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The genetic analysis of the direct and correlated response to selection for chaetae in *Drosophila melanogaster*

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SUMMARY

The direct and correlated response to selection of scutellar microchaetae and scutellar bristles has been analysed by determining the contribution of the three major chromosomes, alone and in combination with each other, to the overall response. The results of the analysis confirm a previous finding, based on a formal statistical approach, that response to selection for microchaetae had highly pleiotropic effects on scutellar bristles. In lines selected, each for high and low microchaetae, genetic changes in the 2nd and 3rd chromosomes are pre-eminent and essentially equal. Inter-chromosomal interactions are of relatively minor importance in interpreting the response to selection for microchaetae but assume greater importance with respect to the correlated character. The results are discussed in terms of the genetic correlation between fitness and the character measured.

1. INTRODUCTION

Although the theory of direct and correlated response to selection minimises the importance of genic interaction (Falconer, 1960; Bohren, Hill & Robertson, 1966), it has been recently shown that genic interactions become apparent during the course of selection (see Scowcroft, 1966; Whittle, 1969). Consequently, these interactions assume major importance in interpreting the response to selection. The object of this paper is to characterize such interactions in respect of direct and correlated response to selection for chaetae in *Drosophila*.

This object was achieved by synthesizing a set of lines in which the 1st, 2nd and 3rd chromosomes of previously selected lines were substituted singly and in all possible combinations into an unselected background. The history and formal statistical analysis of these selection lines was reported by Scowcroft (1968). Briefly, the primary character for selection was scutellar microchaetae which are induced on the scutellum in varying numbers by the mutant gene, *hairy*^{1}, and the correlated character was the normally occurring scutellar bristles. A full-sib analysis of variance yielded a heritability of 0·26 for microchaetae and 0·15 for scutellar bristles with a genetic correlation of 0·83. There was a response to selection for increasing and decreasing numbers of microchaetae such that there was a close correspondence between predicted and realized divergence of the high and low lines. The correlated response of scutellars yielded a genetic correlation of 0·45. Additionally, the behaviour of the correlated character in diallel crosses paralleled that of microchaetae confirming the intimate genetic relationship of the two traits.

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2. MATERIALS AND METHODS

The homozygous combinations of the high and low microchaetae selection lines with the unselected line chromosomes were constructed using various combinations of the following set of chromosomes (Lindsley & Grell, 1968): 1, *FM6*; 2, *SM5*, *SM1*, $In(2R)bw^{VDel}$; 3, *TM3*, $In(3L)D$ and *Sb*. When it was essential that the integrity of the chromosomes be conserved through females only *FM6*, *SM5* or *TM3* were employed. The translocation $T(2;3)ap^{Xa}$ was used to recover specific 2nd and 3rd chromosomes in males and the compound $C(1)RM,yf$ was employed for patroclinous inheritance of specific 1st chromosomes. Fourth chromosome effects were ignored and the *Y* chromosome in each case was that of the unselected line. A typical mating scheme employed, to synthesize a stock (designated UHU) in which the 1st and 3rd chromosomes are from the unselected lines and the 2nd is from the high line is presented in Fig. 1.

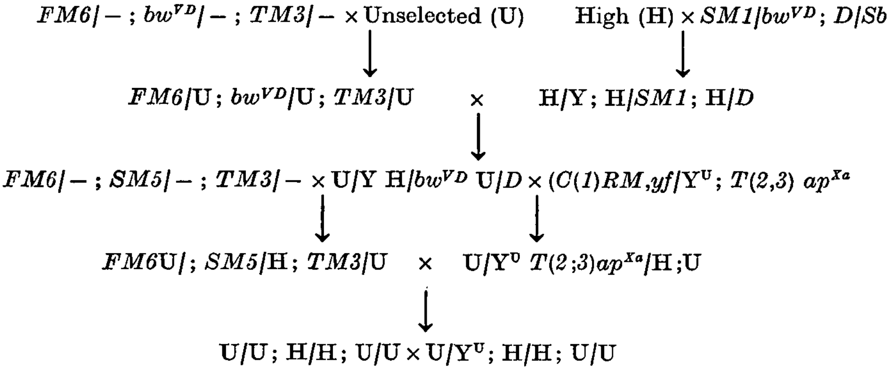

Fig. 1. Representative mating scheme to generate the synthetic line UHU, where U and H refer to chromosomes from the unselected and high lines respectively. Special chromosome designations as per Lindsley & Grell (1968).

To avoid homozygosity by descent in the production of the synthesized lines at least three cultures, each of which had 15 females and 25 males, were used at each step in the procedure.

Mean microchaetae and scutellar bristle number were scored for each of the synthetic stocks. There was no significant replicate variation. The probit transformation (Rendel, 1959) was used for all scutellar bristles scores; all values are measured relative to the 4 bristle–5 bristle threshold. All scores are from females only.

3. RESULTS

(i) *High line substitutions*

The mean microchaetae number and scutellar probit score for the substituted set which involved the high and unselected lines are in Table 1. There was a significant effect of substitution in all cases relative to both the high and low lines. Some of the synthesized lines, e.g. UHU, UUH, HHU and HUH, had the same

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mean microchaetae number but differed significantly in respect of the correlated character, scutellar bristle probit score.

The data of Table 1 was used to derive the contribution of each of the major chromosomes, and of interaction between chromosomes, to the total response to selection (Table 2). The derivation of these values was non-standard in that interaction terms are not statistically independent of each other or from the single chromosome components as would be the case in a classical analysis. The object here was to build up a pattern of single chromosome contributions to selection response and then of interactions between chromosomes. This inflated the interaction terms but such terms were not used to evaluate the statistical significance of the main chromosome effects. The single chromosome components were obtained by difference, i.e. the 1st chromosome component (high microchaetae) = HUU(40·2) − UUU(38·0). The interaction terms were also derived by difference less single chromosome components, i.e. the 1·2 interaction (high line) = HHU(48·9) − UUU(38·0) − component 1(2·2) − component 2(11·5). It should be pointed out that the 2nd-order interaction term is the remainder of the selection response after single chromosome and first order interaction components are accounted for and therefore should be treated with due caution. All components can be derived from two or more of eight independent genotypes scored and standard errors were calculated accordingly.

Table 1. *Mean microchaeta number and probit score for females in the lines synthesized from the high and unselected microchaetae lines*

Genotype 1	2	3	No. of microchaetae	Scutellar bristles: probit score
U	U	U*	38·0 ± 0·34	5·78 ± 0·08
H	H	H*	63·8 ± 0·50	7·71 ± 0·12
H	U	U	40·2 ± 0·39	5·51 ± 0·08
U	H	U	49·5 ± 0·40	6·71 ± 0·13
U	U	H	49·4 ± 0·44	6·93 ± 0·15
H	H	U	48·9 ± 0·61	5·60 ± 0·08
H	U	H	48·8 ± 0·46	7·48 ± 0·25
U	H	H	60·6 ± 0·44	7·48 ± 0·19

* Unselected and high genotypes were not resynthesized.

Single chromsome effects were by far the most important in accounting for the 25·8 microchaetae response in the high line (Table 2). The 2nd and 3rd chromosomes were equally involved in the response, each contributing 11·5 microchaetae. Inter-chromosomal interactions were relatively less important. Interaction of the 1st, both with the 2nd and 3rd chromosomes, depressed the absolute effect of the chromosomes alone. In this case negative and positive interactions cancelled one another.

For the correlated character, interaction assumed far greater importance in interpreting the correlated response of 1·93 probits. The sum of the interaction

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values, regardless of sign, was 2·56 probits while that of single chromosome effects was 2·35. Approximately half of the total interaction components increased the probit score whilst the remainder decreased probit score.

Table 2. *Chromosomal and interaction components of response to selection for microchaetae in the high line and for the correlated character, scutellar bristles*

Component	No. of microchaetae	Scutellar bristles: probit score
1	2·2 ± 0·52	−0·27 ± 0·11
2	11·5 ± 0·53	0·93 ± 0·15
3	11·4 ± 0·57	1·15 ± 0·17
1.2	−2·8 ± 0·89	−0·84 ± 0·19
2.3	−0·3 ± 0·81	−0·38 ± 0·29
1.3	−2·8 ± 0·82	0·82 ± 0·31
1.2.3	6·6 ± 1·28	0·52 ± 0·41

Table 3. *Mean microchaetae number and probit score for females in the lines synthesized from the low and unselected microchaetae lines*

Genotype			No. of microchaetae	Scutellar bristles: probit score
1	2	3		
U	U	U*	38·0 ± 0·34	5·78 ± 0·08
L	L	L*	15·6 ± 0·19	3·21 ± 0·07
L	U	U	37·0 ± 0·31	5·67 ± 0·13
U	L	U	24·3 ± 0·26	4·32 ± 0·08
U	U	L	29·7 ± 0·33	4·92 ± 0·10
L	L	U	21·7 ± 0·28	4·58 ± 0·22
L	U	L	30·1 ± 0·33	4·28 ± 0·11
U	L	L	19·2 ± 0·28	3·74 ± 0·15

* Unselected and low lines not resynthesized.

(ii) *Low line substitutions*

Mean number of microchaetae and probit scores for the low line substitutions are contained in Table 3. The derived chromosomal components (Table 4) show that, as for the high line, the direct contribution of the 2nd and 3rd chromosomes predominated; the sum of the single chromosome contributions closely approximated the overall response of 22·4 microchaetae. There were both positive and negative inter-chromosomal interactions, each of which amounted to approximately 20 % of the overall response to selection.

In respect of the correlated decrease in scutellar bristles, the majority of the chromosome contribution was interpretable in terms of single chromosome effects in the same proportion as that for microchaetae, i.e. the ratio of the 2nd to 3rd chromosome contribution was 1·69 for scutellar bristles and 1·65 for microchaetae. Interaction of a positive and negative nature comprised a smaller component (approximately 50 %) of the overall changes than in the case of the high line.

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Table 4. *Chromosomal and interaction components of response to selection for microchaetae in the low lines and for the correlated character scutellar bristles*

Component	No. of microchaetae	Scutellar bristles: probit score
1	1·0 ± 0·46	0·11 ± 0·15
2	13·7 ± 0·43	1·46 ± 0·11
3	8·3 ± 0·43	0·86 ± 0·17
1.2	1·6 ± 0·60	−0·37 ± 0·28
2.3	−3·2 ± 0·61	−0·28 ± 0·21
1.3	−1·4 ± 0·66	0·53 ± 0·21
1.2.3	2·4 ± 0·83	0·26 ± 0·34

4. DISCUSSION

From this study it can be concluded that:

(1) The genetic changes resulting from selection for microchaetae had a marked effect on scutellar bristles. Direct support for this comes from a consideration of the 2nd and 3rd chromosome contributions. The 2/3 ratio was 1·01 for microchaetae and 0·81 for scutellar probits in the high line and for the low line the ratios were 1·65 and 1·69 for microchaetae and scutellars respectively.

(2) Single chromosome affects were of greater significance for microchaetae than for scutellars. Interactions did occur but these were generally of relatively minor importance. Negative interactions can be accounted for by duplicate gene action in which case interaction terms should be found between the 2nd and 3rd chromosomes. This obtains for the low line but for the high line the significant negative interactions affecting microchaetae occurred between the 1st and 2nd and the 1st and 3rd chromosomes.

(3) Unlike the relatively clear pleiotropism of the single chromosome effects, the chromosomal interaction affecting scutellars could not be predicted from that which was involved in the primary character. In the high line the highly significant 2·3 negative interaction affecting microchaetae had no influence on scutellars; the significant interaction was a positive one involving chromosomes 1 and 3. In the low line the negative interaction between chromosomes 1 and 2 which affected microchaetae also held for scutellar bristles, while that between the 1st and 3rd was negative for microchaetae and positive for scutellars.

In principle these findings support the earlier conclusion (Scowcroft, 1968), based on a statistical analysis, that the correlated response in scutellar bristles appears to be accounted for primarily by genetic changes affecting microchaetae.

These results bear on the question of the interrelationship of any measured character and adaptive significance (Dobzhansky, 1956). Robertson (1955, 1967) believes this to be important to an understanding of the organization of quantitative genetic variation and his original thesis (Robertson, 1955) was that the degree of additive gene action is inversely related to the contribution of the character to reproductive fitness. More recently Robertson (1967) has questioned the rigour of this relationship.

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In a Robertsonian sense microchaetae are adaptively neutral and therefore the underlying genetic variability should be all additive. This view is supported by the close correspondence between predicted and realized response to selection, the lack of regression by either high or low lines upon relaxation of selection (Scowcroft, 1968) and the relative lack of interchromosomal interaction in the above analysis. Further, since natural selection favours the complete absence of microchaetae, thereby favouring a particular allelic state at a single locus, it is intuitively obvious that there is no opportunity for natural selection to modify genetic variability directly associated with the *presence* of microchaetae.

On the other hand, it can be argued that the correlated character, scutellar bristles, is adaptively significant. Although genetically variable (Rendel, 1959; Fraser *et al.* 1965), natural selection has canalized the phenotype such that it assumes minor taxonomic importance. The high negative correlation between fitness and deviation from the norm of four bristles was demonstrated by Latter (1966), who found that with continued selection there was a progressive reduction in fertility along with an increase in generation interval and a marked regression toward the norm following relaxation of selection.

In following this line of reasoning and from a consideration of the above data, it appears that selection for a trait with apparently little relationship to fitness is markedly pleiotropic towards one which is correlated with fitness. Consequently, Robertson's (1955) original thesis does not appear to hold.

To construct an antithesis however, would be futile since implicit in Robertson's hypothesis, and any alternative, is the assumption that a given character can be a sufficient index of fitness. Dobzhansky (1956) points out that 'natural selection does not operate with separate traits'. Reproductive success is a function of the total genetic system. Macrophenotypic analysis looks only at the end-point of many basic processes which are potentially more important to the adaptive process than any one character. Scutellar bristle number when treated in isolation displays the properties of an adaptive trait. On the other hand, analysis of microchaetae variability suggests that it is selectively neutral, yet it has been shown that these two traits are genetically closely related. To discuss their genetic properties in relation to fitness and to each other – and this would apply to any arbitrarily chosen character – requires an analysis in far greater depth than can be done at the quantitative genetic level.

REFERENCES

BOHREN, B. B., HILL, W. G. & ROBERTSON, A. (1966). Some observations on asymmetrical correlated response to selection. *Genetical Research* **7**, 44–57.

DOBZHANSKY, TH. (1956). What is an adaptive trait? *American Naturalist* **90**, 337–347.

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

FRASER, A. S., SCOWCROFT, W. R., NASSAR, R., ANGELES, H. & BRAVO, G. (1965). Variation of scutellar bristles in *Drosophila*. IV. Effects of selection. *Australian Journal of Biological Science* **18**, 619–641.

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

https://doi.org/10.1017/S0016672300012787 Published online by Cambridge University Press

LINDSLEY, D. L. & GRELL, E. H. (1968). Genetic variations of *Drosophila melanogaster*. *Publications. Carnegie Institute of Washington*, no. 627.

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

ROBERTSON, A. (1955). Selection in animals: synthesis. *Cold Spring Harbor Symposia in Quantitative Biology* **20**, 225–229.

ROBERTSON, A. (1967). The nature of quantitative genetic variation. In *Heritage from Mendel*, ed. R. A. Brink. University of Wisconsin Press.

SCOWCROFT, W. R. (1966). Variation of scutellar bristles in *Drosophila*. IX. Chromosomal analysis of scutellar bristle selection lines. *Genetics* **53**, 389–402.

SCOWCROFT, W. R. (1968). Variation of scutellar bristles in *Drosophila*. XI. Selection for scutellar microchaetae and the correlated response of scutellar bristles. *Genetical Research* **11**, 125–134.

WHITTLE, J. R. S. (1969). Genetic analysis of the control of number and pattern of scutellar bristles in *Drosophila melanogaster*. *Genetics* **63**, 167–181.

https://doi.org/10.1017/S0016672300012787 Published online by Cambridge University Press