# RESPONSE TO SELECTION IN SYNTHETIC LINES OF DROSOPHILA MELANOGASTER

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#### Abstract

Response to selection in synthetic lines has been examined by both theoretical and experimental analyses. Synthetic lines were founded from 20 base lines of D. *melanogaster* all derived from the same base population and which had been selected for high sternopleural bristle number. Two methods of synthesis were used: random choice of foundation parents and uniform within-line selection. Selection was then carried out in the synthetic lines, in the best of the 20 base lines, and in the previously unselected base population for 10 generations. The realized heritability in the synthetic lines was about three times that in the best line, and at least as high as that in the base population. By 10 generations the synthetic lines were clearly superior. The results were in broad agreement with theoretical predictions.

# I. INTRODUCTION

Response to selection within a population is based on the use of additive genetic variance. It is therefore natural to expect that a synthetic line formed by pooling several populations will respond to selection more rapidly than a single population. This will be especially the case with highly selected populations which are at or near a selection limit, since the additive genetic variance within such populations is likely to be small. It has been demonstrated, for example by Roberts (1967a), that crosses between plateaued lines may respond to selection, confirming such expectations. He achieved a net gain in body size of mice over the parent line which had reached the larger size at its selection limit. In further work, Roberts (1967b) outcrossed to unselected populations again achieving a clear gain over the original limit attained in the selected line. Robertson (1969), whose lines were used in our synthesis, made crosses with selected lines of Drosophila melanogaster. Further selection gave responses varying from nil in crosses between lines showing poor previous response to rapid where one or both parent lines had previously attained rapid response. Hosgood and Parsons (1967) have studied response to selection in synthetic lines of Drosophila, though the interpretation of their results is complicated by the fact that scutellar bristle number, for which they selected, is a canalized character.

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In practical breeding, it is not only the rate of selection response which is important. If a synthetic line responded rapidly, but began with a mean well below that of its best constituent lines, the delay in reaching that level may be such as to make use of the synthetic line undesirable. For example, in the work of Roberts (1967b) mentioned above, nine generations of selection were required to recover the original limit of the selected parent line. Jackson and James (1970) gave a theoretical analysis of this problem and derived a criterion on which such decisions could be based. In this paper we present a more complete theoretical analysis and the results of an experiment with *D. melanogaster* designed to check on aspects of the theory.

# **II. THEORETICAL ANALYSIS**

We shall suppose that there are N populations, each of size T, available, and that a total of S are to be chosen from among all NT individuals as founders of a selection line. It is assumed that S < T so that all founders may be obtained from one population if so desired. Three methods of founding the selection line will be considered:

- (1) Best line. The population having the highest mean phenotype for the trait of interest is chosen, and the best S individuals in this population are selected as founders.
- (2) Many-line random. In each population S/N individuals are chosen at random and pooled to form the foundation population.
- (3) Many-line selected. In each population the best S/N individuals are selected and pooled to form the foundation population.

In method (2) the mean breeding value of the foundation stock is expected to equal that of all available individuals. In method (1), response to selection both within and between populations will occur if the appropriate genetic variance is present, while response to within population selection is expected with method (3). James (1966) analysed the relative breeding values in this situation and found that mean breeding value of founders from method 1 would exceed that from method (3) if

$$r\phi/h > \log N/(1 \cdot 25 + \log N). \tag{1}$$

Here r is the correlation between population mean phenotype and population mean breeding value,  $h^2$  is the heritability within populations,  $\phi$  is the ratio of between-population genetic standard deviation to within-population genetic standard deviation, and logarithms are to base 10. Inequality (1) is an approximation, slightly favouring method (1).

Jackson and James (1970) derived rates of response in a synthetic line on the assumptions that linkage disequilibrium and selection would have negligible effects on genetic variance. The genetic variance in a synthetic population will now be derived without these restrictions, but retaining the assumption that genetic effects are entirely additive.

Let  $g_j$  denote a gametic value in the *j*th population and  $G_j$  a genotypic value, so that under random mating within populations  $G_j$  is the sum of two independent  $g_j$ values. Thus the genotypic mean  $\overline{G}_j$  is  $2\overline{g}_j$  where  $\overline{g}_j$  is the mean gametic value, while the within-population genotypic variance  $\sigma_{GW}^2$  is  $2\sigma_{gW}^2$ , where  $\sigma_{gW}^2$  is the withinpopulation gametic variance. Furthermore, if  $\sigma_{gW}^2$  and  $\sigma_{gB}^2$  are the betweenpopulation gametic and genotypic variances, then  $\sigma_{GB}^2$  is  $4\sigma_{gB}^2$ . Random mating in a synthetic line formed by pooling all populations is equivalent to random union of the gametes. The variance in the mixed population of gametes is

$$\sigma_{gM}^2=\sigma_{gW}^2+\sigma_{gB}^2,$$

so the genetic variance in the synthetic line is

$$\sigma_{GM}^2 = 2\sigma_{gM}^2 = \sigma_{GW}^2 + \frac{1}{2}\sigma_{GB}^2.$$
 (2)

This is the same as the result given by Jackson and James (1970), but it does not depend on whether or not there is linkage disequilibrium.

The genetic variance between populations is the sum of *n* variances of population mean breeding values and n(n-1) covariances between pairs of loci for all of the *n* loci controlling the trait. The genetic variance in the first generation of the synthetic line does not depend on how  $\sigma_{GW}^2$  is partitioned into these components. However, reassortment under random mating in later generations would reduce any covariance components to zero by establishing linkage equilibrium.

The effect of truncation selection for a normally distributed trait on its mean and variance and those of a correlated trait are well known (e.g. Tallis 1961). If pis the upper tail area removed by truncation at a point x standard deviations above the mean and z is the ordinate at that point, then the mean of the selected fraction is i = z/p while the variance is 1-i(i-x) if the trait is measured in standard units. If a second trait, also measured in standard units, has a correlation  $\rho$  with the selected trait, then its mean in the selected fraction is  $\rho i$  and its variance is  $1-i(i-x)\rho^2$ . The correlation between a gametic value and a phenotypic value is  $h/\sqrt{2}$  so the variance of gametic values after selection is  $1-\frac{1}{2}i(i-x)h^2$  times its value in the unselected population. Genetic variance in the progeny of selected individuals is the variance of the sum of two random gametes, and is thus  $1-\frac{1}{2}i(i-x)h^2$  times that in the unselected parental generation. This result was found by Reeve (1953) using path coefficients.

A normal distribution of gametic values implies a number of loci approaching infinity, with gene effects infinitesimally small. Selection thus produces negligible changes in gene frequency, and the reduction in variance is due to linkage disequilibrium induced by selection. In subsequent generations recombination will reduce the existing linkage disequilibriuum, but selection will provide a new increment, until an equilibrium in reached.

If the gametic variance is  $1-\lambda$  times its value at linkage equilibrium the phenotypic variance is  $1-\lambda h^2$  times its value at linkage equilibrium, so the heritability is  $h^2[(1-\lambda)/(1-h^2)]$ . Then it follows from above that selection will change gametic variance by  $-i(i-x)\frac{1}{4}h^4(1-\lambda)^2/(1-\lambda h^2)$  while recombination will change gametic variance by  $c\lambda \frac{1}{2}h^2$ , where c is a suitable average recombination fraction. Equilibrium occurs when these components sum to zero, when we have

$$\hat{\lambda} = [c + \theta h^2 - (c^2 + 2ch^2(1 - h^2)\theta)^{\frac{1}{2}}/(\theta h^2 + 2ch^2)],$$
(3)

where  $\theta = i(i-x)$ . This result was derived using a different approach by Bulmer (1971). If c = 0 (no recombination),  $\hat{\lambda} = 1$  and genetic variance falls to zero. Except

when there are small numbers of chromosomes, a value of  $c = \frac{1}{2}$  will be fairly accurate (Griffing 1960). If  $h^2/c$  is small, it follows from (3) that

$$\lambda \simeq \frac{1}{2}c i(i-x)h^2$$
,

or when  $c \simeq \frac{1}{2}$ ,  $\hat{\lambda}$  is approximately  $i(i-x)h^2$  or twice the value of  $\lambda$  in the first generation. Further analysis of (3) shows that if  $\theta < 1$ , which is true for all selection intensities,  $\hat{\lambda} < i(i-x)h^2$  when  $c = \frac{1}{2}$ . Thus selection will have its major effect on genetic variance in the first generation, and little error would be involved in ignoring subsequent effects of selection on the variance. This conclusion will clearly not hold for long-term selection where the effects of accumulated gene frequency changes can no longer be neglected.

The implication is therefore that a synthetic line formed by method (3) would have a genetic variance less than that of a synthetic line formed by method (2) by about  $\frac{1}{2}h^2i(i-x)\sigma_{GW}^2$ .

The overall analysis thus leads to the conclusion that if high initial mean breeding value is the aim, method (2) is worst, while if high genetic variance is the aim, method (2) is best, though only slightly better than method (3) in most instances.

### III. MATERIALS AND METHODS

A large number of lines of *D. melanogaster* derived from the Canberra strain and selected for 35 generations for increased sternopleural bristle number on the left side were available from an experiment by Robertson (1969). After Robertson's work the lines were maintained for some 10 generations with about 40 pairs of parents each. Lines which had shown sudden rapid responses to selection in later generations were discarded and 20 of the remaining lines chosen at random. Egg samples were taken from these stocks and cultured in bottles, one per line to establish the 20 lines for the experiment. Mating in all generations was in two replicates, each of two bottles of 10 pairs per line. Flies were cultured on a standard semolina-treacle-yeast medium and kept in a room with constant temperature ( $25^{\circ}$ C) and humidity ( $65^{\circ}$ ). Foundation lines were formed in the following way:

Many lines selected (MS).—The four flies of each sex with highest left sternopleural bristle number from a random sample of 40 flies of each sex were selected from each line. Two lines, each of two replicates with two bottles per line and with 10 pairs per bottle, were formed by random allocation of the selected flies. The progeny of these pooled selected flies are designated generation 0.

Many lines random (MR).—These were formed in the same manner as MS except that four flies of each sex were chosen at random from each of the 20 lines.

*Best line* (BL).—When scoring in the base lines was carried out the line with the highest mean, averaged over sexes, was identified. A new sample of 80 pairs was taken from it and treated as in MR and MS.

*Base population* (BP).—From the Canberra base population a random sample of 80 pairs was taken and treated as in BL.

Two replicate lines of each foundation group were selected for high left sternopleural bristle number for 10 generations. Twenty flies were selected from 40, drawn from both bottles of the replicate, of each sex. Selected flies were allotted at random to the two bottles. The selected lines were designated MSS, MRS, BLS, and BPS, with 1 or 2 denoting the replicate.

The remaining replicate lines were maintained by choosing two sets of 10 pairs at random in each replicate and mating as above. These were designated MSR, MRR, BLR, and BPR, with 1 or 2 denoting the replicate. These random control lines were discontinued after five generations, except for the BPR replicates which were continued for the 10 generations. After the first generation of random mating these lines were used to provide single-pair matings for heritability estimates. One hundred males and virgin females were scored and mated at random in single-pair vials for each line. Five progeny of each sex were scored from each fertile mating.

# **IV. RESULTS**

# (a) Base and Foundation Lines

The means and standard deviations of bristle numbers in the base lines and the theoretical and actual selection differentials obtained in forming MS are shown in Table 1. Line FL15 had the highest mean and was used to form BL. The means of these 20 lines measured following our sampling had changed little from those measured five generations after selection was discontinued. The actual selection differentials were on average 92% of those expected.

Line	Mean	Standard deviation	Theoretical selection differential	Actual selection differential
S13	12.01	1.235	2.088	1.818
S15	9.28	1.019	1.722	1.213
<b>S</b> 16	11.18	1.128	1.906	1.330
F14	11.33	0·999	1.688	1.670
F41	11.99	1.173	1.982	1.893
F42	14.25	1 · <b>2</b> 40	2.095	2.125
F44	13.14	1.193	2.016	1.738
T12	11.80	1.098	1.856	1.625
T13	12.44	1.162	1.963	1·9 <b>3</b> 7
T41	13.40	1 · 294	2.187	2.300
SL11	11.23	1.052	1.778	1.525
SL12	10.83	1.165	1.968	1.913
SL17	12.46	1.073	1.813	1.895
<b>SL46</b>	12.46	1.206	2.038	1.785
FL12	12.86	1.075	1.817	1.913
FL14	11.63	1.116	1.886	1.880
FL15	14.43	1.335	2.256	2.200
FL41	12.10	1.329	2.246	2.025
TL14	12.63	0.980	1.656	1 · 500
TL41	12.76	1.187	2.007	1.737
Mean	12.21	1.153	1 · 949	1 · 801

TABLE 1

MEANS, STANDARD DEVIATIONS, AND SELECTION DIFFERENTIAL FOR STERNOPLEURAL BRISTLE NUMBER ON THE LEFT SIDE IN THE BASE LINES

The means of the foundation parents and their generation 0 progeny, pooled over replicates, are given in Table 2, as are the generation 0 variances. The MS parents averaged 1.76 more bristles than MR parents, while their progeny differed by 0.19 bristles, giving an ostensible within line heritability of 0.11. The BL lines had appreciably higher means. In view of the wide range of base line means, this is as expected.

### (b) Heritability Estimates

The generation 0 phenotypic variances were very similar for MS, MR, and BL, all being about twice that of BP. The high variance of BL could be attributed to a scale effect, but heritability estimates are necessary to discover whether there are increased genetic variance components in MS and MR.

				. 1	ABLE 2					
MEAN	STERNOPLEURAL	BRISTLE	NUMBERS	OF	FOUNDATION	PARENTS	AND	THEIR	PROGENY,	AND
			VARIAN	CES	AMONG PROG	ENY				

Lines	Parental means	Progeny means	Progeny variances	Lines	Parental means	Progeny means	Progeny variances
MSS MSR	14.06 14.04	12.48 12.18 12.16	$2 \cdot 25$ $2 \cdot 09$ $2 \cdot 24$	BLS BLR BDS	$14 \cdot 33$ $14 \cdot 42$ 0.51	13.93 14.06	$2 \cdot 34$ $2 \cdot 34$ $1 \cdot 15$
MRS MRR	$12 \cdot 35$ $12 \cdot 23$	$12 \cdot 16$ $12 \cdot 12$	$2 \cdot 34$ $2 \cdot 58$	BPS BPR	9·51 9·53	9·43 9·27	1.13

Heritabilities were estimated by full-sib correlations and regression of offspring on mid-parent values. The results are shown in Table 3. Because of dominance and common environmental variance the full-sib correlation estimates are expected to exceed the regression estimates. Whatever the cause, this is certainly the case in MR. The regression estimates are also high, but follow the pattern expected on theoretical grounds.

# TABLE 3 HERITABILITY ESTIMATES FROM COVARIANCES BETWEEN RELATIVES IN THE RANDOM CONTROL LINES

Method*	Males	Females	Pooled			
Sibs O-MP	$\begin{array}{c} 0\cdot 341 \pm 0\cdot 089 \\ 0\cdot 311 \pm 0\cdot 075 \end{array}$	$0.496 \pm 0.096 \\ 0.644 \pm 0.102$	$0{\cdot}418{\pm}0{\cdot}066 \\ 0{\cdot}477{\pm}0{\cdot}063$			
Side O-MP	$\begin{array}{c}1\!\cdot\!245\!\pm\!0\!\cdot\!137\\0\!\cdot\!872\!\pm\!0\!\cdot\!053\end{array}$	$\begin{array}{c}1\!\cdot\!282\!\pm\!0\!\cdot\!082\\0\!\cdot\!834\!\pm\!0\!\cdot\!070\end{array}$	$\begin{array}{c} 1 \cdot 263 \pm 0 \cdot 080 \\ 0 \cdot 853 \pm 0 \cdot 043 \end{array}$			
Sibs O-MP	$\begin{array}{c} 0\!\cdot\!200\!\pm\!0\!\cdot\!093\\ 0\!\cdot\!088\!\pm\!0\!\cdot\!142\end{array}$	$0.216 \pm 0.106 \\ 0.374 \pm 0.154$	$\begin{array}{c} 0\!\cdot\!208\!\pm\!0\!\cdot\!071 \\ 0\!\cdot\!231\!\pm\!0\!\cdot\!105 \end{array}$			
Sibs O-MP	$\begin{array}{c} 0\!\cdot\!429\!\pm\!0\!\cdot\!095 \\ 0\!\cdot\!309\!\pm\!0\!\cdot\!126 \end{array}$	$\begin{array}{c} 0\!\cdot\!093\!\pm\!0\!\cdot\!073\\ 0\!\cdot\!233\!\pm\!0\!\cdot\!096\end{array}$	$\begin{array}{c} 0\!\cdot\!261\!\pm\!0\!\cdot\!060\\ 0\!\cdot\!271\!\pm\!0\!\cdot\!079\end{array}$			
	Method* Sibs O-MP Side O-MP Sibs O-MP Sibs O-MP	Method*         Males           Sibs $0.341 \pm 0.089$ O-MP $0.311 \pm 0.075$ Side $1.245 \pm 0.137$ O-MP $0.872 \pm 0.053$ Sibs $0.200 \pm 0.093$ O-MP $0.088 \pm 0.142$ Sibs $0.429 \pm 0.095$ O-MP $0.309 \pm 0.126$	Method*         Males         Females           Sibs $0.341 \pm 0.089$ $0.496 \pm 0.096$ O-MP $0.311 \pm 0.075$ $0.644 \pm 0.102$ Side $1.245 \pm 0.137$ $1.282 \pm 0.082$ O-MP $0.872 \pm 0.053$ $0.834 \pm 0.070$ Sibs $0.200 \pm 0.093$ $0.216 \pm 0.106$ O-MP $0.088 \pm 0.142$ $0.374 \pm 0.154$ Sibs $0.429 \pm 0.095$ $0.093 \pm 0.073$ O-MP $0.309 \pm 0.126$ $0.233 \pm 0.096$			

\* O, offspring; MP, mid-parent.

### (c) Response to Further Selection

Line means (averaged over sexes and replicates) are plotted over the 10 generations of selection in Figure 1. F refers to the foundation parents, while generation 0 was that on which selection was first practised. The unselected lines showed negligible changes over generations, so changes in selection line means are primarily genetic. The greater rate of response in MRS and MSS allowed them to surpass BLS in generations 5 and 7 respectively. The rates of response are in the same order as the heritability estimates given in Table 3.



Figures 2(a)-2(d) show the replicate means and standard deviations for each foundation method over the 10 generations of selection. There was some evidence of a scale effect, since standard deviations tended to rise in S lines as the means increased. Standard deviations showed no consistent changes in the unselected R lines.

Realized heritabilities were calculated in three ways. The first was by regression of line mean on cumulative selection differential. This method has the disadvantage that the standard error of the regression coefficient is an inappropriate measure of error (Hill 1970). The other estimates were both obtained as the ratio of an estimate of total response to the cumulative selection differential giving that response. In one case response was estimated as the difference  $R_{10}$  between means of a line in generations 0 and 10. In the other case response was estimated as the difference  $R_5$ between selected and control line means in generation 5. Line means plotted against cumulative selection differential are shown in Figure 3. Standard errors of these estimates were derived by an argument similar to that of Hill (1971) (see Appendix). Estimates of realized heritabilities for the three methods are shown in Table 4. Heritabilities for the different foundation methods show the predicted ranking, though they are lower than the estimates derived from covariances between relatives.

### V. DISCUSSION

An analysis of variance of the data on which Table 1 is based gave the between line variance component as 1.4105 while the average of the within line variances is 1.3395. The expected variance in a synthetic line would then be  $1.3395 + \frac{1}{2}(1.4105) =$ 2.0448. In fact the average variance of the MR lines was 2.46. The theory for MS lines predicts an expected loss, compared with MR, of  $\frac{1}{2}i(i-x)h^4$  of the within-line variance. Since i(i-x) = 0.84 and  $h^2 = 0.11$  the expected variance in MS is 2.0380, negligibly different from that of MR. The observed value was 2.17. However, little weight can be placed on these differences since the variance of FL15 was 1.78 but in generation 0 as line BL it had a variance of 2.34. Variances are notoriously difficult to estimate accurately, and we must here conclude that the results are not very informative.



Fig. 2.—(a)–(d)Replicate mean bristle number and standard deviation (pooled over sexes) for selection lines over all generations of selection. (a) MSR and MSS lines. (b) MRR and MRS lines. (c) BLR and BLS lines. (d) BPR and BPS lines. F =foundation.

The random-mated lines of all foundation methods showed no great change in mean or standard deviation over the five generations for which they were maintained. The constancy of mean in MSR and MRR suggests that recombination did not break down epistatic gene complexes. The relative stability of the standard deviation likewise suggests that linkage disequilibrium was not a major factor in the variation between lines. A zero average covariance between breeding values at different loci is expected if the lines involved have become differentiated by genetic drift. In populations selected under different regimes a positive contribution to the covariance is



Fig. 3.—Mean bristle number (pooled over sexes and replicates) of all selected foundation lines plotted against cumulative selection differential.

expected, while in lines selected under the same conditions from the same base population a negative covariance is expected, as shown by Latter (1965). The lines used in this experiment were derived from different small (1, 5, or 20 pairs) samples from the Canberra strain and selected at the same intensity for the same trait. Some

REALIZED HERITABILITY ESTIMATES IN THE EXPERIMENTAL LINES							
Lines	Methods						
	10 generation gain	5 generation deviation	Regression				
MSS	$0.28\pm0.026$	$0.29\pm0.064$	$0.29\pm0.011$				
MRS	$0.47 \pm 0.031$	$0.47 \pm 0.081$	$0.46\pm0.019$				
BLS	$0.13 \pm 0.019$	$0.08 \pm 0.040$	$0.12 {\pm} 0.014$				
BPS	$0\cdot 30\pm 0\cdot 28$	$0\cdot 31\pm 0\cdot 068$	$0\!\cdot\!31\!\pm\!0\!\cdot\!029$				

 TABLE 4

 REALIZED HERITABILITY ESTIMATES IN THE EXPERIMENTAL LINES

lines had 5 and others 20 pairs of parents per generation. The similarity of selection would tend to generate a negative covariance while the difference in number of selected parents would tend to generate a positive covariance. These tendencies would appear to have cancelled out or been of such small magnitude relative to the effects of random drift as to have a negligible influence.

Although it was concluded above that the predicted variances were of little value for comparison with observed values, it is nevertheless worthwhile to consider the theoretical expectation of heritability in the synthetic lines. Using the previous values, the genetic variance is  $0.11(1.3395) + \frac{1}{2}(1.4105 = 0.8522)$  and a heritability of 0.8525/2.0448 = 0.4169 for MR. This is much lower than the estimate from covariances, but in good agreement with the realized heritability. The value in MS should differ negligibly, and on averaging realized heritabilities over MSS and MRS we obtain 0.375, quite close to the predicted value.

The realized heritability of about 0.3 in BPS is higher than expected from previous work. Robertson (1969) obtained a realized heritability over 10 generations of 0.16, which agreed well with his estimate of 0.16 from covariances between relatives. The extensive work of Sheridan *et al.* (1968) indicated a heritability of about 0.19, while Latter (1964) obtained an estimate of 0.26, much closer to the present value.

It is very difficult to see any reason why the response should differ appreciably in MSS and MRS. The expected reduction in genetic variance in MSS is too small to have any noticeable effect. The most likely explanation appears to be that the initial MR and MS samples for some reason differed from each other, though what random variation may have occurred is impossible to say.

The experimental results confirm the theoretical conclusion that in practical breeding the optimum method of choosing foundation stock depends on the time during which selection is to be considered. In our case, if a period of one or two generations were considered then the BL method would be favoured, while over 10 generations MR or MS would be superior. Over a period of five generations little difference between the methods occurs. These particular conclusions are of course relevant only to our experimental situation, but the principle applies in general.

We have considered only the extreme case of the founders coming equally from all lines, or entirely from one line. In general, a variable number could be taken from different populations. In a given situation the optimum procedure might well be to select foundation stock from the best few lines, thus making use of some of the initial advantage obtainable from selection between lines, while retaining some part of the increased variance within the synthetic line. Further work along these lines may well be useful.

# **VI.** ACKNOWLEDGMENTS

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### Appendix

Estimation of Standard Errors for Ratio Estimates of Realized Heritabilities

It was shown by Hill (1971, equation 4) that the variance of the difference between the original mean and the mean after t generations of selection is

$$V(R_t) = (\sigma^2/N) \{ th^2 [1 - h^2(1 - p)] + p(2 - \frac{1}{2}h^2) - \frac{1}{2}ph^4 \}.$$

The detailed assumptions are given by Hill, but it may be said that common environmental effects are not allowed for in the formula, and it is assumed that genetic variance has not altered appreciably during selection.

Under these same conditions Hill shows that the mean after t generations of selection has a sampling variance

$$V(\overline{X}_t) = (\sigma^2/N)\{th^2[1-h^2(1-p)]+p(1-\frac{1}{2}h^4)\}.$$

By the same argument the mean of a control line after t generations has a sampling variance

$$V(\overline{X}_t) = (\sigma^2/N)(th^2 + p).$$

Thus if  $R_t$  is measured as the difference between the means of selected and control lines

$$V(R_t) = (\sigma^2/N) \{ th^2 [2 - h^2(1 - p)] + p(2 - \frac{1}{2}h^4) \}.$$

Since  $h^2$  is estimated as  $R_t/S_t$  its variance may be estimated as  $V(R_t)/S^2_t$ . In applying these formulae N has been taken as the actual number of parents. Since the effective number is almost certainly smaller, the standard errors will tend to be underestimated.