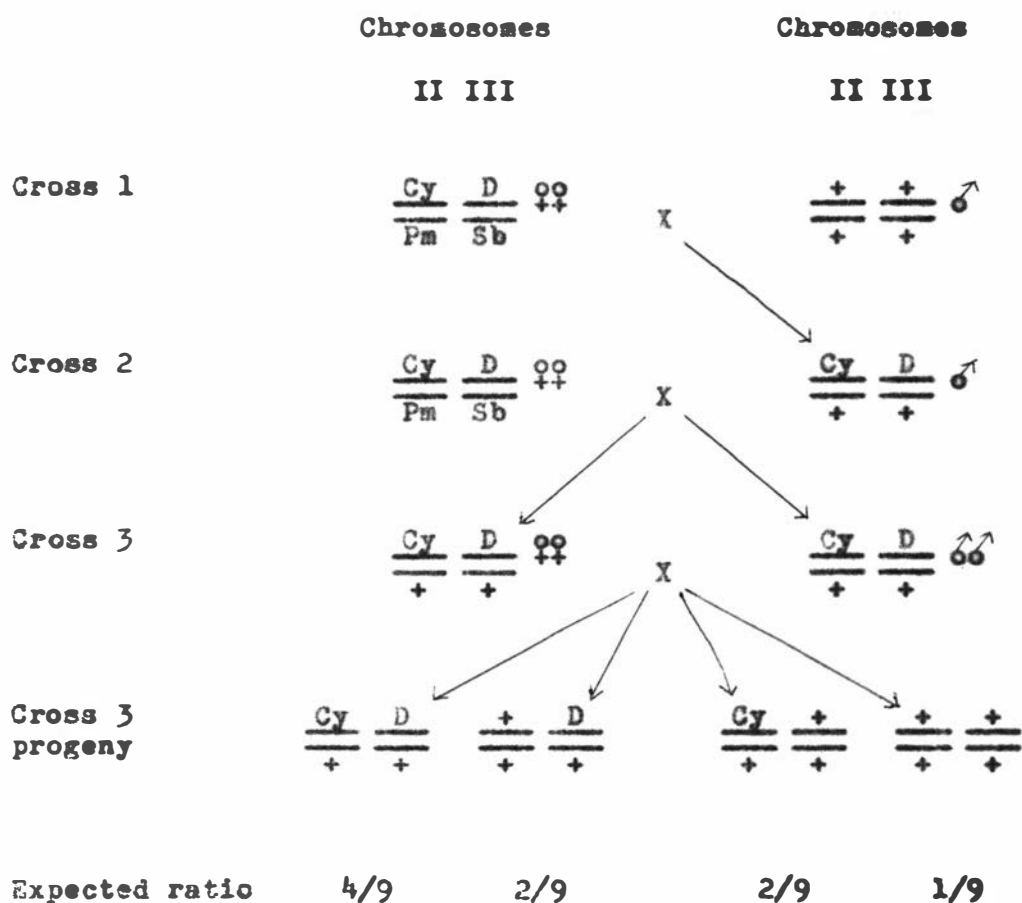
Cross 1: 4 or 5 males were randomly picked from each selection replicate and each was mated to 4 or 5 virgin females of the tester stock.

Cross 2: 6 males were randomly selected from the progeny of each of the Cross 1 matings. Each male was back-crossed to a few tester females. At least six offsprings were tested from each cross to ensure that both the second and third chromosomes (selected chromosomes) of the original sire were being tested.

Cross 3: In order to duplicate the second and third chromosomes from the selection replicate, Cy D males and virgin females from progeny of Cross 2

were mated together. The main reason for using the Cy D markers was that the progeny segregating in the fourth generation could be grouped into their respective phenotypic classes without having to examine under the binocular microscope. The Cy/Cy and D/D homozygotes would be absent from Cross 3 progeny as the mutants are dominant lethals. If neither the second or third chromosomes from the selection replicates are lethal, four phenotypic classes would be present among the Cross 3 progeny. Among the four classes would be the wild-type flies which are homozygous for both the second and third selected chromosomes (+ +), flies with the dominant marker Dichaete (+ D) which are homozygous for the second selected chromosome, progeny which show the Curly (Cy +) which are homozygous for the third selected chromosome and lastly the double heterozygotes (Cy D). If either second or third chromosome contains recessive lethal factors, the phenotypic class with the respective homozygote would be absent. This enabled the frequencies of second and third chromosome lethals in the selection replicates to be assessed directly. The progeny of Cross 3 were sorted into their various phenotypic classes and the numbers recorded.

Table 46: Mating system utilised for detecting recessive lethals in second and third chromosomes in the selection replicates (The male used in Cross 1 is equivalent to a fly from the selection replicate)



## 2. Observations and results

The frequency of second and third chromosome lethals as well as the relative viabilities of the second and third chromosome homozygotes and the interaction between the second and third chromosomes are evaluated according to the method described below. The assumption inherent in this method of estimation is that the genetic background of the tester stock does not have differential effects on the viability of the different phenotypic classes. Under such conditions, if all the progeny are equally viable, the expected ratio of the four phenotypic classes, Cy D, + D, Cy + and ++, would be equal to 4 : 2 : 2 : 1 (Table 47). The observed number of Cy D flies would be taken as the criterion for 100% fitness. If either the second or third chromosome contains recessive lethals, the phenotypic class with the homozygote would be missing. But if the chromosomes are semi-lethal or subvital, the observed number of flies in their respective phenotypic classes would be less than expected.

| Table 47: Method of analysis of the effects of the second and third chromosome homozygotes of the selection replicates on viability |             |                |                |                |
|-------------------------------------------------------------------------------------------------------------------------------------|-------------|----------------|----------------|----------------|
| Phenotypes                                                                                                                          | <u>Cy D</u> | <u>+ D</u>     | <u>Cy +</u>    | <u>++</u>      |
| Expected numbers                                                                                                                    | w           | $\frac{1}{2}w$ | $\frac{1}{2}w$ | $\frac{1}{4}w$ |
| Observed numbers                                                                                                                    | w           | x              | y              | z              |

The viability index of the second chromosome homozygote (S) is obtained by dividing the observed number of + D flies by the expected number, which is half the number of the observed Cy D individuals

( $S = x/\frac{1}{2}w$ ). Similarly, T, the viability index of the third chromosome homozygote is evaluated by dividing the observed number of Cy + flies by the expected ( $T = y/\frac{1}{2}w$ ).

The interaction (I) between the second and third chromosome homozygotes can also be evaluated. If the two chromosome homozygotes are independent in their effects on viability, the expected number of individuals in the ++ class would be equal to  $ST\frac{1}{4}w$ . But if interaction occurs, the actual number of individuals in the ++ class would be equal to:

$$z = I S T \frac{1}{4} w$$

Rearranging the equation and substituting for values of S and T, the interaction can be evaluated by :  $I = wz/xy$ .

The relative viabilities of the homozygotes are classified as shown below. The classification is arbitrary and is adapted from Crow (1968).

- \* V. I. (<0.10) : lethal
- V. I. (0.10-0.50) : semi-lethal
- V. I. (>0.50) : quasinormal

The homozygote is regarded as lethal if the relative viability is less than 0.10. This criterion for lethality has also been adopted by Chung (1962) and Temin (1966). For each selection replicate, about 20-24 chromosomes were tested for lethals. The frequencies of second and third chromosome lethals for each replicate were calculated and expressed as percentages.

#### (i) Frequency of recessive lethals

This analysis shows the relative frequencies of recessive lethals in the selection replicates from different populations. The frequency of lethal second and third chromosomes for each selection replicate is given in percentages in Table 48.

\* (V. I. = viability index)

Table 48: Frequency of lethal second and third chromosomes in high and low selection replicates (n = number of chromosomes tested)

| <u>HIGH SELECTION</u> |         |    |                    |           | <u>LOW SELECTION</u> |         |    |                    |           |
|-----------------------|---------|----|--------------------|-----------|----------------------|---------|----|--------------------|-----------|
| Selection replicate   |         | n  | Freq.of lethals(%) |           | Selection replicate  |         | n  | Freq.of lethals(%) |           |
|                       |         |    | Chrom.II           | Chrom.III |                      |         |    | Chrom.II           | Chrom.III |
| Or-R                  | Rep. II | 19 | 52.6               | 63.2      | Or-R                 | Rep. I  | 23 | 26.1               | 17.4      |
|                       | Rep.III | 22 | 9.1                | 59.1      |                      | Rep.III | 23 | 56.5               | 43.5      |
| +3                    | Rep. I  | 24 | 4.2                | 0.0       | +3                   | Rep. II | 24 | 0.0                | 37.5      |
|                       | Rep.III | 24 | 0.0                | 0.0       |                      | Rep. IV | 23 | 34.8               | 4.4       |
| Cross                 | Rep.III | 21 | 4.8                | 14.3      | Cross                | Rep. I  | 23 | 8.7                | 26.1      |
|                       | Rep. IV | 23 | 4.4                | 0.0       |                      | Rep.III | 24 | 12.5               | 25.0      |

Extremely high frequencies of second and third chromosome lethals were present in Or-RHII and Or-RLIII. For Or-RHIII, only the third chromosome had a high lethal frequency. From such evidence, it is plausible that the poor response of the Oregon-R high replicates and the marked decline in response rate of Or-RLIII from generation seven onwards were due to the selection of recessive lethal factors in their heterozygous state. Since these replicates showed little regression in bristle score over the nine relaxed generations (Fig.15), it could be inferred that these lethals were not selected because of their heterozygote superiority for bristle score. They could be selected because of linkage to genes affecting the selected trait.

A different picture emerged from the +3 population. The two +3 high replicates had extremely low frequency of lethals in the second

chromosome and none were uncovered in the third chromosome. It leaves little doubt that the extremely poor upward response from the +3 population is unlikely to be due to the presence of recessive lethals. The results from the +3 low replicates proved to be rather interesting. There was evidence of high frequency of chromosome III lethals (37.5%) but low frequency of chromosome II lethals in +3LII. The +3LIII on the other hand showed high second chromosome lethals (34.8%) and low third chromosome lethals (4.4%). The marked difference between the two replicates from the +3 population could be due to two possible causes: It could simply be the result of sampling variation, since only a very small sample of flies was tested for lethals from each replicate or; It could also be that recessive lethals were present at low initial frequencies in the +3 base population so that due to sampling variation, some of the recessive lethals were included in one replicate but not in another.

The two Cross high replicates, which gave good responses throughout the 14 generations of selection, had low frequencies of both second and third lethal chromosomes. The Cross low replicates had higher lethal frequencies than the high replicates particularly on the third chromosome.

In conclusion, the replicates from the Oregon-R population as well as the +3 low replicates had high lethal frequencies of over 30%. The other selection replicates tested had frequencies below 25% and in the author's opinion this could not be regarded to have affected selection responses to any large extent since it has been found by other workers that both natural populations as well as laboratory stocks of Drosophila carried lethal frequencies of this order of magnitude. Greenberg and Crow (1960) reported the frequency of the second chromosome lethals in wild and cage populations of D. melanogaster to be about 25%. In studies with a large population of D. melanogaster at equilibrium, Temin (1966)

observed a 23% frequency of second chromosome lethals. More recently, Frankham et al. (1968) found lethal frequencies of 9.5% and 14.5% for the second and third chromosomes respectively in the Canberra cage population.

(ii) Relative viabilities

Omitting the lethals, the average viability indices for the second and third chromosome homozygotes can be computed and are given in Table 49. As mentioned, the viability indices were obtained by comparing the viability of the homozygote with that of the double heterozygote. This is based on the assumption that the marker genes do not affect the viability of the heterozygote either favourably or adversely. Dobzhansky and Spassky (1963) and Dobzhansky, Spassky and Tidwell (1963) reported that the mutant markers they used did not appreciably affect the viability of the heterozygotes.

It must be borne in mind that all the results from the present analysis must be interpreted in the context of the genetic background of the tester stock employed in this particular experiment, as Reeve and F.W. Robertson (1953) and Spassky, Dobzhansky and Anderson (1965) have pointed out that the degree of lethality of a chromosome could be modified by changes in the genetic background.

A feature which stands out from the data in Table 49 is the similarity of results between the two replicates within selection lines and this at least gives some support that the results are not spurious due to high sampling variation of cultures with too few progeny. The +3 and Cross high replicates showed overall high homozygous viabilities, particularly for the third chromosome and this tallied well with the actual observation of high fitness of these replicates throughout the selection programme. The Oregon-R high replicates differed from the +3 and Cross high replicates in that the second chromosome homozygotes had low viabilities and could be



Table 49: Viability indices of second (S) and third (T) chromosome homozygotes of the selection replicates as well as interaction (I)

|                       | Viability Index |                 | Interaction     |
|-----------------------|-----------------|-----------------|-----------------|
|                       | S               | T               | I               |
| <u>HIGH SELECTION</u> |                 |                 |                 |
| Or-R Rep. II          | $0.84 \pm 0.10$ | $0.56 \pm 0.23$ | $0.67 \pm 0.10$ |
| Rep. III              | $0.86 \pm 0.07$ | $0.46 \pm 0.12$ | $1.02 \pm 0.17$ |
| +3 Rep. I             | $0.87 \pm 0.09$ | $1.23 \pm 0.10$ | $1.03 \pm 0.10$ |
| Rep. III              | $0.62 \pm 0.17$ | $1.35 \pm 0.15$ | $1.03 \pm 0.11$ |
| Cross Rep. III        | $0.93 \pm 0.06$ | $1.53 \pm 0.18$ | $1.05 \pm 0.16$ |
| Rep. IV               | $0.77 \pm 0.08$ | $1.63 \pm 0.26$ | $1.11 \pm 0.12$ |
| <u>LOW SELECTION</u>  |                 |                 |                 |
| Or-R Rep. I           | $0.51 \pm 0.09$ | $1.40 \pm 0.12$ | $0.87 \pm 0.13$ |
| Rep. III              | $0.41 \pm 0.09$ | $1.40 \pm 0.18$ | $1.06 \pm 0.14$ |
| +3 Rep. II            | $0.89 \pm 0.11$ | $0.90 \pm 0.13$ | $1.23 \pm 0.64$ |
| Rep. IV               | $0.91 \pm 0.11$ | $0.83 \pm 0.11$ | $0.82 \pm 0.11$ |
| Cross Rep. I          | $0.90 \pm 0.07$ | $0.95 \pm 0.09$ | $0.79 \pm 0.09$ |
| Rep. III              | $0.93 \pm 0.06$ | $0.80 \pm 0.12$ | $1.07 \pm 0.14$ |

regarded as semi-lethals.

The viability of the second and third chromosome homozygotes of the +3 and Cross low replicates fell in the quasinormal range. In contrast, the Oregon-R low replicates had second chromosome homozygotes which could be classified as semi-lethals and third chromosome homozygotes as quasi-normals.

(iii) Interactions

The interactions between the second and third chromosome homozygotes for each replicate are given in Table 49. Interactions between chromosomes could be roughly classified into three types according to the value of  $I$ .

- (a)  $I = 1$  : Viability effects of the second and third chromosome homozygotes are independent (non-synergism).
- (b)  $I < 1$  : reinforcing or positive synergism, where the double homozygote is less viable than either of the single homozygotes.
- (c)  $I > 1$  : opposing or negative synergism, where the deleterious effects of one chromosome homozygote neutralise the detrimental effects of the other homozygote.

There is little literature available on the effects of interactions between homozygous chromosome pairs on viability. There is some evidence that such epistasis may enhance the decline in viability in Drosophila (Dobzhansky, Spassky and Tidwell, 1963; Spassky, Dobzhansky and Anderson, 1965; Mukai, 1967). Crow (1968) found interactions between second and third chromosome homozygotes to be insignificant. In studies utilising the grasshopper, Moraba scurra, Parsons (1964) found evidence of interactions between two pairs of homozygotes which caused a rise in viability. Brown and Bell (1961) reported similar negative synergism between the second and third chromosome homozygotes in a "plateaued" population of D. melanogaster. Results from the present experiment would add further useful information on the effects of such interactions.

The general conclusion from the results of the 12 selection replicates would be that there is a general tendency for non-synergistic interactions. However, positive epistasis occurred in four replicates, Or-RHII, Or-RLI, +3LII and XLI, where the values of  $I$  were below one.

The only instance of negative epistasis was found in the +3LII ( $1.23 \pm 0.64$ ) but this has to be interpreted with caution because of its large standard error.

### 3. Discussion

Results from these lethal tests indicate that balanced lethal systems built up in the second and third chromosomes could be limiting the selection response of the following replicates; Or-RHII, Or-RLIII, +3LII and +3LIV. The low frequency of lethals in the +3 high replicates, in contrast to the high frequency in the +3 low replicates, could mean that in the +3 population the recessive lethals and other detrimental factors are associated with low bristle number so that in the process of selecting for high bristles these factors have been selected out of the high replicates. In all the tested replicates, except the +3 and Cross high replicates, the viabilities of the second and third chromosome homozygotes were lower than the heterozygous viabilities.

With regard to inter-chromosomal interactions on viability, there is strong evidence that in the present genetic background, the interactions tended to be non-significant, that is, the effects of the second and third chromosome homozygotes were independent. There is some evidence for positive epistasis, where the double homozygote has lower viability than either of the single homozygotes. The occurrence of negative epistasis was rare and this was not surprising as it is highly unlikely for such homozygous situations and consequently favourable interactions of this kind, to arise in natural or selected populations. Also, it has been demonstrated that natural selection normally favours heterozygous genotypes because of higher fitness (Wallace and Madden, 1953; Wallace and Dobzhansky, 1962; Dobzhansky and Spassky, 1963). In this respect, it

is more likely for interactions between heterozygous chromosomes to be built up than between homozygous chromosomes. It has also been pointed out by Parsons (1964) that although inter-chromosomal interactions may assume importance in lessening the genetic load in species with low reproductive rate like man, they are much less likely to occur in Drosophila where high mortality could be tolerated.

#### E. DISCUSSION

The main purpose of conducting these series of experiments - relaxation of selection, chromosome analyses and lethal tests - is to elucidate the genetic situation responsible for the observed selection responses. Results from the heritability estimates of the +3 high selection line and the crosses between the +3 high and low selection lines give a clear indication of decline in additive genetic variance and the absence of directional dominance. The rarity of recessive lethals in the second and third chromosomes and the lack of tendency for the +3 high replicates to regress in bristle score when selection was suspended suggest that the lack of upward responses was not due to the selection of superior lethal heterozygotes either for the selected trait or for fitness. It is probable that the sudden cessation of response in the +3 high line, after only about two generations of selection, was due to the rapid fixation of a few genes with large effects on bristle score which were contributing to nearly all the genetic variability found in the +3 base population.

All the selection replicates relaxed for nine generations showed little or no tendency to regress to the unselected population means and thus indicated that the forces of natural selection opposing artificial

selection were not strong. It could also mean that the high frequencies of lethal chromosomes (over 30%) found in replicates, Or-RHII, Or-RHIII, Or-RLIII, +3LII and +3LIV were not maintained because of their heterozygote superiority for bristle number but instead could be selected because of linkage to genes controlling abdominal bristles (Mather, 1949; Frankham et al., 1968).

Another reason to suspect that the lethals were not associated with extreme bristle number was that there appeared to be little correlation between the frequency of lethals in a chromosome and the effects of the chromosome on the selected character. It is expected that if a lethal factor with appreciable effect on the selected character was selected in its heterozygous state, the chromosome in which this factor was located would have a large effect on the selected trait. But this expectation was not observed; for example, in the Or-RHIII, chromosome assays showed that chromosome II had about twice the effect of chromosome III on bristle score but had a lower frequency of lethals than the latter. Similarly, for +3LII where the second chromosome with appreciable effects on low bristle score had no lethals, whereas the third chromosome with smaller effects had high lethal frequency.

The chromosome assays on the whole gave consistent results. Particularly for selection in the high direction, there was marked similarity between replicates within the selection lines and also pronounced differences between the three high lines. In the Oregon-R high replicates, loci controlling high bristle number were located mainly in the second chromosome while in the +3 high replicates they were predominantly in the third chromosome. The Cross high replicates appeared to have the combined properties of both parental strains, with both second and third chromosomes having appreciable effects on bristle score.

The results from the lethal tests were less clear-cut and showed greater heterogeneity between replicates within the selection lines. This is well illustrated in the two +3 low replicates, where a balanced lethal system appeared to be prevalent in the second chromosome in one replicate and the third in the other replicate. This could mean that replicates within the same selection line were truly genetically divergent with regard to the incidence of recessive lethals because of factors like initial sampling errors, random drift and the effects of artificial selection acting on genetic differences. Or it could merely be due to sampling variation since only a small number of flies were tested from each replicate. The author admits that the weaknesses of the lethal tests are not only the smallness of the samples of each replicate which were tested but also that only two replicates of the four from each selection line were tested.

## VII. GENERAL DISCUSSION

## VII. GENERAL DISCUSSION

Since detailed discussions of results and observations have already been made at the end of each separate section of this thesis, the general discussion will be concerned mainly with tying together the results from the different sections.

Preliminary diallel crosses carried out on the two original laboratory strains, Oregon-R and +3, allowed the phenotypic variances in abdominal bristle number to be partitioned broadly into genetic and environmental components. A few differences in variances between the Oregon-R and +3 were noted: the slightly higher additive genetic variance in the +3; some evidence of additive sex-linked effects in the Oregon-R but not in the +3; an indication of the presence of some epistatic variation, mainly of the additive x additive type, in the +3 but not in the Oregon-R. It must be borne in mind that too much reliance should not be placed on these results because of large sampling errors. The components of variation of the two present base populations were also compared with those of the base populations utilised by Clayton et al. (1957), Sheldon (1963) and Sheridan et al. (1968). It was found that the Oregon-R and +3 base populations bore greater resemblance to each other than to any of these other base populations.

The primary aim of this thesis was to evaluate the variability of response of a quantitative character, abdominal bristles, among different base populations. To achieve this, identical selection was practised on the Oregon-R, +3 and the Cross, formed by crossing the two original populations, under uniform environmental conditions. The general expectations from such an experiment would be for greater but more



variable responses from the hybrid stock when compared with those from the two closed populations.

The average high selection responses in these three populations were significantly different, with the +3 giving virtually no response, the Oregon-R poor response and the Cross good response. Also, significant heterogeneity was detected among the high replicates of the Cross but not among those of the other two populations. Thus the high selection responses were in accordance to the above expectations.

Results from the chromosome assays of the selection replicates at the end of the selection programme gave evidence of genetic differences between the three high selection lines. It was found that gene loci controlling high abdominal bristle number were located mainly in chromosome II in the Oregon-R high line. On the other hand, such factors were found predominantly in the chromosome III in the +3 high line. Both the second and third chromosomes of the Cross had large effects on high bristle score. A simple interpretation of these results would be that the high bristle factors in chromosome II of the Oregon-R and chromosome III of the +3 were combined together in the Cross, resulting in greater genetic variability and consequently greater selection response than the two parental strains.

The heritability of about 0.35 estimated in the +3 base population proved to be completely inadequate in predicting the +3 high selection response. This meant that the simple additive selection theory based on the premise that the selected trait is controlled by a large number of additive genes with small effects would not apply to the +3 population for high bristle character. Instead, a different hypothesis was needed to cater for its aberrant behaviour. The hypothesis that high bristle character in the +3 population was controlled by a few additive genes

with large effects, which were subsequently fixed in the early generations of selection, thus causing cessation of response despite continued high selection, seemed to fit in well with the following observations :

- (a) Complete cessation of response in all four +3 high replicates after only three generations of selection
- (b) Consistent low phenotypic variances of the replicates throughout the selection experiment
- (c) Sharp decline in additive genetic variability at the end of selection despite the lack of response
- (d) Absence of directional dominance as indicated by the intermediacy of the hybrids of the +3 high and low selection lines
- (e) Low frequency of recessive second and third chromosome lethals.

An alternative hypothesis proposed by Clarke et al. (1961), of the genetic background of the stock acting as a "barrier" to inhibit the phenotypic expression of the loci controlling the selected character, could also cater for the +3 high responses. Evidence supporting this hypothesis was the large bristle effect of the third chromosome of the +3 high line when transferred to the genetic background of the vg se stock, and also the large upward response in the Cross, which as suggested earlier was made possible partly by the favourable loci from the +3 parental population. An assumption inherent in this hypothesis is that the genetic variance of the character is made up mainly of inter-allelic epistatic variance. Consequently if this hypothesis was correct, one would expect a large amount of epistatic variation to be present in the +3 population. In fact, the amount of epistatic variance found in both the +3 base population and +3 high selection line was relatively small, and thus it presents contradictory evidence to the applicability of this hypothesis.

The low responses from the three different foundation stocks were comparable in both size and general trend. All the three low selection lines gave fair response in the first seven generations or so and showed a definite decline in response rate in the latter seven generations. Unlike the high selection lines where both the largest response and the greatest variability of responses occurred in the Cross high line; for the low selection lines, the +3 gave the greatest low response and the Oregon-R, the largest divergences between replicates.

The similarity of responses from the three different low selection lines suggested that the two original populations, Oregon-R and +3 had comparable array of genes affecting low abdominal bristle number, so that crossing them did not result in any great increase in genetic variability and consequently no greater response from the hybrid base population. Evidence supporting this hypothesis comes from the results of the chromosome analysis of the low selection replicates where the factors affecting low bristle number were found to be located mainly in the second chromosome in all three low selection lines.

A comparable two-directional selection experiment for fecundity was conducted by Richardson and Kojima (1963) using two cage populations of D. pseudobscura and also the hybrid formed by crossing them. Their results differed from those of the present experiment in that their three high selection lines gave comparable responses while among the three low lines, the hybrid yielded greater responses than those of the two parental low lines.

Results from lethal tests conducted on two replicates from each selection line indicated that balanced lethal systems could be present on the second or third chromosome (or on both chromosomes) in the tested Oregon-R high and low replicates as well as in the +3 low replicates.

Evidence such as the small tendency of these replicates to regress in bristle score on relaxation of selection and also the absence of high phenotypic variances in these replicates, suggest that these lethals were not favoured because of their heterozygote superiority on bristle score. A more likely cause of the high lethal frequencies is linkage of these recessive lethals to genes controlling bristle score. In all three populations, the lower viability and higher frequency of second and third chromosome lethals observed in the low replicates than in the high replicates suggested that there was greater tendency for the recessive lethals to be linked to genes affecting low bristle number. Clayton et al. (1957) raised the question as to whether these lethals were originally present in the base populations and were subsequently selected for. If this was the case, it could mean that since the Oregon-R selection replicates had higher frequency of lethals than the +3 replicates, the Oregon-R base population had a greater load of recessive lethals than the +3 base population.

It was mainly because of the differential high selection responses from the three populations that different patterns of asymmetrical response were obtained. Extreme negative asymmetry was observed in the +3, mild negative asymmetry in the Oregon-R and positive asymmetry in the Cross. In relation to extrapolation of selection response of a quantitative character from one population to another, the results from this selection experiment showed that if other factors affecting selection responses were comparable, then extrapolation is reasonable for low selection responses but not for high responses. Different sizes and patterns of asymmetry have been reported by earlier workers using the same selection trait. Positive asymmetry was obtained by Mather and Harrison (1949), Clayton et al. (1957) and Latter and Robertson (1961). Negative asymmetry was

observed by Rasmuson (1955) and Sheldon (1963).

The abdominal bristle character has been classified as a neutral one (A. Robertson, 1955), with little direct effect on fitness, so that the forces of natural selection operating on it are not strong. Thus, the nature of genetic variance of the abdominal bristle character in an unselected population has been shaped mainly by its evolutionary history of chance mutation. This in turn could lead to the diversity of genetic systems governing this character in different base populations, thus resulting in different patterns of selection response, in terms of both the size and trends, from different unselected base populations.

## S U M M A R Y

## S U M M A R Y

This thesis is a study of short-term selection responses from three different base populations of Drosophila melanogaster subjected to identical and concurrent mass selection for increasing and decreasing abdominal bristles on the fourth and fifth sternites. The three populations utilised were two laboratory strains of diverse origins, Oregon-R and +3, and the hybrid formed by crossing them. The results may be summarised as follows :

(1) The +3 population mean exceeded the Oregon-R population mean by about two bristles. The hybrid base population designated as the "Cross" exhibited 5% heterosis and had greater phenotypic variance than those of the two parental strains.

(2) In order to investigate the nature of the two original base populations, Oregon-R and +3, a two sires and two dams diallel cross was carried on each of them. Heritability estimates obtained by parent-offspring regression analysis and from the diallel analysis were highly variable. The weighted average heritabilities of the Oregon-R and +3 were found to be  $0.32 \pm 0.11$  and  $0.37 \pm 0.11$  respectively. There was some indication of sex-linked effects in the Oregon-R base population and some evidence of epistatic variance in the +3 base population.

(3) Fourteen generations of two-directional selection were practised on the Oregon-R, +3 and  $F_3$  of the Cross. In each high and low selection line, there were four replications with nine pairs of parents in each and at 20% selection intensity. A mass-mated unselected control was maintained for each population.

(4) The +3 population exhibited an extreme negative asymmetrical response, the Oregon-R mild negative asymmetry and the Cross positive asymmetry.

(5) With the exception of the Cross high selection line, all other lines declined in rate of response, phenotypic variance and realised heritability.

(6) Significant heterogeneity of average response rate was detected between the four replicates of the Cross high selection line. The high responses from the three foundation stocks were highly variable; with the Cross high line giving excellent sustained response, the Oregon-R weak response and the +3 virtually no response. The trends of the three low selection lines were similar with fair response in the first seven generations and poor response in the later seven generations. Between the two original populations, Oregon-R and +3, the former gave greater upward responses while the latter greater downward responses, so that the divergences between the high and low selection lines of the two populations were remarkably similar.

(7) The trends of variability of response within selection lines were traced by evaluating the variance component between replicates within lines as well as the F-ratios for each generation. Genetic drift could account for the observed divergences between replicates within the Oregon-R and +3 high selection lines but not for the Cross high line. For the Oregon-R and the +3 low lines, genetic drift could be the main cause of variability in the first eight selection generations and thereafter the observed divergences by far exceeded the theoretical.

(8) The heritabilities estimated in the Oregon-R and +3 base populations exceeded the average realised heritabilities of the first selection



generation of both the high and low selection lines of their respective populations. The discrepancies between the estimated base population heritabilities and the average realised heritabilities over 14 generations were even more pronounced.

(9) Predicted responses from the first-generation realised heritabilities exceeded the observed average responses for all selection lines but the discrepancies were less than when base population heritability estimates were used. The first-generation responses proved to be a reasonable predictor of the average response of the first seven populations of the Oregon-R low line and the males of the +3 low line. In general, predictions of short-term selection responses either from the base population or the first-generation selection responses were inadequate.

(10) Various subsidiary tests consisting of relaxation of selection, testing for lethal second and third chromosomes and chromosome analysis, were conducted towards the end of the selection programme to determine the nature of the genetic situation responsible for the observed responses. There was evidence that the plateau which occurred very early in the +3 high selection replicates was due to the fixation of a few additive genes with large effects thus accounting for the low phenotypic and additive genetic variance, the slight regression in bristle score on relaxation, absence of directional dominance and low frequency of recessive lethals.

(11) Five of the 12 selection replicates tested were found to contain high frequencies of second and third chromosome recessive lethals. These lethals were not selected for extreme bristle effect as indicated by the small regression on relaxation of selection and also by the phenotypic

variances within these replicates which were lower than those of their respective unselected controls.

(12) From the chromosome assays it would appear that the two parental strains, Oregon-R and +3, apparently have different array of genes affecting high bristle number and these high bristle factors were located mainly in chromosome II in the Oregon-R high line and chromosome III in the +3 high line. In the Cross high line, high bristle genes were located in both chromosomes II and III. The low bristle factors on the other hand were located predominantly in the second chromosome in the three low lines.

(13) It would appear that crossing the two original strains had successfully combined the different genes favouring high bristles thus allowing greater genetic response in the Cross high line. The same did not occur for low bristles since the response from the Cross low line was comparable to those from the two parental lines.

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