Genet. Res., Camb. (1968), **11**, *pp.* 125–134
With 3 text-figures
Printed in Great Britain

Variation of scutellar bristles in *Drosophila*

XI. Selection for scutellar microchaetae and the correlated response of scutellar bristles

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(*Received* 7 *February* 1967)

1. INTRODUCTION

The understanding of genetic variation associated with any quantitative character rests on the analysis of the phenotypic variation of the character. The disparity between genotype and phenotype for scutellar bristles in *Drosophila melanogaster* leads to difficulties in the interpretation of a genetic analysis. Rendel (1959) employed the probit transformation (Finney, 1947) as a more convenient metric for understanding the genetic variation underlying scutellar bristle number. From a study of the effects of selection on scutellar bristles he concluded that the invariancy in wild type resulted from the canalization of a normally distributed underlying variable. Latter (1964) showed that the heritability of scutellar bristles as measured on the probit scale was constant for an initial thirteen generations of selection. Fraser *et al.* (1965) were more inclined to rely on the untransformed metric in attempting to describe the genetic changes underlying the response to selection for scutellar bristles.

The appearance of an allele of the *hairy* (*h*) locus in one of the author's scutellar bristle selection lines and a similar occurrence found by A. Robertson (personal communication) in a line selected for ocellar bristles, suggested that a study of the mutant *hairy* (*h*) may provide further information as to the nature of the genetic variation underlying scutellar bristle number. Neel (1941, 1943) indicated that h^1 and the extra scutellar mutant, *polychaetoid*, interacted to increase both scutellar microchaetae and bristles. It was even suggested (Falk, 1963) that the four loci *achaete*, *scute*, *hairy* and *Hairy-wing* are involved in a functional relationship analogous to the operon model proposed by Jacob & Monod (1961).

This paper describes the genetic variance associated with, and the effects of selection upon, the mutant *hairy* phenotype and the correlated change in number of scutellar bristles.

2. MATERIALS AND METHODS

The third chromosome mutant allele $hairy^1$ adds microchaetae to the scutellum, halteres and wing veins. In this analysis only scutellar microchaetae will be con-

* Part of this research was supported by National Institutes of Health Grant no. GM 11778-01 from the U.S. Public Health Service while the author was a candidate for the degree of Ph.D. at the University of California, Davis, California, U.S.A.

sidered. These microchaetae are distributed over the dorsal surface and sides of the scutellum, being more heavily concentrated about the anterior scutellar bristles than in any other region.

The heritabilities of, and the phenotypic and genetic correlations between scutellar microchaetae and bristles were estimated from the analysis of variance and covariance between and within related groups of h^1/h^1 individuals. Two analyses were conducted, one based on 20 sires, the other on 10 sires, each with 3 dams per sire and 5 progeny of each sex per dam. All individuals were simultaneously scored for microchaetae and scutellar bristles.

Two selections lines were established from a population segregating for the h^1 allele; one was for increased and the other decreased microchaetae. For both the high and low lines, fifteen unselected single pair matings were established using heterozygous females and h^1/h^1 males. Ten h^1 male progeny were scored per culture and the three males possessing the greatest number of microchaetae (or lowest in the case of the low selection line) were saved from each culture. Of the fifteen cultures scored, the five having the highest (or lowest) mean were retained and five heterozygous ($+/h^1$) virgin females were randomly collected from each culture. These were mated to the five highest (or lowest) males of those males saved from the five selected cultures. After 2 days the twenty-five females were isolated, one per culture and subsequently removed after 5 days. For the next generation fifteen of the twenty-five cultures were chosen at random for scoring. The selection scheme described above was repeated every generation. The selected population segregating for h^1 and its wild-type allele was maintained to check on the recessiveness of the *hairy*^{1} allele during the course of the selection programme. Heterozygous individuals were scored every generation for the presence of microchaetae. Any such individuals which possessed microchaetae were test-crossed to h^1/h^1 sibs and their heterozygous progeny scored for microchaetae.

After eight generations of both high and low selection the number of cultures scored was reduced to nine; three were selected to provide parents for the next generation. At generation 20 and thereafter the number of cultures was reduced to three since there appeared to be a plateau in both the high and low selection lines. In this case the two cultures having the highest (or lowest) male mean microchaeta number were selected. After forty-three generations, selection was terminated and the two lines were maintained as h^1/h^1 mass cultures.

In the high selection line h^1 males and females were scored for scutellar bristles after the third generation of selection. In the low selection line the scutellar bristle number of h^1 males was scored at generations 4, 8, 10 and 12 and every generation thereafter.

An unselected h^1 population was maintained for the duration of the experiment by mass mating.

Two complete diallels were conducted during the course of the selection programme; one at generation 11 and the other fifteen generations (generation 58) after selection was terminated. In the first diallel ten virgin females and ten males were mated in $\frac{1}{2}$ pint cream jars and allowed to lay eggs for 48 h. Approximately

sixty of each sex were scored for both scutellar bristles and microchaetae for each diallel element. In the later diallel each cross was replicated. Twenty-five and 160 individuals were scored per replicate for microchaetae and scutellar bristles respectively.

3. RESULTS

All data analysis was based on microchaetae score *per se* while for scutellar bristles the probit transformation was applied to all data. Unless otherwise stated the probit score reflects the mean of the population relative to the 4/5 bristle threshold.

(i) *Base population parameters*

The mean microchaeta numbers of the progeny of the two base population analyses were significantly different ($P < 0{\cdot}01$), as was the difference between sexes within progenies ($P < 0{\cdot}01$). The heritability estimate was therefore averaged from four separate analyses of variance. The components of variance from which the full sib estimates of h^2 were derived are shown in Table 1.

Table 1. *Components of variance for the derivation of the heritability of scutellar microchaetae in male and female progeny for the two analyses*

	Analysis 1		Analysis 2	
Component	♀♀	♂♂	♀♀	♂♂
Within progenies (σ_w^2)	9·55	6·50	12·65	5·85
Between dams, within progenies (σ_d^2)	2·25	0·88	1·69	0·00
Between sires (σ_s^2)	0·12	0·10	−0·95	0·11
Heritability	0·40 ± 0·12	0·26 ± 0·11	0·11 ± 0·13	0·29 ± 0·15

Although the estimates of σ_d^2 were consistently larger than those of σ_s^2, they were not significantly so and therefore both estimates were pooled to derive the estimated h^2. The average full-sib estimate of heritability was $0{\cdot}26 \pm 0{\cdot}09$. Standard errors of estimate were derived using formulae given by Mode & Robinson (1959).

Similarly, a half-sib analysis of the probit values of full-sib female families yielded a heritability estimate for scutellar bristles of $0{\cdot}15 \pm 0{\cdot}16$, where

$$h^2 = 4\sigma_s^2/(1 + \sigma_d^2 + \sigma_s^2).$$

This is approximately half that calculated by Latter (1964) from the response to selection for increased scutellar bristle number in the Canberra population ($h^2 = 0{\cdot}33$).

A half-sib covariance analysis of full-sib family means for the two analyses yielded a genetic correlation (r_G) of $0{\cdot}82 \pm 0{\cdot}15$. The average of the components used in estimating r_G were: σ_s^2 (scutellars) = 0·012, σ_s^2 (microchaetae) = 0·458, cov_s = 0·061.

The phenotypic correlation (r_P) between scutellar bristles and microchaetae, as estimated from the correlation between family means, was 0·19. The derived

environmental correlation (r_E), from the relationship $r_P = h_x h_y r_G + e_x e_y r_E$, was 0·033, where h_x and h_y are the respective square roots of the heritabilities of the two characters and $e = \sqrt{(1-h^2)}$.

These two characters therefore have heritabilities characteristic of other bristle systems, they have an apparent high genetic correlation but no effective environmental correlation.

(ii) *Response to selection*

The response to selection for both increased and decreased microchaetae is shown in Fig. 1. The nature of the selection scheme employed, i.e. family followed by individual selection, provided generation by generation estimates of the additive

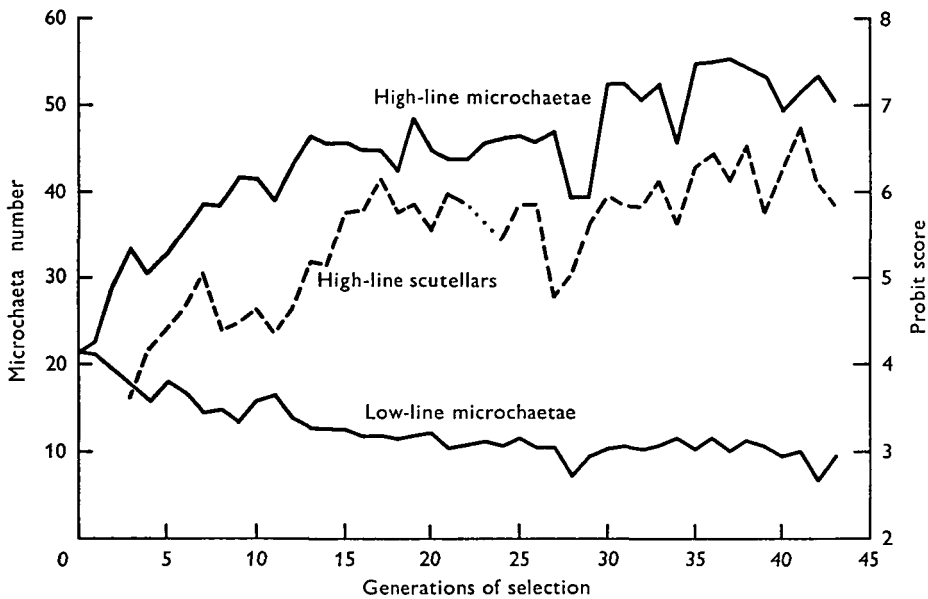

Fig. 1. Response to selection for microchaetae in males of both the high and low selection lines and the correlated response of scutellar bristles in h^1/h^1 males (broken line) of the high selection line.

genetic variance. According to Robertson (1961), the genetic variance among selected families following truncation will be reduced by a proportion $h_f^2[\bar{\imath}(\bar{\imath}-x)]$ where h_f^2 is the heritability of family means, $\bar{\imath}$ is the standardized selection differential and x is the abscissa of the unit normal curve after truncation. Such an estimate was then used to predict the heritability of microchaetae score among individuals of selected families (h_i^2). The expected response to selection in the succeeding generation is a function of both family and individual selection thus:

$$R \text{ (expected response)} = \bar{\imath}_f h_f^2 \sigma_f + \tfrac{1}{2}(\bar{\imath}_i h_i^2 \sigma_i)$$

where $\bar{\imath}_f$ and $\bar{\imath}_i$ are the selection intensities on families and on individuals among selected families respectively. Individual selection was imposed only on males from the selected families. Percent selection was such that $\bar{\imath}_f = 1{\cdot}159$ and $\bar{\imath}_i = 1{\cdot}32$.

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σ_f and σ_i are the phenotypic standard deviations of full-sib male progeny means and among males from selected families respectively.

The initial sixteen generations of selection provided adequate data for a comparison of the expected versus realized response for each generation of selection. Since there was asymmetry in response (see Fig. 1) the more efficient comparison

Table 2. *Estimated heritabilities, expected and realized accumulated responses to selection for increased and decreased microchaetae and the expected and realized divergence (units of change in microchaetae)*

	High line			Low line			Divergence	
Generation	h^2	R_E^1*	R_A^2	h^2	R_E^1	R_A^2	D_E^3	D_A^4
1	0·38	1·89	6·33	0·20	0·71	0·40	—	—
3	0·49	4·79	10·90	0·34	1·94	1·80	4·13	5·67
3	0·20	5·88	7·73	0·03	2·02	3·59	5·29	4·59
4	0·52	9·30	10·10	0·19	2·57	5·56	9·26	8·93
5	0·22	10·35	13·30	0·23	3·32	3·38	11·06	9·95
6	0·22	11·31	16·00	0·15	3·74	4·64	12·45	13·91
7	0·19	12·14	15·60	0·23	4·45	7·24	13·99	16·11
8	0·29	13·58	19·00	0·23	5·15	6·55	16·12	18·82
9	−0·03	13·48	18·70	0·19	5·67	8·32	16·54	20·29
10	0·04	13·61	16·40	0·16	6·16	5·76	17·17	15·43
11	0·12	14·10	20·50	0·15	6·56	5·10	18·06	18·87
12	0·17	14·81	23·69	0·34	7·62	7·48	19·83	24·44
13	0·03	14·88	23·13	0·00	7·62	8·81	19·90	25·21
14	0·03	14·99	22·90	0·10	7·83	8·90	20·21	25·07
15	0·03	15·09	21·40	0·01	7·84	8·96	20·33	23·67
16	0·14	15·60	22·35	0·06	7·96	9·49	20·96	25·11

* Expected (1) and realized (2) accumulated response to selection; and expected (3) and realized (4) accumulated divergence.

was on the basis of divergence. The successive generation estimates of h^2 and the expected and realized accumulated responses to selection for increased and decreased microchaetae are shown in Table 2. The expected and realized accumulated divergences were computed from generation 2 (Table 2) because of the great disparity between the predicted and actual response in the 1st generation of selection in the high line. This was apparently due to a poor estimate of the mean in the first generation of selection, i.e. 22·5 microchaetae versus $26{\cdot}3 \pm 0{\cdot}54$ in the base population. The relationship between the predicted and realized divergence from generation 2 through 16 is depicted in Fig. 2. From generation 2 to 11 there was a consistent relationship between the expected and realized divergence of the high and low selection lines. The slope of the regression line for these ten generations was $1{\cdot}08 \pm 0{\cdot}13$. Generations 12 through 16 by comparison not only had a low predicted divergence but also limited realized divergence. The regression line from generation 2 to 16 had a slope of $1{\cdot}26 \pm 0{\cdot}085$. The reduction in both the estimated additive genetic variance and realized divergence correlates well with the plateaux seen in Fig. 1. It is obvious that the genetic variance available to selection was exhausted by generation 12.

As a result of the unit relationship observed and expected divergence through generation 11, the realized heritability can be derived as the average of those estimates contributing to this relationship. The estimate of realized h^2 is $0{\cdot}21 \pm 0{\cdot}021$ which is statistically non-significantly different from an $h^2 = 0{\cdot}26 \pm 0{\cdot}09$ calculated from the full-sib analysis of variance.

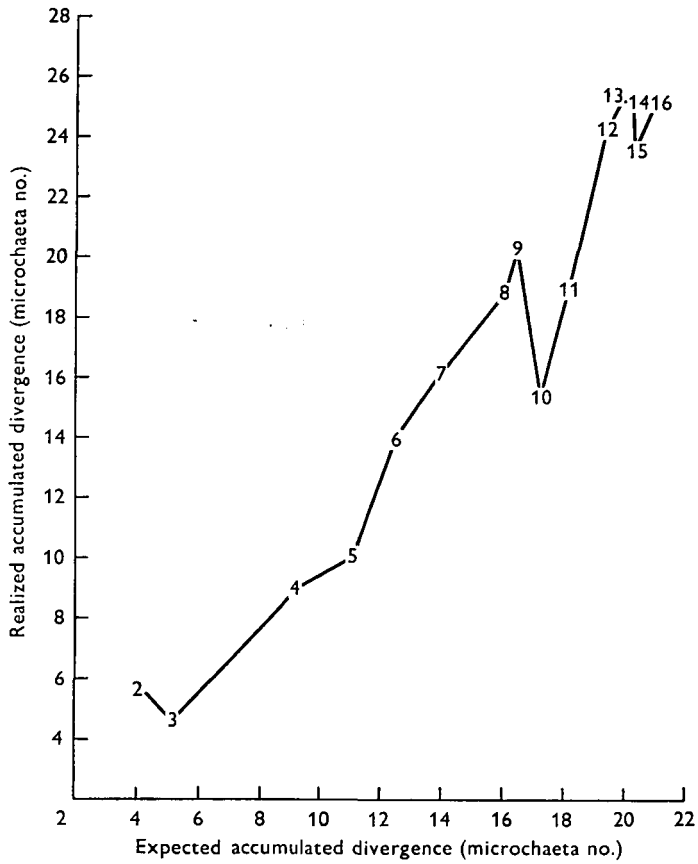

Fig. 2. Realized accumulated divergence between the high and low selection lines as a function of the expected accumulated divergence. (Graph numerals refer to generation number.)

Selection was terminated after 43 generations and the high and low lines were scored every five generations thereafter. During this period of mass mating neither line regressed. The mean number of microchaetae in males in the high and low lines, over the twenty-five generations of mass mating, was $53{\cdot}2 \pm 1{\cdot}52$ and $11{\cdot}15 \pm 0{\cdot}36$ respectively.

For the duration of the selection programme only twenty-two heterozygous ($+/h^1$) individuals, from a total of 3831 scored, possessed at least one microchaeta. None of these individuals possessed more than four microchaetae. These twenty-two individuals were test-crossed to h^1/h^1 sibs and in no case did any of the

heterozygous progeny possess scutellar microchaetae. These twenty-two occurrences were probably due to developmental accidents rather than modification of dominance of the h^1 allele.

(iii) *Correlated response of scutellar bristles*

The correlated change in scutellar bristle number, as measured by the underlying variable (see Fig. 1), essentially paralleled the change in mean number of

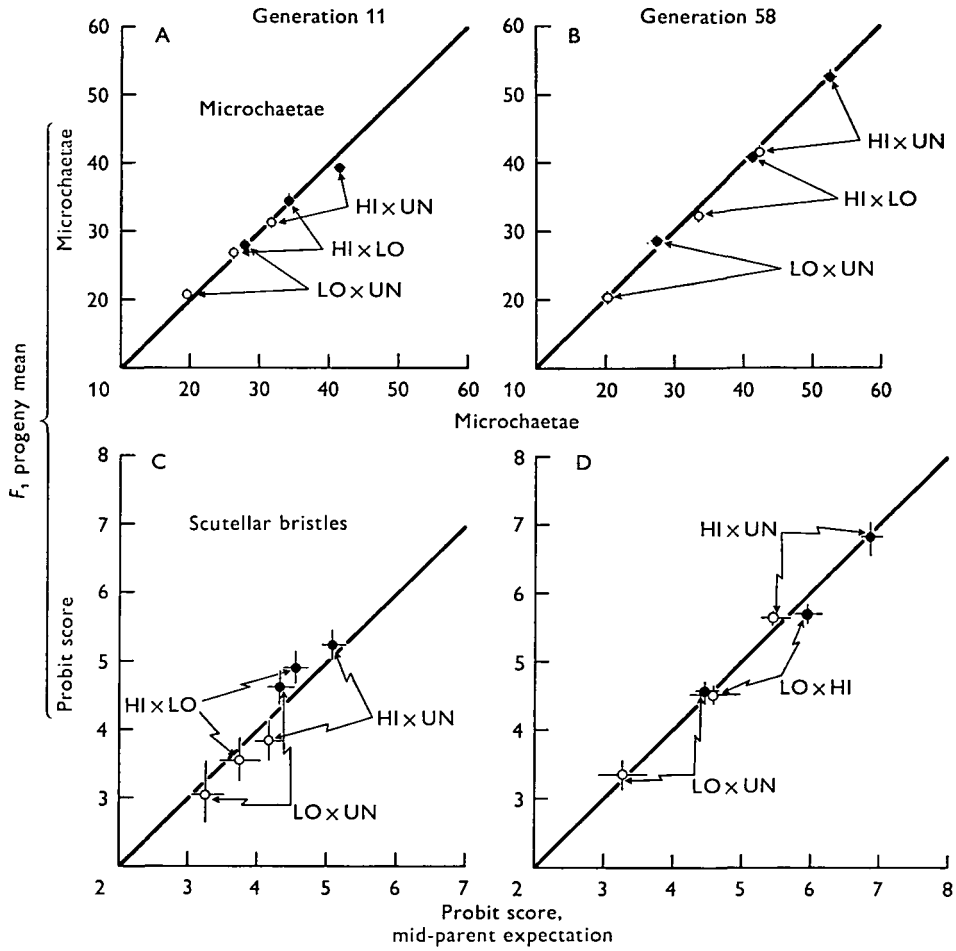

Fig. 3. F_1 progeny means as a function of the mid-parent expectation for the diallel crosses carried out at generations 11 and 58. Solid circles are females and open circles are males. The line with a slope of 1 is the expectation for a completely additive model. Vertical and horizontal lines about each point are confidence intervals (where no such lines are shown the confidence intervals are very small).

microchaetae in h^1/h^1 males of the high incidence line. In the low line there was a decrease in scutellar bristle number to four bristles at generation 8 after which no further change occurred. For the effective period of response of the directly selected character, the realized genetic correlation was calculated according to

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Falconer (1960). Where the direct response to selection in the high line was $1{\cdot}15 \pm 0{\cdot}13$ microchaetae per generation and the correlated response of scutellar bristles was $0{\cdot}12 \pm 0{\cdot}023$ probits per generation, the realized genetic correlation was $0{\cdot}45 \pm 0{\cdot}16$.

This is somewhat less than but not significantly different from $r_G = 0{\cdot}82 \pm 0{\cdot}15$ calculated from the half-sib covariance analysis. The bristle number of heterozygous, $+/h^1$, females in the high line increased by 0·88 probits from the initiation of selection to generation 30 after which no further change occurred. This is approximately 37 % of the correlated response achieved in homozygous, h^1/h^1, females.

(iv) *Diallel analysis*

The results of the two diallel analyses of the primary character and the correlated character are presented in Fig. 3. The slopes of the regression of F_1 progeny means on the mid-parent expectation are shown in Table 3. Since the slopes of the

Table 3. *Slope of the regression of F_1 progeny means on expected value of the F_1*

(Each regression is based on six values; the mean of each of the three two-way crosses for both males and females.)

	Generation 11	Generation 58
Microchaetae	$0{\cdot}84 \pm 0{\cdot}04$	$0{\cdot}98 \pm 0{\cdot}03$
Scutellars (probits)	$1{\cdot}29 \pm 0{\cdot}19$	$0{\cdot}84 \pm 0{\cdot}18$

regression lines are close to unity, the gene effects accumulated under selection for microchaetae would appear to be almost entirely additive. A comparison of Fig. 2A and B and of the respective slopes in Table 3 indicates that the effects of continued selection followed by relaxation of selection has in no way altered the nature of gene effects on microchaetae. This also holds for the correlated character. The apparent sex dimorphism in the G11 analysis of scutellar bristles disappears by G58. This early discrepancy would appear to have been due to the low incidence of extra bristles. By G58 the incidence is increased, thereby improving the estimate of the true mean.

4. DISCUSSION

The use of a major mutant to aid in the understanding of the genetic variation associated with canalized characters has been used to advantage by Fraser, Nay & Kindred (1959) and by Rendel (1959). In this study the third chromosome mutant, *hairy*^{1}, has been employed to effect genetic changes in scutellar chaeta number without using scutellar bristle number *per se* as the selection criteria. This mutant adds microchaetae to the scutellum and in contrast to scutellar bristles is a quasi-continuous character.

The results of a full-sib analysis of variance for microchaetae yielded a heritability estimate of 0·26, somewhat lower, but consistent with that estimated for other bristle systems in *D. melanogaster*. The breeding structure of the micro-

chaetae selection lines allowed a generation-by-generation comparison of the predicted and realized divergence between the high and low microchaetae selection lines. Since the selection régime involved family followed by individual selection, estimates of the additive genetic variance after truncation, and thereby the predicted heritability, were modified according to Robertson (1961).

Unit relationship persisted for eleven generations between predicted and realized divergence, after which both parameters were considerably and essentially equally reduced. The actual divergence declined from 1·08 to 0·25 microchaetae per generation. For all practical purposes the additive genetic variance had been exhausted. The realized heritability (0·21) for the period of unit relationship compares most favourably with that estimated from the full-sib analysis. As far as can be discerned all genetic changes in microchaeta number depended on genes of strictly additive effects, which were apparently fixed early in the selection programme. This is supported by the results of the diallel analysis, where no significant deviation from additivity was observed either early in the programme or after selection was terminated.

Although scutellar bristle number has a low heritability (0·15), as evidenced by a half-sib analysis, the genetic correlation between scutellars and microchaetae is appreciable. The realized genetic correlation was 0·45 while that estimated from a half-sib covariance analysis was 0·83. Thus, approximately 40 % of the variation in scutellar bristles is directly attributable to genic changes affecting microchaetae.

The lack of significant environmental correlation between these two traits is comparable with studies on other related bristle systems in *D. melanogaster*. Any imperfect correlation between chaetae on different but related regions was due largely to localized random variations in development (Reeve & Robertson, 1954; Reeve, 1960).

The behaviour of the correlated character in the diallel crosses paralleled that of microchaetae, suggesting further that genetic changes in the correlated character were a direct result of selection on the primary one.

As was the case with microchaetae, there was no regression of scutellars to the norm upon suspension of selection. This contrasts with Latter (1966), who found a definite tendency for relaxed scutellar bristle selection lines to regress towards the norm of four bristles. In this study genes accumulated under selection had little if any effect on fitness or they had been fixed in a homozygous state.

The canalization of scutellar bristles must primarily involve genes of non-additive effects. In treating the character as a correlated one however, an appreciable amount of additive genetic variance of direct effect on scutellar bristles has been uncovered.

SUMMARY

The third chromosome mutant, *hairy*[1], adds a varying number of microchaetae to the scutellum. The genetic relationship between this character and scutellar bristles was investigated using the conventional techniques of full- and half-sib analysis of variance and covariance, direct and correlated response to selection for

microchaetae and scutellars respectively and diallel crosses at two stages in the programme. There was a good correspondence between the predicted and realized divergence resulting from selection for increased and decreased microchaetae. The correlated response in scutellar bristles appears to be accounted for primarily by genetic changes in microchaetae.

I am grateful to Professor A. S. Fraser for his helpful discussion during the course of this research and to Dr B. D. H. Latter for detailed and constructive evaluation of the manuscript.

REFERENCES

FALK, R. (1963). A search for a gene control system in *Drosophila*. *Am. Nat.* **97**, 129–132.

FALCONER, D. S. (1960). *Introduction to Quantitative Genetics*. Edinburgh: Oliver and Boyd.

FINNEY, D. J. (1947). *Probit Analysis*. Cambridge University Press.

FRASER, A. S., NAY, T. & KINDRED, B. M. (1959). Variation of vibrissa number in the house mouse. *Aust. J. Biol. Sci.* **12**, 331–339.

FRASER, A. S., SCOWCROFT, W., NASSAR, R., ANGELES, H. & BRAVO, G. (1965). Variation of scutellar bristles in *Drosophila*. IV. Effects of selection. *Aust. J. Biol. Sci.* **18**, 619–641.

JACOB, F. & MONOD, J. (1961). Genetic regulatory mechanisms and the synthesis of proteins. *J. molec. Biol.* **3**, 318–356.

LATTER, B. D. H. (1964). Selection for a threshold character in *Drosophila*. I. An analysis of the phenotypic variance on the underlying scale. *Genet. Res.* **5**, 198–210.

LATTER, B. D. H. (1966). Selection for a threshold character in *Drosophila*. II. Homeostatic behaviour on relaxation of selection. *Genet. Res.* **8**, 205–218.

MODE, C. J. & ROBINSON, H. F. (1959). Pleiotropism and the genetic variance and covariance. *Biometrics* **15**, 518–537.

NEEL, J. V. (1941). Studies on the interaction of mutations affecting the chaetae of *Drosophila melanogaster*. I. The interaction of *hairy*, *polychaetoid*, and *Hairy-wing*. *Genetics* **26**, 52–68.

NEEL, J. V. (1943). Studies on the interaction of mutations affecting the chaetae of *Drosophila melanogaster*. II. The relation of character expression to size in flies homozygous for *polychaetoid*, *hairy*, and *Hairy-wing* and the combination of these factors. *Genetics* **28**, 49–68.

REEVE, E. C. R. (1960). Some genetic tests on asymmetry of sternopleural chaeta number in *Drosophila*. *Genet. Res.* **1**, 151–172.

REEVE, E. C. R. & ROBERTSON, F. W. (1954). Studies in quantitative inheritance. VI. Sternite chaeta number in *Drosophila*; a metameric quantitative character. *Z. indukt. Abstamm.- u. VerebLehre* **86**, 269–288.

RENDEL, J. M. (1959). Canalization of the *scute* phenotype. *Evolution* **13**, 425–439.

ROBERTSON, A. (1961). Inbreeding in artificial selection programmes. *Genet. Res.* **2**, 189–194.