VARIATION OF SCUTELLAR BRISTLES IN DROSOPHILA VI. DOMINANCE AND EPISTASIS*

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Summary

Selection for extrascutellar bristles has resulted in two main levels of selection response, in several sets of lines. Crosses between these lines have shown that there are two genetic systems controlling the number of scutellar bristles.

Two components of the selection advance have been compared at different levels of the background genotype, and one, the A9 component, shows a marked correlation of its effect with deviation from the norm of four bristles, having little if any effect at the norm and a marked effect at a mean of six bristles. The other component (the A15 component) did not show such a correlation.

I. INTRODUCTION

Selection for extrascutellar bristles in *Drosophila* is characterized by an extreme heterogeneity of response, both between lines, and between generations within lines (see Payne 1918; Sismanidis 1942; Fraser and Hansche 1964; Fraser *et al.* 1965). Similar patterns of response to selection have been found for sternopleural chaetae number in *Drosophila* (Thoday and Boam 1961). Mather (1941, 1943) suggested that the heterogeneity of response was due to the existence of relationally balanced polygenes, and Fraser (1957) showed by computer simulation that his explanation was sufficient to explain the results. Fraser, Miller, and Burnell (1965) have shown by computer simulation that selection for an intermediate norm will lead to the evolution of repulsion relational balance, and Mather's (1941) hypothesis can be accepted as fully sufficient. This does not, however, exclude the possibility of other mechanisms of genetic balance (see Reeve and Robertson 1953).

Fraser *et al.* (1965) found in their A set of extrascutellar selection lines that there were two ranges of bristle number at which selection was ineffective. These two ranges were termed the second and third levels of response. Unselected lines in which the majority of individuals have the norm of four scutellars are termed first level. Although recombination of relationally balanced polygenes is probably involved in these responses to selection, it appears most likely that each of the three levels at which selection is ineffective represent an adaptive peak (Fraser *et al.* 1965). This interpretation has been supported by the results of Scowcroft and of Kuhn (personal communications). Scowcroft found that reversal of selection in a second level line could effect a return to the first level. A further reversal could then effect a return to the second level. This genetical plasticity contrasts with the stability of sublines at the second level in which selection was relaxed. Kuhn showed in a thirdlevel line that reverse selection had a definite but limited response in returning

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towards the second level. Sublines in which selection was relaxed showed a marked regression to the third level. A schematic representation of these results is given in Figure 1.

A further complication was found in crosses between lines of the three levels, which showed a marked regression towards the first level, indicating a dominance of the norm (Fraser 1963; Fraser *et al.* 1965). Results from a more detailed set of crosses are presented and discussed in this paper.



GENERATIONS OF SELECTION

Fig. 1.—Responses to forward, reverse, and relaxed selection found by Kuhn for a third-level line and by Scowcroft for a second-level line are shown schematically.

II. MATERIAL AND METHODS

The A set of extrascutellar lines has been described by Fraser *et al.* (1965). Six of these were used for the present study. Three had been stabilized at the third level for over 30 generations (lines 1, 9, and 18). The other three lines had similarly stabilized at the second level (lines 4, 6, and 15). The pattern of response to selection in these lines is shown by Fraser *et al.* (1965). Crosses were made between these lines, in a complete diallel, and also between these lines and a set of unselected lines (lines 70, 71, and 73). These latter lines have been described by Pennycuik and Fraser (1964).

All crosses were of 4 females with 8 males in quarter-pint bottles at 72° F. Two replicates were set up for each cross. 50 females and 50 males were scored in the first cultures. 50 females were scored in the second culture.

A further set of crosses was made of a number of the B set of selection lines to the six selected A lines. These crosses were not made to form a complete diallel each B line was crossed with all six of the A lines, but no crosses were made between the different B lines.

III. RESULTS AND DISCUSSION

The mean scutellar numbers of progeny in crosses between the A set of lines are given in Tables 1 and 2 for female and male progeny respectively. Female progeny were scored in the replicate cultures and there is a strong correlation between replicates (r = 0.91) indicating that considerable weight can be given to the values of individual crosses. A similarly strong correlation occurs between the female progeny of reciprocal crosses, showing that maternal effects do not need to be considered in any explanation of the differences between this set of lines. Comparisons of male

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MEAN SCUTELLAR NUMBER OF FEMALE PROGENY IN CROSSES BETWEEN THE A SET OF SELECTION LINES

Female				Male I	Parent		
Parent		A9	A18	Al	A15	$\mathbf{A4}$	A6
A9	R_1	7.59	$7 \cdot 19$	7.58	$4 \cdot 86$	$6 \cdot 32$	$5 \cdot 06$
	R_2	$7 \cdot 28$	$6 \cdot 84$	$6 \cdot 94$	$4 \cdot 90$	$5 \cdot 98$	$4 \cdot 98$
	$ar{x}$	$7 \cdot 43$	7.01	7.26	4 · 88	$6 \cdot 15$	$5 \cdot 02$
A18	R_1	6.77	7.04	$7 \cdot 15$	4.84	5.72	$4 \cdot 48$
	R_2	$7 \cdot 02$	$7 \cdot 12$	$6 \cdot 06$	$5 \cdot 14$	$4 \cdot 92$	$4 \cdot 26$
	x	6.88	7.08	6.60	4.99	$5 \cdot 32$	$4 \cdot 37$
 A1	R_1	7.12	$6 \cdot 48$	6.78	4.84	$6 \cdot 32$	4.74
	R_2	$7 \cdot 28$	6.38	$6 \cdot 84$	$4 \cdot 90$	$6 \cdot 50$	$4 \cdot 86$
		$7 \cdot 20$	$6 \cdot 43$	6.81	4 · 87	6.41	4 · 80
A15	R_1	4.78	4.58	$5 \cdot 20$	$5 \cdot 47$	$4 \cdot 94$	4 ·77
	R_2	$4 \cdot 82$	$5 \cdot 08$	$4 \cdot 94$	5.68	$4 \cdot 66$	$4 \cdot 48$
	\bar{x}	4.80	$4 \cdot 83$	$5 \cdot 07$	$5 \cdot 57$	4 ·80	$4 \cdot 62$
A4	R_1	6.04	$5 \cdot 50$	$7 \cdot 14$	$4 \cdot 64$	$5 \cdot 42$	4.74
	R_2	$5 \cdot 84$	$5 \cdot 32$	$5 \cdot 63$	4.70	$5 \cdot 44$	$4 \cdot 72$
	\bar{x}	$5 \cdot 94$	$5 \cdot 41$	$6 \cdot 38$	$4 \cdot 67$	$5 \cdot 43$	$4 \cdot 73$
A6	R_1	5.57	4.71	4.78	4.78	$4 \cdot 62$	4.71
	R_2	$4 \cdot 64$	$4 \cdot 24$	4.78	$4 \cdot 28$	4.76	$5 \cdot 18$
	\bar{x}	$5 \cdot 10$	4.47	4.78	$4 \cdot 53$	4 .69	4 · 94

 R_1 and R_2 are values for replicate cultures. \bar{x} is mean over replicates

TABLE 2

MEAN SCUTELLAR NUMBER OF MALE PROGENY IN CROSSES BETWEEN THE ${f A}$ set of selection lines

Female				Male 1	Parent		
Parent		A9	A18	Al	A15	A4	A6
A9	R_1	6.71	6.11	$6 \cdot 25$	$4 \cdot 25$	5.77	4.31
A18	R_1	$5 \cdot 91$	$6 \cdot 15$	$6 \cdot 11$	$4 \cdot 28$	$5 \cdot 22$	$4 \cdot 10$
Al	R_1	$6 \cdot 52$	5.96	6.00	$4 \cdot 12$	5.86	$4 \cdot 24$
A15	R_1	4.78	$4 \cdot 64$	4.55	$4 \cdot 84$	$4 \cdot 81$	$4 \cdot 57$
	R_2	$4 \cdot 20$	$4 \cdot 38$	4.14	$4 \cdot 96$	$4 \cdot 09$	$4 \cdot 17$
	\bar{x}	$4 \cdot 49$	$4 \cdot 51$	$4 \cdot 34$	$4 \cdot 90$	$4 \cdot 45$	$4 \cdot 37$
$\mathbf{A4}$	R_1	$5 \cdot 62$	$5 \cdot 02$	$5 \cdot 42$	$4 \cdot 13$	$4 \cdot 91$	4.18
$\mathbf{A6}$	R_1	$4 \cdot 26$	$4 \cdot 19$	$4 \cdot 21$	$4 \cdot 13$	$4 \cdot 31$	$4 \cdot 33$
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 R_1 and R_2 are values for replicates. \bar{x} is mean over replicates

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progeny between reciprocal crosses also show no consistent differences except for crosses involving lines A4 and A15. The simplest explanation is that these lines have sex-linked components of +0.25 scutellars in line A15, and -0.25 in line A4. This will be discussed further below.



Fig. 2.—Mean scutellar number of the F_1 's from crosses between the A set of lines are shown plotted against the mid-parent expectation. The graphs titled "all crosses" give the results for all crosses between both the A and B sets of lines.

The results of the separate crosses averaged over replicates and reciprocals are shown in Figure 2 plotted against the mid-parent expectation. There are several conclusions which can be drawn from these data:

(1) The three third-level lines (A1, A9, and A18) show an agreement with the mid-parent expectation in their crosses with each other. The genetic basis of their advance is either allelic in the three lines, or basically additive. Scowcroft (see Fraser et al. 1965) has shown that the chromosomal locations of the advances are not identical—the advance in line A9 is predominantly located on chromosome III, whereas lines A1 and A18 show a location of the advance on both chromosomes I and III with a strong interaction term. This shows that the genetic basis of the advances are not, at least in part, allelic and it follows that they must be additive relative to each other. This contrasts with Scowcroft's finding that the advance to the third level was recessive relative to the "inversion balanced" chromosomes which were used.

- (2) The three second-level lines (A4, A6, and A15) show a marked regression below the mid-parent expectation. This is especially evident in the male progeny. It would appear that the advance to the second level involves a different genetic system to that involved in the advance to the third level. This is in agreement with Scowcroft (see Fraser *et al.* 1965) who found that negative interactions between chromosomal components were a prominent feature of second-level lines.
- (3) Crosses between the second- and third-level lines divide into two groups. This is evident from the male progeny and it is less clear but also evident from the female progeny. Crosses of lines A6 and A15 with the third-level lines show a marked regression below the mid-parent expectation. A feature of crosses involving these two lines is that there is a noticeable similarity of their scutellar number, regardless of whether the other parent is a second-or third-level line. The crosses regress to a level which is independent of the difference between the second and third levels. These results contrast with those from crosses involving the other second-level line (line A4). Crosses of line A4 with the third-level lines do not show the same regression below the mid-parent expectation which is such a marked feature of lines A6 and A15. Clearly, there is a marked heterogeneity between the second-level lines in their possession of a component of the selection advance which can interact additively with that of the third-level lines.

Р	ar	ents	Pro	geny	F	Par	\mathbf{ents}	Pro	geny	Р	ar	ents	Pro	geny
Male	×	Female	Male	Female	Male	×	Female	Male	Female	Male	X	Female	Male	Female
Al	×	70	$4 \cdot 03$	$4 \cdot 21$	A1	×	71	$4 \cdot 02$	4.11	Al	×	73	4.00	4.04
$\mathbf{A4}$	X	70	$4 \cdot 04$	$4 \cdot 29$	$\mathbf{A4}$	Х	71	$4 \cdot 05$	$4 \cdot 13$	$\mathbf{A4}$	Х	73	$4 \cdot 00$	$4 \cdot 05$
$\mathbf{A6}$	Х	70	$4 \cdot 05$	$4 \cdot 11$	$\mathbf{A6}$	Х	71	$4 \cdot 03$	$4 \cdot 21$	$\mathbf{A6}$	×	73	$4 \cdot 00$	4.09
$\mathbf{A9}$	Х	70	$4 \cdot 05$	4.68	$\mathbf{A9}$	Х	71	$4 \cdot 10$	$4 \cdot 25$	$\mathbf{A9}$	Х	73	4.00	$4 \cdot 05$
A15	×	70	$4 \cdot 02$	$4 \cdot 26$	A15	×	71	$4 \cdot 07$	$4 \cdot 36$	A15	Х	73	$4 \cdot 00$	$4 \cdot 06$
A18	\times	70	$4 \cdot 04$	$4 \cdot 25$	A18	×	71	$4 \cdot 07$	$4 \cdot 17$	A18	×	73	$4 \cdot 01$	$4 \cdot 08$

TABLE 3

MEAN SCUTELLAR NUMBER OF PROGENY IN CROSSES BETWEEN THE FIRST-LEVEL LINES (70, 71, AND 73) AND THE A SET OF SELECTION LINES

A further set of crosses were made of the A set of selection lines with the firstlevel unselected lines (70, 71, and 73). The results are given in Table 3. There is a marked regression towards the first level with little, if any, real differences between the second- and third-level lines, except in the cross of A9 with line 70. This discrepancy will be discussed below.

A second set of extrascutellar lines were crossed to the A set of lines. These were all members of the B set of selection lines (see Fraser *et al.* 1965). The aim was to determine whether the results from the A set of lines were generally valid for all extrascutellar lines. Seven B lines were used. Their patterns of response to selection have been described by Fraser *et al.* (1965).

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	SCUTELLAR
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	geny	Female	4 · 43 4 · 76	$4 \cdot 73$ $4 \cdot 56$	4 30 4 46	$5 \cdot 16$ $4 \cdot 70$	4 · 76 4 · 70	$\begin{array}{c} 4\cdot 33\\ 4\cdot 46\end{array}$	$4 \cdot 33$
	Pro_{0}	Male	$4 \cdot 13$ $4 \cdot 30$	$4 \cdot 23$ $4 \cdot 16$	$\begin{array}{c} 4\cdot 10\\ 4\cdot 16\end{array}$	$4 \cdot 43$ $4 \cdot 66$	$4 \cdot 10$ $4 \cdot 43$	$4 \cdot 13$ $4 \cdot 16$	$4 \cdot 16$
SET	Parents	Male \times Female	$\begin{array}{ll} \mathbf{A1} & \times \mathbf{B6} \cdot 2 \\ \mathbf{B6} \cdot 2 & \times \mathbf{A1} \end{array}$	$\begin{array}{llllllllllllllllllllllllllllllllllll$	$\begin{array}{llllllllllllllllllllllllllllllllllll$	$\begin{array}{llllllllllllllllllllllllllllllllllll$	$\begin{array}{llllllllllllllllllllllllllllllllllll$	$\begin{array}{lll} A18 & \times B6 \cdot 2 \\ B6 \cdot 2 & \times A18 \end{array}$	$B6 \cdot 2 \times B6 \cdot 2$
CH THE A	geny	Female	$5 \cdot 16$ $5 \cdot 26$	4.96 4.96	$5.26 \\ 4.93$	5 · 53 5 · 90	$5 \cdot 50$ $4 \cdot 86$	$5 \cdot 43$ $4 \cdot 73$	6 · 70
LINES WI	Prog	Male	$4 \cdot 53$ $4 \cdot 56$	$4 \cdot 53$ $4 \cdot 36$	4 · 36 4 · 53	4 • 56 5 • 00	$4 \cdot 33$ $4 \cdot 56$	$4 \cdot 60$ $4 \cdot 13$	5.62
THE B SET OF	Parents	ale $ imes$ Female	floor X = floor X	$\begin{array}{ccc} \mathbf{t} & \times & \mathbf{B7} \cdot 3 \\ 7 \cdot 3 & \times & \mathbf{A4} \end{array}$	$3 \times B7 \cdot 3$ $7 \cdot 3 \times A6$	$\begin{array}{ll} 0 & \times \mathbf{B7.3} \\ 7.3 & \times \mathbf{A9} \end{array}$	$f [5 imes B7 \cdot 3] \ 7 \cdot 3 imes A15$	$\begin{array}{ll} \mathbf{B} & \times \mathbf{B7} \cdot 3 \\ 7 \cdot 3 & \times \mathbf{A18} \end{array}$	$1 \cdot 3 \times B7 \cdot 3$
SES OF		le M	B. A.	B' A	B7	B7	B. A.	B7 B7	B
DF CROS	geny	Fema	4.60 4.96	$4 \cdot 56$ $4 \cdot 53$	4.63 4.56	5 · 03 5 · 23	4 · 60 4 · 56	$4 \cdot 83$ $4 \cdot 53$	4.50
UMBERS (Pro	Male	$\begin{array}{c} 4\cdot 06\\ 4\cdot 20\end{array}$	$\begin{array}{c} 4\cdot 16\\ 4\cdot 23\end{array}$	$4 \cdot 13$ $4 \cdot 23$	$4\cdot 26$ $4\cdot 60$	$4 \cdot 06 \\ 4 \cdot 36$	$4 \cdot 13$ $4 \cdot 03$	$4 \cdot 03$
EAN SOUTELLAR N	Parents	Male \times Female	$\begin{array}{ll} \mathrm{AI} & \times \ \mathrm{B13}{\cdot}2 \\ \mathrm{B13}{\cdot}2 & \times \ \mathrm{AI} \end{array}$	$\begin{array}{lll} {\rm A4} & \times \ {\rm B13}{\cdot}2 \\ {\rm B13}{\cdot}2 & \times \ {\rm A4} \end{array}$	$egin{array}{cccc} { m A6} & imes { m B13}{ m \cdot}2 \ { m B13}{ m \cdot}2 & { m A6} \ { m B13}{ m \cdot}2 \end{array}$	$\begin{array}{lll} \mathbf{A9} & \times \ \mathbf{B13\cdot 2} \\ \mathbf{B13\cdot 2} \times \mathbf{A9} \end{array}$	$\begin{array}{lll} \mathbf{A15} & \times \mathbf{B13\cdot 2} \\ \mathbf{B13\cdot 2} & \times \mathbf{A15} \end{array}$	$\begin{array}{ll} A18 & \times B13 \cdot 2 \\ B13 \cdot 2 & \times A18 \end{array}$	$B13 \cdot 2 \times B13 \cdot 2$
M	$\mathbf{Progeny}$	Female	5 · 08 5 · 06	$5.32 \\ 4.96$	5 · 26 5 · 30	$6 \cdot 02$ $5 \cdot 72$	4.86 5.00	5 · 38 5 · 02	5.72
		Male	4 • 48 4 • 48	4 • 56 4 • 38	4 • 45 4 • 18	5 · 06 5 · 04	$4 \cdot 18$ $4 \cdot 62$	$4 \cdot 50$ $4 \cdot 28$	4.73
	Parents	$\mathrm{Male} \times \mathrm{Female}$	$\begin{array}{ll} \mathrm{A1} & \times \ \mathrm{B2}{\cdot}2 \\ \mathrm{B2}{\cdot}2 & \times \ \mathrm{A1} \end{array}$	$egin{array}{ccc} { m A4} & imes { m B2}{ m \cdot}2 \ { m B2}{ m \cdot}2 \ { m A4} \ { m B2}{ m \cdot}2 \ { m A4} \end{array}$	$egin{array}{ccc} { m A6} & imes { m B2}{ m \cdot}2 \\ { m B2}{ m \cdot}2 & imes { m A6} \end{array}$	$egin{array}{ccc} { m A9} & imes { m B2\cdot2} \ { m X9} { m B2\cdot2} & imes { m A9} { m B2\cdot2} \end{array}$	$\begin{array}{lll} \mathrm{A15} & \times \ \mathrm{B2}{\cdot}2 \\ \mathrm{B2}{\cdot}2 & \times \ \mathrm{A15} \end{array}$	$\begin{array}{lll} A18 & \times B2 \cdot 2 \\ B2 \cdot 2 & \times A18 \end{array}$	$B2 \cdot 2 \times B2 \cdot 2$

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	Pro£	geny	Parents	Ρroξ	geny	Parents	Prog	eny
Ma	le	Female	$Male \times Female$	Male	Female	Male \times Female	Male	Female
4 4	48	5 · 57 5 · 37	$\begin{array}{c} AI \\ BII\cdot 2 \times AI \\ \end{array}$	$4 \cdot 31$ $4 \cdot 23$	4 · 48 4 · 94	$B11 \cdot 3 imes A1$	$4 \cdot 20$	$4 \cdot 53$
4 4	57 43	5 · 08 5 · 30	$\begin{array}{l} {\rm A4} \qquad \times {\rm B11}{\cdot 2} \\ {\rm B11}{\cdot 2} \times {\rm A4} \end{array}$	$\begin{array}{c} 4\cdot 20\\ 4\cdot 36\end{array}$	$\frac{4\cdot 72}{5\cdot 05}$	$ m B11\cdot3 imes A4$	$4 \cdot 23$	$4 \cdot 50$
44	24 13	5 · 44 5 · 13	$\begin{array}{ll} \mathrm{A6} & \times \mathrm{B11}{\cdot}2 \\ \mathrm{B11}{\cdot}2 \times \mathrm{A6} \end{array}$	$4 \cdot 13$ $4 \cdot 20$	$4 \cdot 72$ $4 \cdot 77$	$B11 \cdot 3 imes A6$	$4 \cdot 00$	4.60
44	84 55	$5 \cdot 37$ $5 \cdot 41$	$\begin{array}{ll} A9 & \times B11 \cdot 2 \\ B11 \cdot 2 \times A9 \end{array}$	$\begin{array}{c} 4\cdot 40\\ 4\cdot 65\end{array}$	$\frac{4\cdot 94}{5\cdot 43}$	$B11 \cdot 3 imes A9$	$4 \cdot 23$	$5 \cdot 20$
44	83 63	$5 \cdot 10$ $5 \cdot 38$	$\begin{array}{ll} A15 & \times B11\cdot 2 \\ B11\cdot 2 & \times A15 \end{array}$	$\begin{array}{c} 4\cdot 69\\ 4\cdot 33\end{array}$	$4 \cdot 82$ $4 \cdot 43$	$B11 \cdot 3 imes A15$	$4 \cdot 20$	$4 \cdot 70$

TABLE 4 (Continued)

 $4 \cdot 40$ $4 \cdot 26$

 $4 \cdot 23$ $4 \cdot 06$

 $\begin{array}{l} A18 \hspace{0.2cm} \times \hspace{0.2cm} B11 {\cdot} 2 \\ B11 {\cdot} 2 \hspace{0.2cm} \times \hspace{0.2cm} A18 \end{array}$

 $\begin{array}{ll} A18 & \times & B11 \cdot 1 \\ B11 \cdot 1 & \times & A18 \end{array}$

 $\rm B11\cdot3\times B11\cdot3$ $\rm B11\cdot3\times A15$

 $5 \cdot 52$

 $4 \cdot 37$

 $B11 \cdot 2 \times B11 \cdot 2$

 $7 \cdot 19$

 $5 \cdot 94$

 $B11 \cdot 1 \times B11 \cdot 1$

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MEAN SCUTELLAR NUMBERS OF THE CROSSES OF EACH SELECTION LINE TO THE A SET OF LINES

 R_1 is the mean over the crosses where the A lines were the male parents. R_2 is the mean over the reciprocal crosses. M is the mean over all crosses. The means over reciprocals for crosses with an A9 line are shown as "A9 cross". The "A9 component" is the difference of "A9 cross" from the mean over all crosses

			A	lales					Fei	males		
Line Tested	T inc	Means	over Test (Crosses	9 Q	40	Tino	Means	over Test (Crosses	40	0 V
	Mean	R_1	R_2	W	Cross	Component	Mean	R_1	R_2	М	Cross	Component
A9	7.43	$6 \cdot 29$	$6\cdot 22$	$6\cdot 25$	7.43	1.18	6.71	5.57	5.58	5 · 57	$6 \cdot 71$	1 · 14
A18	7.08	5.87	$5 \cdot 87$	5.87	$6 \cdot 94$	$1 \cdot 07$	$6 \cdot 15$	$5 \cdot 29$	5.32	$5 \cdot 30$	$00 \cdot 9$	0.70
Al	6.81	6.08	$6 \cdot 15$	$6 \cdot 11$	$7 \cdot 23$	$1 \cdot 12$	$6 \cdot 00$	5.52	5.38	5.45	$6 \cdot 38$	0.93
A15	$5 \cdot 57$	4.94	$4 \cdot 91$	$4 \cdot 92$	$4 \cdot 84$	-0.08	$4 \cdot 90$	4.51	$4 \cdot 30$	$4 \cdot 40$	$4 \cdot 37$	-0.03
A4	$5 \cdot 43$	5.42	5.46	5.44	$6 \cdot 04$	0.60	4.91	4.88	5.08	4.98	$5 \cdot 69$	0.71
A6	$4 \cdot 94$	4.75	$4 \cdot 74$	4.74	$5 \cdot 06$	0.32	$4 \cdot 33$	$4 \cdot 23$	$4 \cdot 25$	$4 \cdot 24$	$4 \cdot 28$	$0 \cdot 04$
$B2 \cdot 2$	5.72	5.32	$5 \cdot 17$	$5 \cdot 24$	$5 \cdot 87$	0.63	$4 \cdot 73$	$4 \cdot 49$	$4 \cdot 53$	$4 \cdot 51$	$5 \cdot 05$	$0 \cdot 54$
$B13 \cdot 2$	$4 \cdot 50$	4.70	$4 \cdot 72$	4.71	$5 \cdot 13$	0.42	$4 \cdot 03$	$4 \cdot 27$	$4 \cdot 13$	$4 \cdot 20$	$4 \cdot 43$	0.23
$B7 \cdot 3$	$6 \cdot 70$	5.30	$5 \cdot 10$	$5 \cdot 20$	$5 \cdot 76$	0.56	$5 \cdot 62$	$4 \cdot 52$	$4 \cdot 48$	$4 \cdot 50$	$4 \cdot 78$	0.28
$B6 \cdot 2$	4.33	$4 \cdot 61$	$4 \cdot 60$	$4 \cdot 60$	$4 \cdot 93$	0.33	4.16	$4 \cdot 31$	$4 \cdot 18$	$4 \cdot 24$	$4 \cdot 54$	$0 \cdot 30$
BII·I	$7 \cdot 19$	$5 \cdot 27$	$5 \cdot 25$	$5 \cdot 26$	$5 \cdot 39$	$0 \cdot 13$	5.94	4.45	$4 \cdot 58$	4.51	4.69	$0 \cdot 18$
$B11 \cdot 2$	5.52	4.69	$4 \cdot 92$	$4 \cdot 80$	$5 \cdot 18$	0.38	4.37	$4 \cdot 35$	$4 \cdot 30$	$4 \cdot 32$	$4 \cdot 52$	0.20
B11.3	$4 \cdot 26$		4.65	4.65	$5 \cdot 20$	0.55	4.06		$4 \cdot 18$	$4 \cdot 18$	$4 \cdot 23$	0.05

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Each of the seven B lines was crossed to all six of the A set of lines. The mean scutellar numbers of these crosses are given in Table 4. The average values over reciprocal crosses are plotted against the mid-parent expectation in Figure 2. There is a general agreement with the results found in the A set of crosses. The results are plotted separately for each of the B lines in Figure 3.

A major point of difference between the A and B sets is in the behaviour of crosses involving the third-level lines. Lines $B7 \cdot 3$ and $B11 \cdot 1$ showed a major response to selection which is analogous to that of the third-level lines of the A set. However, crosses of $B7 \cdot 3$ and $B11 \cdot 1$ with the third-level A lines show a marked regression to values characteristic of second-level lines. It would appear that the advance to the third level can involve different genetic systems: one which is essentially additive in crosses between third-level lines, and another which is markedly non-additive in crosses between third-level lines.



Fig. 3.—Mean scutellar number of the F_1 's from crosses between the B set of lines and the A set of lines are shown separately for each of the B lines. The F_1 values are plotted against the midparent expectation. \bigcirc Males. \spadesuit Females.

The results from both the A and B sets of crosses can be considered as a set of test crosses of the selection lines to a group of test stocks. The results are given in Table 5 on this basis, with the mean scutellar number of each selection line shown with the average over all of its crosses with the A set of lines. The results are averaged separately for the reciprocal sets. The agreement between the reciprocals is extremely close, allowing considerable weight to be given to the average over reciprocals. There is a positive correlation between the value of the selection line, and the average of its crosses with the test lines. This could simply be expressed by fitting a regression line, assuming homogeneity of the data, but this would obscure the very real heterogeneity, which is apparent in Figure 4 in which the average over all crosses is plotted against the mid-parent expectation. Lines A1, A4, A9, and A18 form one group, with lines A6, A15, B6 $\cdot 2$, B7 $\cdot 3$, B13 $\cdot 2$, and the B11 set forming another group. Line B2 $\cdot 2$ is an uncertain quantity which may belong to either group if the female progeny are considered. There is no doubt considering the male progeny— $B2 \cdot 2$ is homogeneous with the second group. This separation into two groups is the same as that found in the consideration of the individual crosses, and the separation of the selection lines

	ence		-0.25		-0.06	-0.16		+0.02
	Diffe	$\begin{array}{c} -0.44 \\ -0.13 \\ -0.15 \\ -0.15 \\ -0.32 \\ -0.20 \end{array}$		$\begin{array}{c} + 0 \cdot 07 \\ - 0 \cdot 17 \\ - 0 \cdot 07 \\ + 0 \cdot 14 \\ - 0 \cdot 16 \\ - 0 \cdot 18 \end{array}$			$+ 0 \cdot 04$ 0	
	Male Progeny	$5 \cdot 86$ $4 \cdot 31$ $5 \cdot 77$ $4 \cdot 45$ $5 \cdot 22$	$5 \cdot 12$	$\begin{array}{c} 4 \cdot 16 \\ 4 \cdot 53 \\ 4 \cdot 23 \\ 4 \cdot 43 \\ 4 \cdot 36 \\ 4 \cdot 56 \end{array}$	$4 \cdot 38$	4.75	$4 \cdot 03$ $4 \cdot 00$	$4 \cdot 01$
	\times Male	× × × × × A4 × × × × × × × × × A4 A4		$\begin{array}{c} \times & A4 \\ A4 \\ \times & \times & A4 \\ \times & \times & A4 \\ \times & A4 \\ A4 \\ A4 \\ A4 \\ \end{array}$			$\begin{array}{c} \times \ \mathbf{A4} \\ \times \ \mathbf{A4} \\ \times \ \mathbf{A4} \end{array}$	
	Female	A1 A6 A9 A15 A18		$\begin{array}{c} B13\cdot 2\\ B7\cdot 3\\ B6\cdot 2\\ B11\cdot 1\\ B111\cdot 2\\ B11\cdot 2\\ B11\cdot 2\\ B2\cdot 2\end{array}$			70 73	
	Male Progeny	$5 \cdot 42$ $4 \cdot 18$ $5 \cdot 62$ $5 \cdot 02$ $5 \cdot 02$	4.87	$\begin{array}{c} 4 \cdot 23 \\ 4 \cdot 36 \\ 4 \cdot 16 \\ 4 \cdot 57 \\ 4 \cdot 57 \\ 4 \cdot 20 \\ 4 \cdot 28 \end{array}$	$4 \cdot 32$	$4 \cdot 59$	$4 \cdot 07$ $4 \cdot 00$	$4 \cdot 03$
	ightarrow Male	$\begin{array}{c} \times & \times & \\ \times & \times & \times & \\ \times & \times & \times & \\ \times & & & \\ \end{array}$		$\begin{array}{c c} \times & B13\cdot 2\\ \times & B7\cdot 3\\ \times & B6\cdot 2\\ \times & B6\cdot 2\\ \times & B11\cdot 1\\ \times & B11\cdot 2\\ \times & B2\cdot 2\end{array}$			× 70 × 73	
and 73	Female	A4 A4 A4 A4 A4		A4 A4 A4 A4 A4 A4			$\mathbf{A4}$ $\mathbf{A4}$	
- 02	ence		+0.25		+0.31	+0.29		+0.11
	Differ	+0.22 + 0.32 + 0.24 + 0.24 + 0.24 + 0.23		$\begin{array}{c} + \ 0 \cdot 30 \\ + \ 0 \cdot 23 \\ + \ 0 \cdot 33 \\ + \ 0 \cdot 33 \\ + \ 0 \cdot 36 \\ + \ 0 \cdot 44 \end{array}$			$+ 0 \cdot 10 + 0 \cdot 13$	
	Male Progeny	$\begin{array}{c} 4 \cdot 12 \\ 4 \cdot 13 \\ 4 \cdot 13 \\ 4 \cdot 25 \\ 4 \cdot 28 \end{array}$	4.18	$\begin{array}{c} 4 \cdot 06 \\ 4 \cdot 33 \\ 4 \cdot 10 \\ 4 \cdot 63 \\ 4 \cdot 63 \\ 4 \cdot 33 \\ 4 \cdot 18 \end{array}$	$4 \cdot 27$	4 · 22	$4 \cdot 05$ $4 \cdot 00$	
	e × Male	$\begin{array}{c} \times & \mathrm{A15} \\ \times & \mathrm{A15} \end{array}$		$\begin{array}{c} \times & \mathrm{A15} \\ \times & \mathrm{A15} \end{array}$			$\begin{array}{c} \times \ A15 \\ \times \ A15 \\ \times \ A15 \end{array}$	
	Female	A1 A4 A6 A9 A18		$\begin{array}{c} B13\cdot 2\\ B13\cdot 3\\ B7\cdot 3\\ B6\cdot 2\\ B11\cdot 1\\ B11\cdot 1\\ B11\cdot 2\\ B11\cdot 2\\ B11\cdot 2\\ B2\cdot 2\end{array}$			70 73	
	Male Progeny	4.34 4.45 4.37 4.37 4.49 4.51	$4 \cdot 43$	4 · 56 4 · 56 4 · 43 4 · 43 4 · 63 4 · 62	$4 \cdot 58$	4.51	$4 \cdot 15$ $4 \cdot 13$	
	Female imes Male	$\begin{array}{c} \mathrm{A15} \times \mathrm{A1} \\ \mathrm{A15} \times \mathrm{A4} \\ \mathrm{A15} \times \mathrm{A4} \\ \mathrm{A15} \times \mathrm{A6} \\ \mathrm{A15} \times \mathrm{A9} \\ \mathrm{A15} \times \mathrm{A18} \\ \mathrm{A15} \times \mathrm{A18} \end{array}$	ũ	$\begin{array}{llllllllllllllllllllllllllllllllllll$	<i>s</i> i	Mean of means	$\begin{array}{rrrr} \mathrm{A15} & \times & 70 \\ \mathrm{A15} & \times & 73 \end{array}$	

TABLE 6

MEAN SCUTELLAR NUMBERS OF MALE PROGENY IN RECIPROCAL CROSSES OF LINES A15 AND A4 WITH THE A AND B SETS OF SELECTION LINES AND LINES

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into two groups on the basis of their behaviour in crosses appears to be a valid generalization, which could be a useful focus for further work. Some observations by Erway (personal communication) are pertinent. He observed that the third-level lines of the A set had increased frequencies of extra bristles at other than the scutellar positions. He did not find an analogous correlated response in any of the second-level lines which he examined except line A4. There is clearly a correlation between the separation of the A lines into two groups on the basis of their behaviour in crosses, and on the basis of the correlated response in other bristles than scutellars.



Fig. 4.—Mean values of the crosses of each line with the A set of lines (M, see Table 5) are shown plotted against the average mid-parent expectation. The differences between lines A1, A4, A9, A18, and the rest of the lines are emphasized by showing the results for the former as open circles, and the latter as closed circles.

The existence of sex-linked components of the selection advance were indicated by the differences between male progeny of reciprocal crosses involving lines A4 and A15. This possibility can be further examined for the B set of crosses. The results are shown in Table 6. There is a resaonable agreement between the A and B sets for the A15 component, but there is a marked discrepancy for the A4 component. This difference could be due to the A4 component only being exhibited in the A set of crosses or the differences in the A set could be fortuitous. The A15 sex-linked component is not large—approximately 0.3 bristle, but it is interesting in its being relatively insensitive to the background genotype. This can be seen from Figure 5 in which the differences between male progeny of reciprocal crosses involving line A15 are plotted against the average scutellar number of male progeny. There is no correlation but the range of levels is not very large, and it is possible that a significant correlation could be detected over a wider range of genetic backgrounds. Reciprocal crosses were made in replicate between A15 and two first-level lines (70 and 73). The results are given in Table 6. There is a difference between the male progeny which is consonant with an A15 sex-linked component of 0.11 bristle. This reduction of the effect of the sex-linked component could be a consequence of the threshold at four bristles (see Rendel 1959). It should be possible to isolate the A15 sex-linked component and then substitute this into a number of selection lines which would allow decision on the sensitivity of the effect of this component relative to the background genotype.

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The results of the crosses of each line to the A set of lines are shown in Figure 3. A feature of almost all of these sets of crosses is that the cross with the A9 line has a greater value than the mean over the set of crosses. The means over each set of crosses are given in Table 5 with the values for the crosses with the A9 line. The A9 mean exceeds the mean over the set of crosses in all but the test of A15. This A9 component has a mean value of 0.49 bristle over all selection lines. There is a marked difference of effect of the A9 component between the third-level lines of the A set (lines 1, 9, and 18) and the other selection lines. This difference may be due to a real heterogeneity, or it may represent an extreme value in the correlation of the effect of the A9 component with the background genotype (see Fig. 5). Crosses of



Fig. 5.—(a) Mean values of the crosses of each lines (M, see Table 5) are shown plotted against the deviation of the cross with A9 from M. This latter is termed the "A9 component". (b) Difference between male progeny of reciprocal crosses involving line A15 is shown plotted against the mean scutellar number over the reciprocal crosses. The former is termed the "A15 component". • Males. \bigcirc Females.

the A set with the first-level lines (70, 71, and 73) are inconsistent with regard to the A9 component. This has a value of 0.38 for the crosses with line 70, 0.05 for line 71, and -0.01 for line 73. These values have been included in Figure 5. They emphasize the probability that the effect of the A9 component is correlated with the background genotype. The results for the B11.1 and A15 lines do not fit such a hypothesis. An analogy can be drawn with the modification of the effect of the *Bare* gene in *D. simulans* by the level of selection for missing scutellars (Fraser 1963). Modification of the background genotype changes an isoallelic into an oligogenic difference. The detailed analysis of these lines has resulted in the identification of two components of the selection advance: the A15 component which is insensitive to the effects of the background genotype, and the A9 component which is very sensitive to the background genotype.

IV. CONCLUSION

Three main hypotheses have been presented to explain the patterns of response to selection for extrascutellars in *Drosophila*. Mather (1941, 1943) and Sismanidis (1942) proposed a model of recombination in relationally balanced polygenes. They based their discussions on the relational balance involving repulsion linkages. Rendel (1959) proposed a model of developmental canalization in which the actions of a genetically simple scutellar genotype are conditioned by a non-linear relationship of the actions of this genotype to its effect on scutellar number. Reeve and Robertson (1953) suggested that the results from which Mather (1941) deduced the existence of relational balance could be explained by the modification of isoalleles into oligogenes. Fraser (1963) found that such a modification occurred in a selection line for missing scutellars in D. simulans.

Two further hypotheses have not been specifically applied to the problem of the genetic determination of scutellar number, but they are obviously pertinent. Clayton, Morris, and Robertson (1957) have suggested that heterogeneity of response to selection can be due to sampling deviations in a genetic system of many loci without need for introduction of complexities due to linkage, canalization, etc. Lerner (1954) proposed a similar hypothesis, with the addition of overdominance of developmental stability to explain the maintenance of a high degree of heterozygosity in unselected populations. A feature of Lerner's model of "genetical homeostasis" is that heterozygosity increases the developmental stability.

The results of our experiments (Fraser 1963; Fraser and Green 1964; Pennycuik and Fraser 1964; and Fraser *et al.* 1965) cannot be explained solely by any one of these hypotheses, and it is probable that a final explanation will require the incorporation of features of many, if not all, of these hypotheses.

The results which need to be explained are:

- (1) Directed selection can produce a response which exceeds any predictions which can be made from the variability of the initial population, i.e. a large fraction of the genetic variability is maintained in a phenotypically unexpressed form. The majority of our selection lines for extrascutellars were initiated from single fertilized females, and Mather (personal communication) has emphasized that this was an important feature of his experiments, arguing that it is difficult to explain the responses to selection which he found unless the potential variability is held in the form of relationally balanced polygenes, with repulsion linkages.
- (2) Responses to selection lead to a limited number of end points. This is particularly evident from the A set of selection lines. Fraser *et al.* (1965) have emphasized that this is not due to there being a limited number of genetic end points, but rather to the occurrence of a limited number of ranges of scutellar number with high fitness. The results of Kuhn and Scowcroft (personal communications) support this conclusion.
- (3) Selection in the presence of scute produces a correlated response in wild-type segregants (Rendel 1959) whereas selection in the presence of wild-type does not produce a correlated response in scute segregants (Fraser and Green 1964). The latter have suggested an explanation based on substitution at the scute locus controlling the activity of two multigenic systems: a "scute" system which is operative in the presence of the scute allele, and a "wild-type" system which is operative in the presence of the wild-type allele. Support of this hypothesis comes from the very different patterns of response

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to selection in *scute* and *wild-type*. Response to selection in *scute* is homogeneous over long time periods which contrasts with the heterogeneity of response to selection found in *wild-type*.

- (4) Selection on a restricted genetic base is more effective than selection on a wide genetic base. Nassar and Fraser (1965) have shown that selection for extrascutellars in stocks which are isogenic for all but chromosome III is more effective than selection in stocks where all chromosomes are variable. An explanation can be phrased in terms of compensative interactions between chromosomes masking the expression of intra-chromosome variability (see Fraser et al. 1965).
- (5) Crosses between selection lines show a complex pattern of interactions, which indicate the existence of at least two separate genetic systems determining the number of scutellar bristles. An extension of the *scute* model can explain many features of these results. Suppose substitution at a locus acts as a switch, determining which of two genetic systems is operative. This substitution would not be under selection, except in the presence of an advantageous combination of the genetic systems which it controls. In the presence of such a combination, this substitution would be oligogenic, whereas in its absence the substitution would be isoallelic. Selection could be expected to be initially ineffective for such a system, and the best way of achieving an initial advance would be to combine inbreeding with selection, over a large number of independent lines—this was the pattern used in the A and B sets of selection lines.

The analysis of variation of number of scutellar bristles has reached a stage where explicitly detailed hypotheses can be proposed and experiments of analogous detail designed to test the validity of these hypotheses. The phase of general exploration is effectively over—further work will be based on the identification of components of the selection advance, e.g. the A15 and A9 components, and on the description of patterns of development of scutellar bristles. Erway (personal communication) has shown that this approach will be of value. It has been discussed by Waddington (1957), and Fraser and Short (1960) have developed it in consideration of the genetic control of the structure of the fleece.

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