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Selection for a threshold character in *Drosophila*

I. AN ANALYSIS OF THE PHENOTYPIC VARIANCE ON THE UNDERLYING SCALE

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1. INTRODUCTION

In this series of papers, it is proposed to describe a number of aspects of the behaviour of a wild-type population of *Drosophila melanogaster* under artificial selection. The character for which selection has been practised, viz. the number of macrochaetae on the scutellum, is almost invariant in wild-type populations, and the arrangement and orientation of the bristles are both precisely defined. There is normally present an anterior and a posterior pair of bilaterally symmetrical bristles in each sex, but it is not uncommon to find individuals with supernumerary macrochaetae: much more rarely one may find individuals with less than the normal complement (Sismanidis, 1942; Rendel & Sheldon, 1960).

Payne (1918) and Sismanidis (1942) have shown that under selective breeding, the incidence of extra-bristle individuals in a population can readily be increased, and the expression of the character greatly enhanced. The trait is particularly convenient for quantitative genetic studies in that it may very rapidly be scored, and it is in addition strongly influenced by natural selection (Latter, 1963). However, the incidence of abnormal phenotypes in most wild-type populations is of the order of 2% or less, and the effects of selection in the absence of deliberate inbreeding have not therefore been previously documented.

In this paper, the short-term response to selection for increased scutellar bristle number is to be described in terms of a bivariate threshold model, which enables the underlying variation to be analysed into its principal components. Comparisons are then to be made with analyses of the variation displayed in the same population by two related characters, viz. abdominal and sternopleural hair number.

2. THE ALTERNATIVE THRESHOLD MODELS

We shall adopt the conventional statistical model which postulates the existence of a continuous underlying variable influenced both by genetic and environmental factors, with threshold values corresponding to the occurrence of particular grades of expression of the character (Fisher, 1930). The metric can be chosen initially to give a normal distribution of frequency of the underlying variable about its mean, though there can be no assurance that the variable will be normally distributed in other regions of the scale so defined.

Two alternative models of this sort will be employed in the present study. The simpler one, the *univariate model*, takes as the observed phenotype the total number of bristles on the scutellum, and assumes a 1 : 1 correspondence between the bristle-number classes and precisely defined intervals of the underlying scale (Rendel, 1959): the model does not attempt to specify in any way the locations of supernumerary bristles. The *bivariate model* takes as the observed phenotype the number of bristles on the left side of the scutellum (L), and the number on the right side (R), as separate observations. A single underlying scale of measurement is taken to be appropriate to both variables, but a developing individual is supposed to have two distinct phenotypic values, p_l amd p_r, and the observed phenotype is determined by the relationship of each of these values to the threshold levels on the underlying scale.

It is easy to see that expectations based on the univariate and bivatiate models do not exactly correspond. Consider a phenotypic value which falls just short of the 4/5 threshold value on the scale postulated by the univariate model, leading to a 4-bristle phenotype: the corresponding values of p_l and p_r may differ sufficiently in a particular individual for p_l to fall short of the 2/3 threshold postulated by the bivariate model, while p_r falls beyond the threshold, leading to a (2:3) phenotype. In fact, it is only when p_l and p_r are perfectly correlated in the population that the two models are equivalent.

3. THE INITIAL RESPONSE TO SELECTION FOR INCREASED SCUTELLAR BRISTLE NUMBER

The stock of *D. melanogaster* which has been used in this study was derived from a collection made in Canberra, Australia, during the late summer of 1959. The foundation population was based on well over 100 pairs of breeding individuals, and the stock has been maintained at 25° C. with approximately 500 pairs of parents per generation, with periodic exchange of individuals between replicate culture bottles. The stock cultures were always crowded, but bristle counts have been taken on flies raised under uncrowded conditions at 25° C.

Three selection lines, Sc 1, Sc 2, and Sc 3, were commenced after the base population had been in the laboratory for 7, 63 and 66 generations respectively. In Sc 1, 100 females taken from a single bottle culture were scored in each of the first five generations, only those with supernumerary bristles on the scutellum being retained for breeding: artificial selection was not practised among males during this period. The numbers of breeding individuals exceeded fourteen pairs in each generation, so that inbreeding was kept to a minimum. In subsequent generations both males and females were scored, selection of breeding individuals being determined solely on the basis of total bristle count. Over a period of ten cycles of selection, the harmonic mean of the number of selected individuals per generation was 19·4 pairs, and the selection differential calculated on the basis of the univariate model ($\sum \bar{i}_u$) was 10·42.

The behaviour of this line has been described in very general terms elsewhere (Latter, 1963). Since the decline in reproductive fitness over the ten-generation interval was very marked, the procedure of selection in Sc 2 was designed to provide

information on the fertility and productivity of individual pairs of flies. In each generation, 500 virgin females were scored, ten from each of fifty tubes, and the fifty with highest score retained for breeding. A single male was also retained from each tube, and the chosen males and females mated in pairs at random. Although the proportion of females selected was almost constant throughout, the selection differential varied according to the distribution of scores over the discrete bristle-number classes (Table 1).

The selection régime in Sc 3 was very similar to that in Sc 1. Selection was practised only among females during the first seven cycles, and thereafter both sexes were scored each generation. Over a period of ten generations, the harmonic mean of the number of selected individuals per generation was 22·3 pairs, and the accumulated selection differential was 9·18, based on the univariate model. Both Sc 1 and Sc 3 have been maintained throughout as single-bottle cultures, parents being removed in time to ensure the development of their offspring under uncrowded conditions.

The response to selection, measured in terms of mean bristle number, has been found to be continuous but markedly curvilinear, the distribution of bristle scores changing in a regular fashion to give a symmetrical and essentially normal distribution of frequency at a mean of six bristles (Table 1). It is important to stress that

Table 1. *Distribution of bristle scores in females of line Sc 2*

Generation	$\sum i_u$*	$\sum i_b$*	Bristle-number distribution (%) 4	5	6	7	8	9	Mean
1	0·22	0·24	93·1	6·5	0·4				4·07
2	0·85	0·93	94·8	4·9	0·3				4·05
3	1·57	1·72	83·1	15·1	1·8				4·19
4	2·35	2·57	83·9	14·3	1·7				4·18
5	3·12	3·42	71·2	24·2	4·4	0·2			4·34
6	3·87	4·24	72·6	21·3	5·4	0·4	0·2		4·34
7	4·64	5·12	61·2	25·1	12·0	1·6	0·2		4·55
8	5·45	6·12	43·4	31·2	21·9	2·4	0·9	0·2	4·87
9	6·18	6·95	37·1	34·8	23·9	4·2			4·95
10	6·89	7·77	33·5	30·1	29·5	5·8	1·1		5·11
11	7·64	8·66	14·4	28·8	35·8	16·9	3·9	0·2	5·68
12	8·41	9·57	9·9	28·5	36·4	20·9	4·0	0·2	5·81
13	9·15	10·47	8·4	20·0	36·2	25·2	9·3	0·9	6·09

* Accumulated selection differentials appropriate to the univariate (u) and bivariate (b) models, respectively.

the change in mean bristle count in these early generations is due primarily to an increase in the number of bristles close to the two *anterior* scutellar loci. A 6-bristle fly normally has two pairs of anterior scutellars and one pair of posteriors, and an 8-bristle fly most commonly shows three pairs of anterior bristles. However, asym-

metrical individuals with three bristles near one anterior locus and one bristle at the other, are not uncommon. Bristles in a position intermediate between the anterior and posterior loci occurred in approximately 8% of females in Sc 2 towards the end of the thirteen-generation period, and fine apical bristles between the posterior pair of loci occurred in about 4% of individuals.

(i) *Realized heritability based on the univariate model*

The curve of response on the bristle-number scale can readily be transformed to give a plot of progress on the underlying probit scale, assuming the univariate model to be appropriate. In each generation, the mean of the population relative to the position of the 4/5 threshold, can be estimated from a table of probit values as a direct function of the observed proportion of individuals showing extra bristles. A regression line can then be fitted by a method which weights each mean according to its error of estimation, allowing for heterogeneity between means due either to genetic sampling or to environmental differences among generations (Finney, 1947). The resulting plot for Sc 2 is shown in Fig. 1.

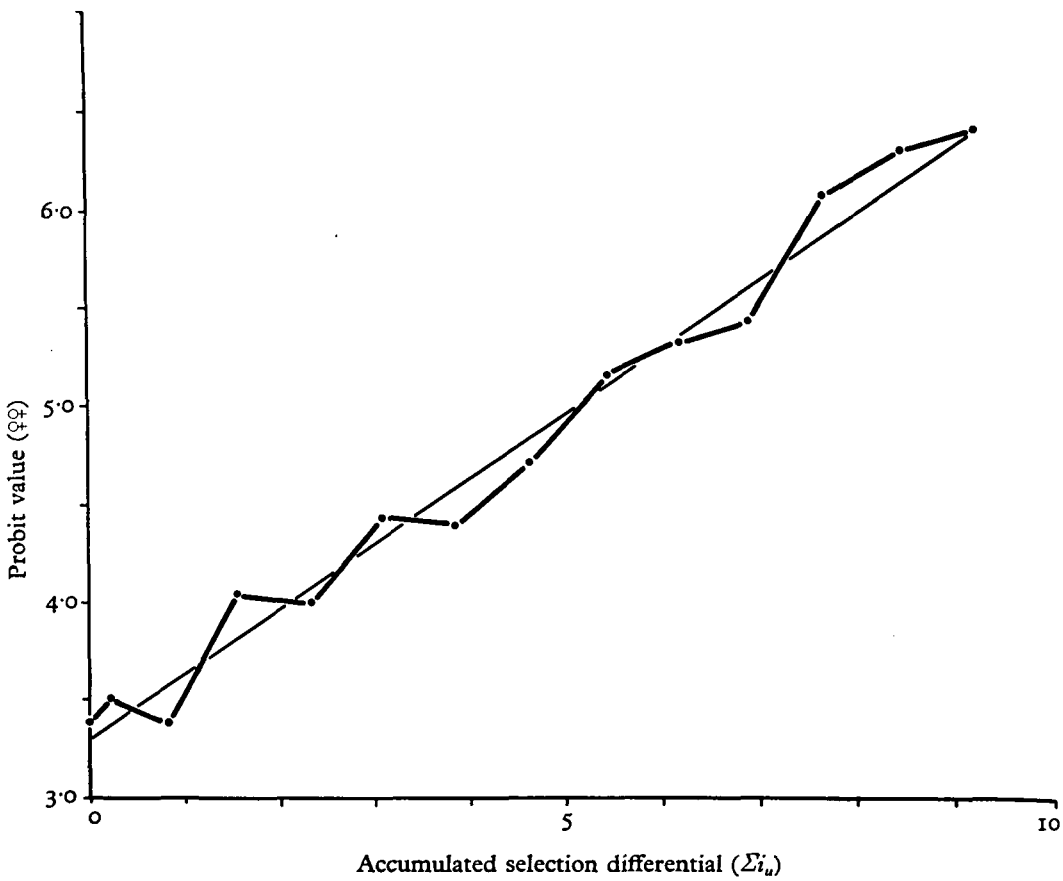

Fig. 1. The response to selection for extra scutellar bristles in Sc 2, measured on the underlying scale.

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In Table 2 are given parameters which summarize the response to selection in each of the three lines, up to the point at which almost all individuals exceeded the 4/5 threshold. This point corresponds to values of $\sum i_u$ of 7·61, 9·15 and 9·18 in Sc 1, Sc 2 and Sc 3. None of the selected lines showed a significant departure from linearity of response, and since genetic advance has been expressed here in phenotypic standard deviations, the heritability of the character on the underlying scale must therefore have remained constant over this initial period of response.

Table 2. *Parameters of regression lines measuring response on the univariate scale in phenotypic standard deviations, as a function of the accumulated selection differential*

Selection line	Males		Females	
	Intercept	Slope	Intercept	Slope
Sc 1	$-2{\cdot}07 \pm 0{\cdot}23$	$0{\cdot}399 \pm 0{\cdot}040$	$-1{\cdot}19 \pm 0{\cdot}07$	$0{\cdot}360 \pm 0{\cdot}020$
Sc 2	—	—	$-1{\cdot}70 \pm 0{\cdot}08$	$0{\cdot}335 \pm 0{\cdot}015$
Sc 3	$-2{\cdot}23 \pm 0{\cdot}16$	$0{\cdot}302 \pm 0{\cdot}021$	$-1{\cdot}61 \pm 0{\cdot}14$	$0{\cdot}296 \pm 0{\cdot}025$
Means		$0{\cdot}322 \pm 0{\cdot}018$		$0{\cdot}335 \pm 0{\cdot}011$

The intercepts given in Table 2 provide indirect estimates of the position of the base population mean relative to that of the 4/5 threshold, at the time of initiation of the line concerned. The mean of females in the base population can be estimated from the table to be $0{\cdot}71 \pm 0{\cdot}15$ phenotypic standard deviations greater than that in males, averaging over the three lines. It can also be estimated that the base population mean, averaged over the two sexes, changed by $-0{\cdot}45 \pm 0{\cdot}09$ standard deviations over a period of roughly fifty-eight generations in the laboratory.

(ii) *The measure of developmental error*

It has previously been emphasized that expectations based on the univariate and bivariate models will correspond only if p_l and p_r, the phenotypic values on the underlying scale of the bivariate model, are perfectly correlated. Since flies with five scutellar bristles are very frequent in populations produced by artificial selection, and 6-bristle flies showing bilateral asymmetry are not uncommon, it is obvious that the variables p_l and p_r must be to some extent independent. If it can be assumed that the *genetic* correlation between them is unity, then their *phenotypic* correlation, ρ, measures the proportion of the total variation of each variable which is due to genetic segregation and to common environmental effects. The residual, $1-\rho$, can then be defined as a measure of 'developmental error' in the expression of the character on the underlying scale.

An accurate estimate of ρ is essential if the bivariate model is to be used in the interpretation of observed responses to selection. By reference to tables of volumes of the bivariate normal distribution (Pearson, 1931), it is possible to estimate ρ from observations of the proportions of individuals in a population with phenotypes L = 2, R = 2; L > 2, R = 2; L = 2, R > 2; and L > 2, R > 2. A total of thirty-one

such estimates have been obtained from observations of the early generations of the three selection lines, the unweighted means of the estimates being $0{\cdot}354 \pm 0{\cdot}054$ for males and $0{\cdot}366 \pm 0{\cdot}028$ for females. The standard errors are only approximate, having been calculated from the observed variance among the individual estimates. The weighted mean over the two sexes is $\hat{\rho} = 0{\cdot}362 \pm 0{\cdot}026$.

(iii) *Realized heritability based on the bivariate model*

On the assumption that the variables p_l and p_r are normally distributed with correlation ρ and identical means and variances, there is no difficulty in estimating the probability that p_r will exceed the 2/3 threshold in any given population, and hence the position of the population mean relative to the threshold value. However, the determination in each generation of the effective selection differential, $\bar{\imath}_b$, imposed on the variable p_r, given that selection has been based on total bristle score, L + R, is more involved.

If the values of p_l and p_r had been directly observed, and if selection had been based on the index $I = p_l + p_r$, the change in the mean value of p_r under selection is expected to be

$$\Delta G = \bar{\imath} r_{ia} \sigma_a$$

where $\bar{\imath}$ denotes the selection differential in standard units imposed on the index I, r_{ia} is the correlation between the value of the index and the breeding value of the individual in respect of the variable p_r, and σ_a is the standard deviation of the distribution of breeding values in the population. The correlation r_{ia} can be shown to be equal to $[2h^2/(1+\rho)]^{1/2}$ where h^2 is the heritability of the variable p_r, so that the response to selection can be expressed as

$$\Delta G = \bar{\imath}[2/(1+\rho)]^{1/2} h \sigma_a.$$

The effective selection differential imposed on p_r, expressed in standard units, is therefore $\bar{\imath}[2/(1+\rho)]^{1/2}$.

The value of $\bar{\imath}$ is defined to be $[E(p_l + p_r)][2\sigma_p{}^2(1+\rho)]^{-1/2}$ where $E(p_l + p_r)$ denotes the expected value of $p_l + p_r$ in the selected group of breeding individuals, and $\sigma_p{}^2$ is the phenotypic variance of p_r. In any population, the mean value of $p_l + p_r$ following truncation can readily be estimated from tables of volumes of the bivariate normal distribution, using formulae given by Young & Weiler (1960).

In Table 1 the accumulated selection differential, $\Sigma\, \bar{\imath}_b$, is given in detail for line Sc 2. The plot of the population mean on the underlying scale as a function of this selection differential, differs little from that shown in Fig. 1 for the univariate model, apart from the change in scale. The response to selection does not depart significantly from linearity, so that we may take the regression coefficient, $0{\cdot}272 \pm 0{\cdot}009$, as an estimate of the realized heritability of the variable p_r (or p_l). It is not possible to estimate the corresponding regression coefficients for lines Sc 1 and Sc 3, since complete records of the partition of total bristle score were not kept.

(iv) *Probit distances spanned by the bristle-number classes*

If it is assumed that successive threshold levels on the underlying scale maintain the same relative positions throughout this early phase of response, then any

systematic change in the phenotypic variance of the population, or of the shape of the distribution on the underlying scale, will lead to changes in the probit distances spanned by the bristle-number classes. The ratio of the spans of different classes will of course be unaffected by changes in variance alone, since each is expressed in terms of the prevailing phenotypic standard deviation.

A summary is given in Table 3 of the observed trends in the span of the 5- and 6-bristle classes in the three selection lines, based on the *univariate* model. The regression coefficients are derived from a weighted analysis carried out separately on each sex, covering periods of response corresponding to total selection differentials of 14·0, 13·3, and 15·1 in Sc 1, Sc 2, and Sc 3 respectively. Though the individual estimates suggest a reduction in the span of the 5-bristle class in Sc 2, and an increase in the span of the 6-bristle class in Sc 3, the means of the regression coefficients over all three lines give no clear indication of a trend in the span of either class.

Table 3. *The regression of the span of individual bristle-number classes on the value of* Σi_u.

Line	Bristle class	Regression coefficient	Mean span	
			Males	Females
Sc 1	'5'	$0{\cdot}0208 \pm 0{\cdot}0160$	$0{\cdot}902 \pm 0{\cdot}057$	$0{\cdot}919 \pm 0{\cdot}051$
Sc 2	'5'	$-0{\cdot}0238 \pm 0{\cdot}0096$	—	$0{\cdot}899 \pm 0{\cdot}022$
Sc 3	'5'	$0{\cdot}0010 \pm 0{\cdot}0213$	$0{\cdot}880 \pm 0{\cdot}055$	$0{\cdot}913 \pm 0{\cdot}048$
		Mean	$0{\cdot}891 \pm 0{\cdot}040$	$0{\cdot}904 \pm 0{\cdot}019$
Sc 1	'6'	$0{\cdot}0042 \pm 0{\cdot}0166$	$1{\cdot}130 \pm 0{\cdot}060$	$1{\cdot}015 \pm 0{\cdot}059$
Sc 2	'6'	$-0{\cdot}0099 \pm 0{\cdot}0097$	—	$1{\cdot}017 \pm 0{\cdot}023$
Sc 3	'6'	$0{\cdot}0408 \pm 0{\cdot}0144$	$1{\cdot}095 \pm 0{\cdot}059$	$0{\cdot}943 \pm 0{\cdot}056$
		Mean	$1{\cdot}112 \pm 0{\cdot}042$	$1{\cdot}007 \pm 0{\cdot}020$
Weighted means				
	'5'	$-0{\cdot}0086 \pm 0{\cdot}0072$	$0{\cdot}902 \pm 0{\cdot}017$	
	'6'	$0{\cdot}0060 \pm 0{\cdot}0072$	$1{\cdot}027 \pm 0{\cdot}018$	

Also given in Table 3 are the weighted means of the probit distances spanned by the 5- and 6-bristle classes. There is no clear-cut evidence of a difference in variance between the sexes: the mean span of the 6-bristle class in males exceeds that in females by approximately 10%, and this difference is on the borderline of statistical significance, but the means for the span of the 5-bristle class are in excellent agreement.

Consider now the application of the *bivariate* model to the female scores in Sc 2. The regression coefficient measuring the change in the span of the 3-bristle class as a function of Σi_b, over the period of response from generation Sc 2/3 to generation Sc 2/15, is $0{\cdot}0088 \pm 0{\cdot}0124$, again suggesting that the phenotypic variance on the underlying scale has not been altered by directional selection. The weighted mean span of this bristle class in females is $1{\cdot}608 \pm 0{\cdot}031$.

Since the above analyses have failed to show any conspicuous change in the span

of the 5- and 6-bristle classes of the univariate model, or of the 3-bristle class of the bivariate model, the overall means of these intervals can be taken as providing an indirect measure of the phenotypic variance of the base population. In subsequent papers, these means will be used in assessing the extent of the variability retained in a number of derived populations.

4. AN ANALYSIS OF THE VARIATION SHOWN BY ABDOMINAL AND STERNOPLEURAL HAIR NUMBER

The application of the bivariate model has provided us with a useful picture of the composition of the phenotypic variance shown by the variable underlying scutellar bristle number. The rate of response to selection has indicated that $27{\cdot}2 \pm 0{\cdot}9\%$ of the total is additive genetic variance, and developmental error variance has been shown to account for a further $63{\cdot}8 \pm 2{\cdot}6\%$. The remaining $9{\cdot}0 \pm 2{\cdot}7\%$ of the variance must therefore be due to environmental differences among individuals and to non-additive genetic effects.

There is some similarity between the results of this analysis and those described by Reeve & Robertson (1954) and by Clayton, Morris & Robertson (1957) for abdominal hair number, and by Reeve (1960) for sternopleural hair number, in wild-type laboratory populations (Table 4). The figures for sternopleural hairs have been derived from Tables 1 and 7 of Reeve (1960), using the data on the PdL wild stock. The last two rows of his Table 7 contain errors because σ_s^2 was not calculated as the sum of the components of variance within and between families from his Table 1. The correct figures, which Dr Reeve has asked me to quote, are:

PdL wild stock	σ_s^2	$2\sigma_i^2$	$2\sigma_c^2$	r_{LR}
Males	3·08	1·69	0·70	+0·293
Females	3·42	1·84	0·79	+0·300

For a single side, the total variance is $\sigma_c^2 + \sigma_i^2$, and the fraction of σ_c^2 due to additive genetic effects is estimated as $h^2\sigma_s^2/(\sigma_s^2 - 2\sigma_i^2)$.

Table 4. *Percentage composition of the variance shown by abdominal and sternopleural hair number in wild-type populations, each on the basis of a single score (i.e. single side or segment)*

Component (%)	Abdominals*	Abdominals†	Sterno-pleurals‡
Additive genetic	39·3	37·6	15·8
Environmental	2·3	7·0	13·8
Developmental error	58·4	55·4	70·4

* Reeve & Robertson (1954).
† Clayton *et al.* (1957).
‡ Reeve (1960).

It has been observed in the present selection experiment that both of these hair characters increase in mean in lines selected over a long period for increased scutellar bristle number, and it was therefore decided to make an accurate comparison of the variance components of the three characters in the same wild-type population.

(i) *Abdominal hair number*

The response to selection for abdominal hair number in the Canberra population has been observed in two pairs of lines, AH 1, AL 1, and AH 2, AL2. In each line, selection was imposed at an intensity of 10/20 in each sex, in each of five sub-cultures. The five sets of selected parents were then mated at random to provide the five sub-cultures of the following generation. Selection was based on the total number of hairs on the 4th and 5th sternites, and the realised heritability of this selection

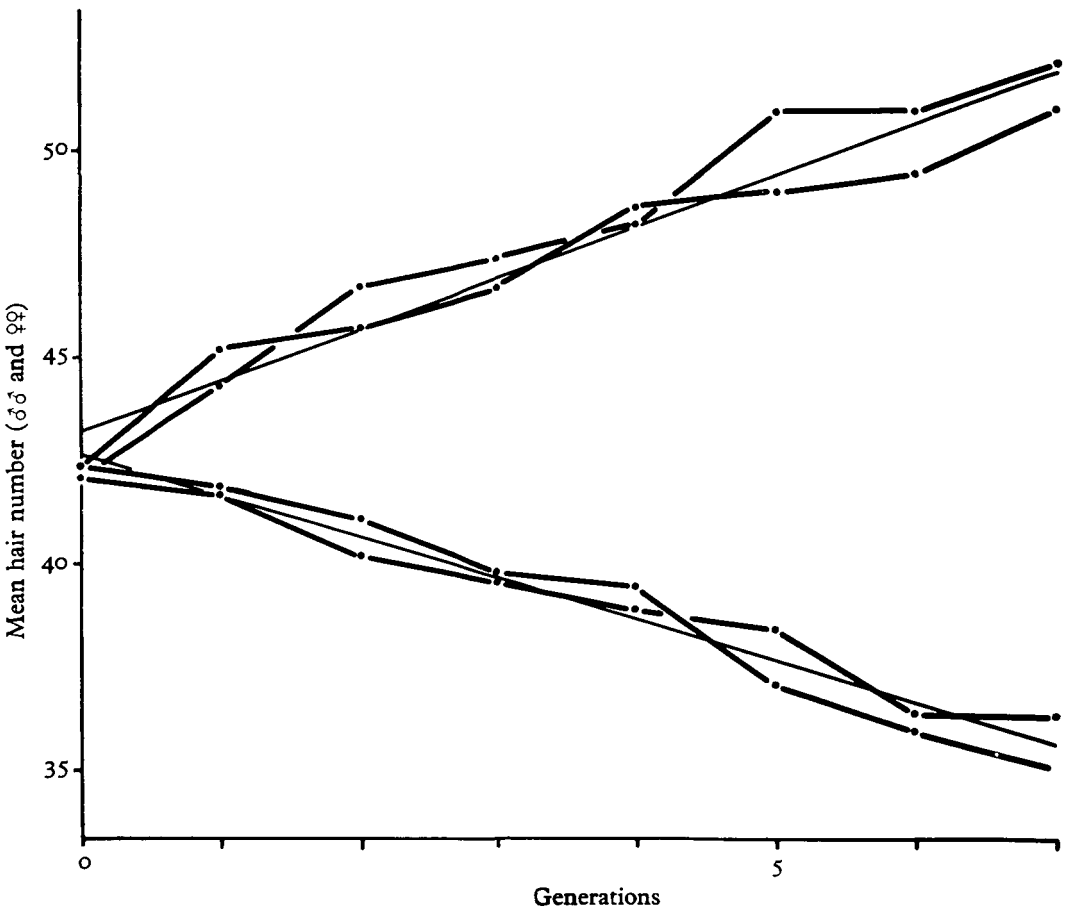

Fig. 2. The response to selection for abdominal hair number.

criterion, h_s^2, has been estimated from the response over the first seven generations of selection (Fig. 2). During this period a linear rate of response was maintained in all four lines.

In Table 5 are given the parameters of the unweighted linear regression lines measuring response in total hair number, averaged over the two sexes, as a function of the number of generations of selection. The mean response over all four lines is $1{\cdot}103 \pm 0{\cdot}045$ hairs per generation.

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Table 5. *The regression of mean abdominal hair number, measured as the sum of the scores on the 4th and 5th sternites, on the number of generations of selection*

Line	Intercept	Slope
AH 1	$43{\cdot}05 \pm 0{\cdot}47$	$1{\cdot}322 \pm 0{\cdot}113$
AH 2	$43{\cdot}31 \pm 0{\cdot}40$	$1{\cdot}091 \pm 0{\cdot}096$
AL 1	$42{\cdot}21 \pm 0{\cdot}25$	$-0{\cdot}879 \pm 0{\cdot}059$
AL 2	$42{\cdot}95 \pm 0{\cdot}36$	$-1{\cdot}121 \pm 0{\cdot}085$
Mean H	$43{\cdot}18 \pm 0{\cdot}31$	$1{\cdot}206 \pm 0{\cdot}074$
Mean L	$42{\cdot}58 \pm 0{\cdot}22$	$-1{\cdot}000 \pm 0{\cdot}052$

The within-culture phenotypic standard deviation of the sum of the hair counts on the 4th and 5th sternites, σ_s, was $3{\cdot}174 \pm 0{\cdot}062$ and $3{\cdot}730 \pm 0{\cdot}072$ in males and females respectively of the base population. The realized heritability of the selection criterion is then

$$\hat{h}_s^2 = \frac{1{\cdot}103}{\frac{1}{2}(0{\cdot}768)(6{\cdot}904)} = 0{\cdot}416 \pm 0{\cdot}018.$$

The phenotypic correlations in the base population between the scores on the 4th and 5th sternites, were $\hat{\rho}_m = 0{\cdot}369 \pm 0{\cdot}024$ and $\hat{\rho}_f = 0{\cdot}427 \pm 0{\cdot}023$, so that the heritability of abdominal hair number, on the basis of a single sternite, can be calculated as $\hat{h}_m^2 = 0{\cdot}285 \pm 0{\cdot}013$, and $\hat{h}_f^2 = 0{\cdot}297 \pm 0{\cdot}013$. This leads to the analysis presented in Table 6, where the standard errors have been calculated by means of large-sample formulae which take account of the covariances among the various estimates involved.

Table 6. *Percentage composition of the variance shown by abdominal hair number in the Canberra population*

Component (%)	Males	Females	Combined
Additive genetic	$28{\cdot}5 \pm 1{\cdot}3$	$29{\cdot}7 \pm 1{\cdot}3$	$29{\cdot}1 \pm 1{\cdot}2$
Environmental	$8{\cdot}4 \pm 2{\cdot}4$	$13{\cdot}0 \pm 2{\cdot}4$	$10{\cdot}7 \pm 1{\cdot}9$
Developmental error	$63{\cdot}1 \pm 2{\cdot}4$	$57{\cdot}3 \pm 2{\cdot}3$	$60{\cdot}2 \pm 1{\cdot}6$

(ii) *Sternopleural hair number*

The heritability of sternopleural hair number in the Canberra population has been determined from two series of experiments, each involving only one generation of selection. In the first series, sets of fifty males and females from the base population were scored for the total number of sternopleural hairs on both sides, the ten males with highest score being mated to the ten females with highest score in a single bottle culture, and similarly with the lowest scoring individuals. The second series of observations involved the same procedure with a selection intensity of 5/40.

The mean selection differential over four sets of observations in the first series was 4·44 hairs, and the response to selection, measured as the difference in mean between

the high and low selections, amounted to $1{\cdot}80 \pm 0{\cdot}28$ hairs. The realized heritability is therefore $0{\cdot}406 \pm 0{\cdot}069$, where the standard error includes a term due to genetic sampling (Prout, 1962). The four sets of observations in the second series gave a mean response of $1{\cdot}91 \pm 0{\cdot}35$ hairs, the mean selection differential being 4·98 hairs, leading to a realized heritability estimate of $0{\cdot}383 \pm 0{\cdot}079$. The weighted mean of the two estimates is then $\hat{h}_s^2 = 0{\cdot}396 \pm 0{\cdot}052$.

The phenotypic correlations in the base population between the counts on the left and right sides, were $\hat{\rho}_m = 0{\cdot}266 \pm 0{\cdot}028$ and $\hat{\rho}_f = 0{\cdot}327 \pm 0{\cdot}028$, so that the heritability of sternopleural hair number, on the basis of a single count, can be estimated to be $\hat{h}_m^2 = 0{\cdot}251 \pm 0{\cdot}033$, and $\hat{h}_f^2 = 0{\cdot}263 \pm 0{\cdot}035$. The results of the analysis are summarized in Table 7.

Table 7. *Percentage composition of the variance shown by sternopleural hair number in the Canberra population*

Component (%)	Males	Females	Combined
Additive genetic	$25{\cdot}1 \pm 3{\cdot}3$	$26{\cdot}3 \pm 3{\cdot}5$	$25{\cdot}7 \pm 3{\cdot}4$
Environmental	$1{\cdot}5 \pm 4{\cdot}0$	$6{\cdot}4 \pm 4{\cdot}1$	$4{\cdot}0 \pm 3{\cdot}7$
Developmental error	$73{\cdot}4 \pm 2{\cdot}8$	$67{\cdot}3 \pm 2{\cdot}8$	$70{\cdot}3 \pm 2{\cdot}0$

5. DISCUSSION

As far as short-term response in a wild-type population is concerned, both the univariate and bivariate threshold models have been shown to provide a satisfactory statistical transformation of the scale of measurement. The former model has the advantage of simplicity, and is to be preferred from an operational point of view. The latter model has intuitive appeal in that the threshold phenomenon is virtually identified as the appearance of an additional bristle at a specified locus, supernumerary bristles almost invariably being located in the vicinity of the anterior scutellar locus. The bivariate model has the further advantage that it enables a more penetrating analysis to be made of the underlying phenotypic variation.

The response to artificial selection, measured on the underlying scale, has been shown to be a linear function of the accumulated selection differential in each of three replicate lines, over a number of generations sufficient to raise the incidence of extra bristles to almost 100%. The heritability of the character is therefore virtually constant on the underlying scale, over this initial phase, and observations of the probit distances spanned by the bristle-number classes suggest that the phenotypic variance is also constant. No significant change could be detected in the relative position of the means of the two sexes.

An analysis of the variation shown by the underlying variable postulated by the bivariate model, has indicated that the genetic variance is almost entirely additive, and that the phenotypic variance is remarkably similar in composition to that shown by the two hair characters studied (Table 8). The dominating feature of the analyses is the magnitude of the 'developmental error' component, which accounts for more than 60% of the phenotypic variance of each of the three characters. The available

evidence supports the contention that in unselected populations, such a low correlation between the expression of the same character in different regions is due primarily to chance effects of an independent nature, rather than to the effects of phenomena such as competition for substrate between regions. It has been shown by Reeve & Robertson (1954) that in genetically homogeneous material raised under optimal environmental conditions, the correlation between hair numbers on the 3rd, 4th and 5th abdominal sternites is virtually zero. In a similar study with sternopleural hairs, Reeve (1960) did record a negative correlation between the left and right sides in homozygous material derived from the Renfrew population ($r = -0{\cdot}16$), but it is of a very low order in crosses among the inbreds ($r = -0{\cdot}02$): in lines derived from other populations, Reeve found the correlations to be consistently positive. Plunkett (1927) came to a similar conclusion in respect of variation in the number of dorsocentral and other bristles in the presence of the mutant gene Dichaete.

Table 8. *A comparison of the components of variance estimated for scutellar bristle number, and for abdominal and sternopleural hair number, in the Canberra population*

Component (%)	Abdominals	Sterno-pleurals	Scutellars
Additive genetic	$29{\cdot}1 \pm 1{\cdot}2$	$25{\cdot}7 \pm 3{\cdot}4$	$27{\cdot}2 \pm 0{\cdot}9$
Environmental	$10{\cdot}7 \pm 1{\cdot}9$	$4{\cdot}0 \pm 3{\cdot}7$	$9{\cdot}0 \pm 2{\cdot}7$
Developmental error	$60{\cdot}2 \pm 1{\cdot}6$	$70{\cdot}3 \pm 2{\cdot}0$	$63{\cdot}8 \pm 2{\cdot}6$

In view of the similarity in variance composition, it seems justifiable to suggest that the hair-number characters are the direct phenotypic expression of variables comparable to that underlying the expression of the canalized bristle character. If the necessary statistical precautions are observed, scutellar bristle number may therefore serve as an extremely useful model character for quantitative genetic experiments. It has a distinct advantage over the hair characters in being susceptible to analysis on the basis of the pattern of structures formed, even when the total number of bristles on the scutellum is of the order of 14. In advanced selection lines, such an analysis may provide clues to the reasons for such phenomena as temporary barriers to progress under selection, or the occurrence of spectacular increases in phenotypic variance.

SUMMARY

The short-term response to artificial selection in a wild-type population for increased scutellar bristle number, has been interpreted in terms of two alternative threshold models. Both models have been shown to give a satisfactory transformation of the scale of measurement, in that the underlying variable shows an effectively linear response in terms of the accumulated selection differential, and the phenotypic variance on the underlying scale remains virtually unchanged over a period of generations sufficient to increase the incidence of extra-bristles to almost 100%.

A genetic analysis based on the bivariate model, which to a large extent takes

account of the location of the supernumerary bristles, has shown the phenotypic variance on the underlying scale to have the following composition: the additive genetic variance is $27{\cdot}2 \pm 0{\cdot}9\%$ of the total, and the developmental error or 'chance' variance accounts for a further $63{\cdot}8 \pm 2{\cdot}6\%$, so that the remaining $9{\cdot}0 \pm 2{\cdot}7\%$ of the variance must be due to environmental differences among individuals and to non-additive genetic effects.

The relative magnitudes of these parameters are remarkably similar to those observed for two quasi-continuous variables in the same population, viz. abdominal and sternopleural hair number. In view of the ease with which scutellar bristles may be scored, the character can therefore serve as an extremely useful model character for quantitative genetic experiments.

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