GENETIC HETEROGENEITY AMONG THE FOUNDERS OF LABORATORY POPULATIONS OF *DROSOPHILA MELANOGASTER*

III.* STERNOPLEURAL CHAETAE

By P. A. Parsons †

Summary

Single, inseminated females of *D. melanogaster* derived from the same population have led to discrete strains for sternopleural chaeta number, in agreement with earlier work on other traits. The discrete stains indicate that wild populations have genes which are polymorphic for sternopleural chaeta number. As well as showing characteristic mean chaeta numbers, there was some indication that the strains had characteristic levels of variability. No significant correlations were found between sternopleural and scutellar chaeta numbers.

I. INTRODUCTION

Parsons and Hosgood (1967) and Hosgood and Parsons (1967a) described experiments where a number of strains of *Drosophila melanogaster* derived from single inseminated females, collected from the same population in the wild, led to genetically discrete strains for three quantitative traits, namely scutellar chaeta number, percentage of pairs mated in 60 min, and duration of copulation. The differences between strains were genetic arising from differences between the founder females, as was confirmed for some of the strains by diallel crosses between them. The genetic heterogeneity between the founder females derived from the same population implies that the population must be polymorphic for genes (or polygenes) determining these traits (Parsons, Hosgood, and Lee 1967). The polymorphism for additional scutellar chaetae has been exploited by Hosgood and Parsons (1967b), who found extremely rapid responses when directional selection for high chaeta number was based on those strains derived from single inseminated females which had a high scutellar chaeta number.

Parsons, Hosgood, and Lee (1967) and Lee and Parsons (1968) argued that polymorphism for polygenes would be ubiquitous for quantitative traits. In this paper we extend our observations to mean sternopleural chaeta number and its variability. Correlation with scutellar chaeta number will be considered in some of the data. It seemed important to extend our work to sternopleural chaeta number, since the results may be more applicable to the usual types of traits handled by quantitative geneticists than scutellar chaeta number which in many strains is rigidly canalized to four chaetae. No such rigid canalization is apparent for sternopleural chaeta number.

P. A. PARSONS

TABLE 1

MEAN STERNOPLEURAL CHAETA NUMBERS ($\bar{x}$), WITH STANDARD DEVIATIONS (s), AND COEFFICIENTS OF VARIATION ($s/\bar{x}$) FOR THE 18 STRAINS

Strains 1–3 were collected in December 1963, and strains 20–34 in December 1965

Strain	Females (count 1, $n = 50$)			Males (count 1, $n = 50$)			Females (count 2, $n = 30$)			Males (count 2, $n = 30$)		
	$\bar{x}$	s	$s/\bar{x}$	$\bar{x}$	s	$s/\bar{x}$	$\bar{x}$	s	$s/\bar{x}$	$\bar{x}$	s	$s/\bar{x}$
1	18·02	1·48	0·082	17·52	1·54	0·088	18·07	1·36	0·075	17·03	1·65	0·097
2	17·40	1·54	0·088	16·66	1·53	0·092	16·77	1·46	0·087	15·90	1·49	0·094
3	16·50	1·67	0·101	16·26	1·52	0·094	16·27	1·14	0·070	15·50	1·50	0·097
20	18·14	1·63	0·090	16·84	1·54	0·092	17·00	1·58	0·093	16·50	1·78	0·108
21	18·58	1·58	0·085	17·78	1·67	0·094	17·27	1·46	0·085	16·17	1·68	0·104
22	19·16	1·83	0·096	18·70	1·90	0·101	18·60	1·98	0·106	18·67	2·17	0·116
23	21·46	2·45	0·114	18·70	1·63	0·087	20·07	2·24	0·112	18·87	2·16	0·115
24	18·36	2·05	0·112	16·82	2·14	0·127	18·50	1·55	0·084	17·37	2·13	0·122
25	20·12	1·79	0·089	19·20	1·51	0·079	19·10	1·30	0·068	18·20	1·30	0·071
26	19·74	2·15	0·109	18·72	1·86	0·100	19·57	2·15	0·110	19·00	2·38	0·125
27	21·30	2·89	0·136	20·82	1·75	0·084	21·67	2·81	0·130	21·43	2·73	0·127
28	17·32	1·63	0·094	16·34	1·44	0·088	17·07	1·26	0·074	15·77	1·25	0·079
29	19·24	1·53	0·080	18·04	2·04	0·113	19·80	1·99	0·101	18·80	1·61	0·085
30	19·48	1·73	0·089	17·74	2·01	0·113	19·27	1·41	0·073	17·43	1·96	0·112
31	20·10	1·95	0·097	18·68	1·87	0·100	19·27	2·13	0·111	18·70	2·00	0·107
32	19·46	1·93	0·099	18·74	1·47	0·078	18·57	2·24	0·121	18·20	1·81	0·099
33	18·66	1·86	0·100	17·56	2·24	0·128	18·10	1·88	0·104	17·73	2·41	0·136
34	20·68	2·26	0·109	19·98	1·94	0·097	18·17	1·34	0·074	18·20	1·83	0·100

Analysis of Variance of Chaeta Number

Source of Variation	Degrees of Freedom	Mean Square	F	P
Counts	1	137·59	40·17	$< 0·001$
Sexes	1	623·47	182·03	$< 0·001$
Strains	17	262·35	76·59	$< 0·001$
Interactions:				
Counts $\times$ sexes	1	12·94	3·78	
Counts $\times$ strains	17	16·86	4·92	$< 0·05$
Sexes $\times$ strains	17	9·47	2·77	
Counts $\times$ sexes $\times$ strains	17	2·88	0·84	
Error	2808	3·43		

Analysis of Variance of the Coefficients of Variation

Source of Variation	Degrees of Freedom	Mean Square	F	P
Strains	17	0·000542	4·92	$< 0·01$
Sexes	1	0·000561	5·05	$< 0·05$
Counts	1	0·000031	0·28	
Interactions:				
Strains $\times$ sexes	17	0·000247	2·22	
Strains $\times$ counts	17	0·000164	1·46	
Sexes $\times$ counts	1	0·000741	6·68	$< 0·05$
Error	17	0·000111		

II. Method

Eighteen *D. melanogaster* strains were derived from single, inseminated females collected (3 in December 1963, and 15 in December 1965) at Leslie Manor near Camperdown, Vic., and set up in half-pint bottles at 25°C; the strains were transferred every 3 weeks to set up the next generation. Scoring was carried out in April 1967 (count 1) and four generations later in July 1967 (count 2), in order to see whether there was stability between generations. In count 1, 50 flies per sex were scored for both sternopleural and scutellar chaetae, and in count 2, 30 flies per sex were scored for sternopleural chaetae only. In order to minimize environmental variables, eggs were collected and newly hatched larvae were placed in vials at a density of 50 per vial in the generation before scoring, since it is known that larval density affects fly size and also sternopleural chaeta number (Parsons 1961).

III. Results

(a) Mean Sternopleural Chaeta Numbers

Mean sternopleural chaeta numbers are given in Table 1, with corresponding standard deviations and coefficients of variation, and an analysis of variance of the chaeta numbers showing significant main effects due to counts, sexes, and strains. The counts effect presumably reflects some overall environmental effect, since in general the means for the first count were slightly higher than the second. The most likely reason would be because count 1 was done in entirety by the author, and count 2 by a research assistant. The significant sexes effect reflects the usual observation of more sternopleural chaetae in females than in males. The strains effect is of most interest in the present context, and shows that there are significant differences between the 18 strains under consideration as found for the various traits cited in the introduction, and that this is maintained over the four generations between the two counts, since the interaction terms are negligible as compared with the main effects. This was confirmed by computing correlation coefficients between the 18 female and 18 male means for the two counts, which came to $0 \cdot 8526$ and $0 \cdot 8766$ for females and males respectively and are both significantly > 0 ($P < 0 \cdot 001$).

(b) Correlations with Scutellar Chaeta Numbers

In count 1, scutellar chaetae were also scored (Table 2) by recording the number of flies with more than four chaetae (additional chaetae) in each strain. The object was to see what, if any, correlation between sternopleural and scutellar chaeta numbers occurred. The reason for doing this was because Rendel (1963) found a positive correlation between the number of scutellar and abdominal chaetae in *scute* (*sc/sc*) males, but in *sc*+ and ++ males the correlations were negative. On selection the correlation became positive, perhaps because the total resources for making chaetae were increased. Such negative correlations as were observed can probably be explained by assuming that the proportion of total resources going to the two kinds of chaetae is varied. Since in this paper 18 strains which vary somewhat amongst themselves are under analysis, both for scutellar (Parsons and Hosgood 1967) and sternopleural chaeta numbers, it seemed reasonable to see if information could be obtained on the simultaneous distribution of the two chaetae types. After applying the angular transformation to the scutellar chaeta data, correlation coefficients between the mean sternopleural chaeta number and incidence of additional scutellar chaetae

came to −0·1707 in females and +0·1929 in males. Neither of the correlation coefficients differ significantly from 1, and thus the data, so far as they go, do not indicate any strong association of the two types of chaetae. If the same polygenes were affecting both traits in a similar way, then an association would have been expected. These results thus seem to indicate the likelihood that to some extent different genes affect the two traits in wild populations. Further information on this point will be collected during the continuation of a selection experiment previously reported (Hosgood and Parsons 1967b).

TABLE 2

NUMBERS OF FLIES OUT OF 50 WITH ADDITIONAL SCUTELLAR CHAETAE IN COUNT 1

Strain	Females	Males	Strain	Females	Males
1	1	0	26	3	1
2	13	9	27	4	1
3	0	0	28	2	0
20	1	0	29	1	0
21	0	0	30	0	0
22	0	0	31	0	1
23	0	0	32	0	0
24	4	1	33	0	0
25	5	5	34	0	2

(c) *Variability of Sternopleural Chaetae*

It has been shown that the mean sternopleural chaeta numbers differ between strains; thus, to compare variability between strains, it was thought best to base arguments on coefficients of variation $s/\bar{x}$ (Table 1), where the mean is $\bar{x}$ and the standard deviation is s. The use of coefficients of variation is an attempt to avoid a bias due to correlations between s and $\bar{x}$. An analysis of variance of the coefficients of variation was carried out (Table 1), and showed a significant strains effect ($P < 0.01$), so indicating that the strains, at least for the four-generation period under study, do show a characteristic level of variability, i.e. there are some strains having consistently high and others having consistently low levels of variability.

The significant sexes effect occurs because the males in general show slightly more variability than females, and the sexes × counts interaction is a little difficult to interpret. Even so, the most highly significant effect in the data is the strains effect.

The strains effect also clearly emerges from the correlation coefficients between the 18 strains. The correlation coefficient for females came to 0·5065 and for males to 0·4942, both of which are significantly >0 ($P < 0.05$), but are less than the correlation coefficients quoted earlier between means as might be expected.

IV. DISCUSSION

The significant variation between strains for mean sternopleural chaeta number is in agreement with the work cited in the Introduction, for scutellar chaeta number and the mating behaviour traits. Many selection experiments have been

carried out in the past for chaeta number traits, often with extreme variability of response, even when selection is carried out on the same trait using identical breeding procedures. The polymorphic nature of populations for polygenes (see Introduction) perhaps helps to explain this, since the founder females in selection lines may differ genetically. It is apparent from the literature that the base population is often very small, both in directional selection and in disruptive selection experiments (see Parsons, Hosgood, and Lee 1967 for references). Some of these experiments were begun from strains derived from single inseminated females, where the founder effect would be expected to be most important. Hosgood and Parsons (1967*b*) carried out directional selection experiments for scutellar chaeta number based on those strains having a high incidence of flies with additional chaetae. Thus, basing selection on a hybrid of the four strains showing the highest incidence of flies with additional chaetae out of 16 strains led to a dramatic response to selection to a mean of 10·6 chaetae in 12 generations in one line (Hosgood, MacBean, and Parsons unpublished data), which represents a continuous accelerated response to selection, and is far more rapid than has previously been reported in the literature for this trait. Since accelerated responses to selection represent the steepest part of a selection response curve, a continuous accelerated response represents the most rapid possible response. Another line based on the same hybrid of the four strains, and two lines based on the strain having the highest incidence of flies with additional chaetae, all led to very rapid responses, compared with a hybrid of all 16 strains. Thus selection among the 16 strains clearly has led to the choosing of desirable genes from the point of view of the selection objective. Suggestive evidence shows that the exploitation of variability between such strains may be effective for selection for duration of copulation (MacBean, unpublished data). In conclusion, therefore, it may be predicted that exploiting variability for sternopleural chaeta number between strains set up from single inseminated females may lead to more rapid responses to selection than have usually been observed.

The lack of correlation between sternopleural and scutellar chaeta number is perhaps surprising, and shows that at the natural population level the genes for the two traits may be relatively independent. The results given may not, however, be particularly sensitive, because in a number of strains all flies had four scutellar chaetae as would be expected, since this trait is often highly canalized to four chaetae, perhaps with different underlying genetic architectures in different strains. Even so, if there were a strong tendency for the genetic architectures of the two traits to be similar, some correlation might have been expected. It seems difficult to say much more without locating the genes controlling the two traits, as has been done for sternopleural chaeta number by Thoday (1961) and his colleagues. A start has been made by Miller, Erway, and Fraser (1966) for scutellar chaeta number. Such a study would enable a much more definite answer to be given as to the degree of pleiotropy or independent gene action controlling the traits, and would be of considerable importance in applied fields where the question of the simultaneous selection for two traits often arises.

Finally, we turn to the variability data, which show that some strains have high and others low variability. The interpretation of this result follows fairly directly from the interpretation of the differences between means as being due to each strain

receiving initially different genes by chance. In the high-variability strains, perhaps there are genes of larger effect segregating than in the low-variability strains. The low-variability strains may be relatively homozygous or some segregating genes may be at a low frequency. Probably all of these points are relevant. If variability data are available as well as data on means, it may be worth taking both into account when selecting the strains to be used to commence a selection experiment, since a high-variability strain may have genes segregating that could be rapidly altered in frequency by selection. However, it may well be that there may not be adequate data, since far fewer flies need to be counted to obtain an assessment of means compared with variances. In this respect the scutellar chaeta system is rather different, since usually the highly variable strain will be divergent from four chaetae, so that variability can usually be assessed by the mean. This is because of the frequent high levels of canalization to four chaetae.

V. Acknowledgments

VI. References

Hosgood, S. M. W., and Parsons, P. A. (1967a).—Genetic heterogeneity among the founders of laboratory populations of *Drosophila melanogaster*. II. Mating behaviour. *Aust. J. biol. Sci.* **20**, 1193–203.

Hosgood, S. M. W., and Parsons, P. A. (1967b).—The exploitation of genetic heterogeneity among the founders of laboratory populations of *Drosophila* prior to directional selection. *Experientia* **23**, 1066–7.

Lee, B. T. O., and Parsons, P. A. (1968).—Selection, prediction and response. *Biol. Revs* (In press.)

Miller, D., Erway, L., and Fraser, A. (1966).—Switch genes and polygenic systems determining number of scutellar bristles. [Abstr.] *Genetics, Princeton* **54**, 348.

Parsons, P. A. (1961).—Fly size, emergence time and sternopleural chaeta number in *Drosophila*. *Heredity* **16**, 455–73.

Parsons, P. A., and Hosgood, S. M. W. (1967).—Genetic heterogeneity among the founders of laboratory populations of *Drosophila melanogaster*. I. Scutellar chaetae. *Genetica* **38**, in press.

Parsons, P. A., Hosgood, S. M. W., and Lee, B. T. O. (1967).—Polygenes and polymorphism. *Mol. Gen. Genet.* **99**, 165–70.

Rendel, J. M. (1963).—Correlation between the number of scutellar and abdominal bristles in *Drosophila melanogaster*. *Genetics, Princeton* **48**, 391–408.

Thoday, J. M. (1961).—The location of polygenes. *Nature, Lond.* **191**, 368–70.