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Genetic Heterogeneity among the Founders of Laboratory Populations of *Drosophila melanogaster*

V. Sternopleural and Abdominal Chaetae in the Same Strains

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Summary. 1. Single inseminated females of *Drosophila melanogaster* derived from the same population led to discrete strains for both sternopleural and abdominal chaeta number in agreement with other work, which indicates that the wild populations have genes polymorphic for these traits. Variability varied significantly between strains for sternopleural but not abdominal chaeta number.

2. Overall, the data show a weak correlation between the two traits. Considering this by strain, the correlations go from negative (but not significantly < 0) to positive (but significantly > 0). Therefore just as the rate of response to directional selection has been shown to be extremely rapid when based on strains extreme in the direction of the required selection response, it seems that a similar process may be useful for directional selection based on two traits simultaneously, by using only those strains showing a positive correlation.

Introduction

In a recent series of papers (Parsons and Hosgood, 1967; Hosgood and Parsons, 1967a, 1968; Parsons, MacBean and Lee, 1969, and Parsons, 1968, 1970) experiments have been described which show that strains set up from single inseminated females differ genetically for a number of quantitative traits. These are morphological (sternopleural and scutellar chaeta number), behavioural (mating speed and duration of copulation) and physiological (resistance to high temperatures, dessication, and irradiation with Co^{60}-γ rays). Often where tested, the differences between extreme strains are mainly additive, as is indicated by diallel crosses between extreme strains for scutellar chaeta number and radioresistance. This means that at least some of the traits are likely to be amenable to detailed genetic analysis, in order to look at their genetic architecture. The two behavioural traits tested pose difficulties, since they involve an interaction between the two sexes, but a fair degree of additivity is often found (Hosgood and Parsons, 1967a). The differences between strains are often large, which suggests genes of fairly large effect, rather than many polygenes of small effect. Unpublished work of ours confirms this for radioresistance and scutellar chaeta number, as does published work of Fraser et al. (1965) and Miller, Erway and Fraser (1966) for scutellar chaeta number and Thoday, Gibson and Spickett (1963, 1964) for sternopleural chaeta number.

Assuming genes of fairly large effect differentiating the strains, one implication is that it should be possible to obtain extremely rapid responses to directional selection by basing selection on extreme strains. This has been demonstrated by Hosgood and Parsons 1967b and Hosgood, MacBean and Parsons (1968) for scutellar chaeta number where the 10 flies out of 100 with the highest chaeta number were selected in each generation. Thus taking the strain with the highest mean initially out of 16 strains, there was a 31% increase in mean scutellar chaeta number in females over the first 7 generations of directional selection, and for a hybrid population derived from the 4 strains with the highest mean initially there was a 46% increase, compared with an increase of 13% for a hybrid population made up from all 16 strains. This last situation would be more analogous to the heterogeneous population upon which directional selection is often based. The initial selection of favourable strains in this way may not of course mean that the ultimate total response to selection is greater than using a larger heterogeneous population, but the initial selection of favourable strains does lead to early and rapid responses to selection, which often may take many generations to occur when using large and heterogeneous populations. Another trait in *D. melanogaster* for which the exploitation of variability between strains set up from single inseminated females has been effective is duration of copulation (MacBean and Parsons, 1967), and an example can be cited in cotton (see Manning, 1956).

Some selection programs are based on the simultaneous selection of two or more traits, and the question arises as to whether variability between strains as described above can be exploited to obtain more rapid responses to selection than based on a large heterogeneous population. Selection based on two or more traits involves the setting up of selection indices which take into account correlations between traits, and clearly a positive correlation between two traits implies the likelihood that selection would be effective on both traits simultaneously, as compared with the situation where there is a negative correlation between two traits. In order to look into this, 18 strains set up from single inseminated females were assayed simultaneously for sternopleural chaeta number, and abdominal chaeta number on the fourth segment of the abdomen. It seemed reasonable to select traits for which some correlation is expected, thus selection for chaeta number in one region of a fly often leads of correlated responses to selection in other regions of flies, indicating that perhaps one of the effects of selection is to increase the total resources for making chaetae (Rendel, 1963; Hosgood, MacBean and Parsons, 1968). However, there is no doubt that to some extent the genetic control of chaeta number in different regions of flies is unique for each particular region.

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, Victoria, and set up in half-pint milk bottles at 25 °C. The strains were transferred every 3 weeks to set up the next generation. Fifty flies per sex were scored for sternopleural and abdominal chaeta number. In order to minimize environmental variables, eggs were collected and newly hatched larvae were placed in vials at a density of 25 per vial in the generation before scoring, since it is known that larval density affects fly size (Parsons, 1961).

Results

(*a*) *Means and coefficients of variation*

Means $\bar{x}$ are given in Table 1, with analyses of variance of chaeta numbers in Table 2a showing significant effects for sexes and strains for both sternopleural and abdominal chaeta number, and a small but significant interaction between sexes and strains for abdominal chaeta number. The significant sexes effect reflects the usual observation of more chaetae in females than males, but this is more pronounced for abdominal chaeta number, which is probably reasonable as the abdomen is the region where the main sex-differentiating traits occur. The significant strains effects are of most significance in the present context, and show that there are significant differences between the 18 strains under consideration as found for the various traits cited in the introduction (including sternopleural chaeta number).

Parsons (1968) found strains to differ in variability as measured by coefficients of variation $s/\bar{x}$ (where s = the standard deviation) for sternopleural chaeta number. Coefficients of variation were used in an attempt to avoid a bias due to correlations between s and $\bar{x}$. The interpretation of Parsons' (1968) results was that some strains show high and some low variability, perhaps because the high variability strains have genes of larger effect segregating than in the low-variability strains, or that the low-variability strains may be relatively homozygous, or any segregating genes may be at a low frequency in them.

An analysis of variance of the coefficients of variation was carried out and gave a significant strains effect for sternopleural chaeta number as found by Parsons (1968), but there was no such significant effect for abdominal chaeta number. It is difficult to interpret this, except to suggest that there may be fewer major genes controlling abdominal chaeta number than sternopleural chaeta number. The chaetae on the sternopleural plate may well make up a fairly complex system (Spickett, 1963) parts of

Table 1. *Mean sternopleural and abdominal chaeta numbers ($\bar{x}$) with coefficients of variation ($s/\bar{x}$) for the 18 strains*

Strain	Sternopleural chaeta number				Abdominal chaeta number			
	Females		Males		Females		Males	
	s	$s/\bar{x}$	s	$s/\bar{x}$	s	$s/\bar{x}$	s	$s/\bar{x}$
1	19.00	.1003	18.94	.1085	19.04	.0949	16.00	.0945
2	16.68	.0910	16.24	.1081	23.24	.0751	18.32	.0945
3	16.96	.0875	16.14	.0840	21.24	.0816	16.66	.0975
20	16.90	.1370	16.52	.1068	20.48	.1189	16.88	.0877
21	17.32	.1006	16.58	.1284	20.82	.0750	16.90	.0912
22	17.30	.1026	16.78	.1131	20.68	.0887	16.56	.0962
23	17.80	.0970	17.16	.1062	19.16	.0799	16.26	.1210
24	19.00	.1135	17.64	.1003	20.04	.0800	16.10	.0898
25	19.70	.0901	19.08	.1004	21.72	.0883	18.18	.0921
26	18.68	.0901	18.18	.1115	21.88	.0859	17.50	.0881
27	21.36	.1272	21.06	.1306	21.14	.0956	17.62	.0979
28	16.14	.0937	15.80	.0990	19.78	.0909	17.26	.0834
29	21.30	.1166	21.24	.1202	21.84	.0819	18.38	.0899
30	18.50	.1279	17.58	.1360	19.92	.0854	16.24	.0710
31	18.60	.1053	17.54	.1057	20.30	.0834	15.98	.1031
32	17.34	.0837	16.24	.0783	20.98	.0864	16.92	.0725
33	18.02	.0857	17.42	.0876	21.32	.0755	17.54	.0712
34	18.88	.0955	18.24	.0862	20.82	.0762	17.16	.0680

which may be controlled by different loci, since they can be divided into macrochaetae and microchaetae; a distinction which cannot be made for abdominal chaetae. Because of this complexity, there may be more genes of major effect involved, than for abdominal chaeta number.

Table 2a. *Analyses of variance of sternopleural and abdominal chaeta numbers*

Source of variation	Degrees of freedom	Sternopleural chaeta number Mean Square	Sternopleural chaeta number F	Abdominal chaeta number Mean Square	Abdominal chaeta number F
Sexes	1	171.13	46.30***	6410.89	2301.94***
Strains	17	226.90	61.39***	75.17	26.99***
Sexes × strains	17	3.00	0.81	8.86	3.18***
Error	1764	3.70		2.79	

*** $P < 0.001$

Table 2b. *Analyses of variance of the coefficients of variation for sternopleural and abdominal chaeta numbers*

Source of variation	Degrees of freedom	Sternopleural chaeta number Mean square	Sternopleural chaeta number F	Abdominal chaeta number Mean square	Abdominal chaeta number F
Sexes	1	0.000120	1.36	0.000121	0.92
Strains	17	0.000420	4.78**	0.000147	1.11
Error	17	0.000088		0.000132	

** $P < 0.01$

(b) *Correlations between sternopleural and abdominal chaeta number*

Table 3 gives the correlation coefficients for the 50 paired observations for each of the 18 strains, taking sexes separately. The coefficients for the total data for each sex are also given, which are positive and significant, although the degree of correlation is quite low. Even so, these last coefficients indicate that in a heterogeneous population (which would be simulated by pooling the data or all 18 strains), there is a low level of correlation between the number of chaetae at the two sites under consideration. This is also indicated from the correlation coefficients based on the means for the 18 strains in table 1, which are positive but not significant.

Looking now at the correlation coefficients for each of the 18 strains, there are more coefficients deviating significantly from 0 than would be expected by chance, and all of these are for $r > 0$, again confirming the low level of positive correlation as above. This can be seen naively in another way. For the 18 strains, there are 36 correlation coefficients of which 29 are positive and 7 negative, whereas on a hypothesis of no correlation between the two sites, 18:18 would be expected, and comparing observed with expected gives $\chi_1^2 = 13.44$ ($P < 0.001$). Thus we conclude that there tends to be a weak positive correlation between the number of chaetae at the two sites. This is most pronounced for strain 20 where $r > 0$ significantly in both sexes ($P < 0.05$ in females and < 0.001 in males). Thus if one were wishing to select simultaneously for chaeta number at both sites, this might be one good strain to use.

Table 3. *Correlation coefficients* (r) *between sternopleural and abdominal chaeta numbers*

Strain	n	Females	Males
1	50	0.2193	0.1248
2	50	0.0219	0.1219
3	50	0.0594	0.2168
20	50	0.2948*	0.5482***
21	50	−0.2409	−0.0441
22	50	0.4123**	0.0078
23	50	−0.0958	0.3184*
24	50	0.0767	0.1260
25	50	−0.0791	−0.0619
26	50	−0.0639	0.3362*
27	50	0.2881*	0.1941
28	50	0.2817*	0.2862*
29	50	0.1304	0.2732
30	50	0.1673	0.0225
31	50	0.2092	−0.1501
32	50	0.2974*	0.0912
33	50	0.1287	0.2212
34	50	0.2562	0.0899
From the means in table 1	18	0.0971	0.3418
From the total data	900	0.1298***	0.1993***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (for deviation from $r = 0$)

Discussion

Some of the points raised have been discussed in recent publications, e.g. those specifically relating to significant differences in means and coefficients of variation between strains set up from single inseminated females. The point not discussed previously is whether selection among certain strains set up from single inseminated females is a useful procedure when carrying out directional selection simultaneously for two or more traits. In this case the two traits involve chaetae, and it would often happen that selection programs involving 2 or more traits would be based on traits of a similar nature. The tentative conclusion is that selection among strains, before initiating a directional selection program, may be useful even when 2 or more traits are involved, if some strains show positive correlations. Clearly the responses are likely to be far less dramatic than for directional selection based on one trait, but the responses may well be more rapid than based on a large and heterogeneous population. Directional selection experiments analogous to those of Hosgood and Parsons (1967b) for scutellar chaeta number, exploiting extreme strains, have not so far as I am aware, been carried out for two traits simultaneously, but would certainly be worthwhile. Even so, as indicated several times in the literature (see for example Lee and Parsons, 1968), if the actual genes controlling quantitative traits can be located and studied individually, as has been carried out for some quantitative traits (see introduction) then the direct effects of the genes could be assayed and their correlated effects. This would enable them to be manipulated in a Mendelian manner to achieve a desired object. Thus ultimately, one can envisage the selection experiment, as is known today, being partly replaced by the manipulation of genes into certain combinations, and a start in this direction has been made by selection among the founder females as in the work of Hosgood and Parsons (1967b). Needless to say, complications may occur, since new combinations of genes may emerge not predicted by gene manipulations, since in new genetic environments, it is possible for genes to change radically in their effects.

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Literature

1. Fraser, A. S., Scowcroft, W., Nassar, R., Angeles, H., Bravo, G.: Variation of scutellar bristles in *Drosophila* IV. Effects of selection. Aust. J. Biol. Sci. **18**, 619—641 (1965). — 2. Hosgood, S. M. W., MacBean, I. T., Parsons, P. A.: Genetic heterogeneity and accelerated responses to directional selection in *Drosophila*. Mol. Gen. Genetics **101**, 217—226 (1968). — 3. Hosgood, S. M. W., Parsons, P. A.: Genetic heterogeneity among the founders of laboratory populations of *Drosophila melanogaster* II. Mating behaviour. Aust. J. Biol. Sci. **20**, 1193—1203 (1967a). — 4. Hosgood, S. M. W., Parsons, P. A.: The exploitation of genetic heterogeneity among the founders of laboratory populations of *Drosophila* prior to directional selection. Experientia **23**, 1066 (1967b). — 5. Hosgood, S. M. W., Parsons, P. A.: Polymorphism in natural populations for the ability to withstand temperature shocks in *Drosophila*. Experientia **24**, 727—728 (1968). — 6. Lee, B. T. O., Parsons, P. A.: Selection, prediction and response. Biol. Reviews **43**, 139—174 (1968). — 7. MacBean, I. T., Parsons, P. A.: Directional selection for duration of copulation in *Drosophila melanogaster*. Genetics **56**, 233—239 (1967). — 8. Manning, A.: Yield improvement from a selection index technique with cotton. Heredity **10**, 303—322 (1956). — 9. Miller, D., Erway, L., Fraser, A. S.: Switch genes and polygenic systems determining number of scutellar bristles. Genetics **54**, 348 (1966). — 10. Parsons, P. A.: Fly size, emergence time and sternopleural chaeta number in *Drosophila*. Heredity **16**, 455—473 (1961). — 11. Parsons, P. A.: Genetic heterogeneity among the founders of laboratory populations of *Drosophila melanogaster*. Aust. J. Biol. Sci. **21**, 297—302 (1968). — 12. Parsons, P. A.: Genetic heterogeneity in natural populations of *Drosophila melanogaster* for ability to withstand dessication. Theor. Appl. Gen. **40**, 261—266 (1970). — 13. Parsons, P. A., Hosgood, S. M. W.: Genetic heterogeneity among the founders of laboratory populations of *Drosophila*. I. Scutellar chaetae. Genetica **38**, 328 to 339 (1967). — 14. Parsons, P. A., MacBean, I. T., Lee, B. T. O.: Polymorphism in natural populations for genes controlling radioresistance in *Drosophila*. Genetics **61**, 211—218 (1969). — 15. Rendel, J. M.: Correlation between the number of scutellar and abdominal bristles in *Drosophila melanogaster*. Genetics **48**, 391—408 (1963). — 16. Spickett, S. G.: Genetic and developmental studies of a quantitative character. Nature **199**, 870—873 (1963). — 17. Thoday, J. M., Gibson, J. B., Spickett, S. G.: Some polygenes. Heredity **18**, 553—554 (1963). — 18. Thoday, J. M., Gibson, J. B., Spickett, S. G.: Regular responses to selection. 2. Recombination and accelerated response. Genet. Res. **5**, 1—19 (1964).

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