

GENETIC HETEROGENEITY AMONG THE FOUNDERS OF
LABORATORY POPULATIONS OF *DROSOPHILA*.
I. SCUTELLAR CHAETAE

P. A. PARSONS and SALLY M. W. HOSGOOD

School of Biological Sciences, La Trobe University, Melbourne.

(Received February 10, 1967)

The incidence of flies with more than four scutellar chaetae (additional chaetae) has been followed for 45 generations in three strains set up from single inseminated females of *Drosophila melanogaster* collected in the wild from the same locality at the same time. Each strain differed in the incidence of additional chaetae over this time, and the differences between strains were found to be controlled largely by additive genes.

Fifteen further such strains were followed for 9 generations and each maintained consistent incidences of additional chaetae.

Thus there may be genetic differences between populations derived from single inseminated females present in a given wild population, so lending support to a role for genetic drift (as a founder effect) in these situations. These differences may be maintained for many generations.

Some possibilities for obtaining rapid responses in directional selection experiments based on the initial selection of favourable strains derived from single individuals are discussed briefly.

Introduction

In experiments on interspecific competition between *Tribolium castaneum* and *T. confusum*, one species invariably displaces the other, such that in certain environments *T. castaneum* wins, in others *T. confusum*, and in intermediate environments the result is unpredictable (PARK, 1954; PARK & LLOYD, 1955). LERNER & DEMPSTER (1962) have shown that the indeterminacy in the intermediate environments is largely removed by inbreeding. Under inbreeding the genotypes are specified precisely, so making the results of replicate competing cultures predictable in each individual case. Other suggestive evidence comes from the greater uniformity of results when 10 pairs of beetles of each species were used to initiate the cultures of both species instead of two. Presumably the aggregate genetic effects

in competition of sets of 20 genotypes taken at random are much more uniform than the aggregate effects of four genotypes. Thus the apparent indeterminacy is largely the result of genetic heterogeneity among the founders of the different cultures. LERNER & DEMPSTER (1962) consider that their experiments lend great emphasis to the importance of the founders of small isolates as advocated by MAYR (1954, 1963). More generally, they ascribe a role to genetic drift in evolution.

In *D. pseudoobscura*, significant differences in mating speed have been found between different strains within the karyotypes ST/ST (Standard) and CH/CH (Chiricahua) collected from Mather, California at the same time (PARSONS & KAUL, 1967). SPIESS, LANGER & SPIESS (1966) reported similar results for strains of AR/AR and PP/PP karyotypes, which may be a partial explanation of differences between some of their results and those of PARSONS & KAUL (1966). The variation between strains within karyotypes may reflect genetic heterogeneity among the founders of the strains which is preserved over a number of generations. If common, this type of heterogeneity may be important in explaining differences between experimenters for various traits.

Less variation between strains within the karyotypes ST/ST and CH/CH was found for duration of copulation (PARSONS & KAUL, 1967) than for mating speed. However, if we can argue from *D. melanogaster*, there may be less genetic variance controlling this trait than mating speed (PARSONS, 1964; MACBEAN & PARSONS, 1966).

Thus although it is still difficult to assess the exact importance of genetic heterogeneity among the founders in evolution, it is a factor of some importance in laboratory populations. In this paper, evidence for genetic heterogeneity for scutellar chaeta variation between strains of *D. melanogaster* set up from the same population at the same time will be presented. Variation will be assessed by the incidence of flies having more than the usual four chaetae on the scutellum.

Method

The scutellum normally has 4 chaetae near its edge, namely 2 anterior and 2 posterior. Extra chaetae may occur anterior to the anterior chaetae, between the anterior and posterior chaetae (inter-

stitial chaetae), or between the posteriors. In this paper any fly with more than 4 chaetae is classified as having additional scutellar chaetae. Flies with fewer than 4 chaetae are of course found, but will not be considered. In any case, such flies were very rare in the strains to be discussed.

In the first experiment to be described the incidence of additional scutellar chaetae was analysed for 45 generations in 3 strains set up from single inseminated females collected in December 1963 at Leslie Manor near Camperdown, Victoria. Scoring was carried out every generation in the early generations, and at longer intervals in the later generations, but in no case was the interval more than five generations. The strains were kept in half pint milk bottles at 25°C and were transferred every 3 weeks to set up the next generation. At the twenty-fourth generation in the laboratory, the three strains were crossed together in all possible combinations so forming a complete 3×3 diallel cross, in order to look into the genetic basis of the trait.

In the second experiment 15 strains from single inseminated females collected at Leslie Manor in December 1965 were analysed for the incidence of additional scutellar chaetae at the 2nd, 3rd, 5th, 7th and 9th generations in the laboratory.

Results

The incidence of additional scutellar chaetae for the three strains from the first experiment is given in Fig. 1 plotting sexes separately. Each point on these graphs is based on about 150 flies, but the sample size varied somewhat between generations.

For all strains the incidence in males is far lower than in females in agreement with other work (FRASER, 1963). In both sexes, however, strain 2 has the highest incidence of additional chaetae (15 to 30% in females and 3 to 10% in males), followed by strain 1, and strain 3 has the lowest incidence. In females this sequence is maintained in all generations tested, and in males for the great majority of generations. It is remarkable that this pattern is maintained for a 45 generation period, with little apparent temporal trend except for a tendency for strain 2 to have a small increased incidence of additional chaetae with time.

Because of this consistency, it is likely that the differences between

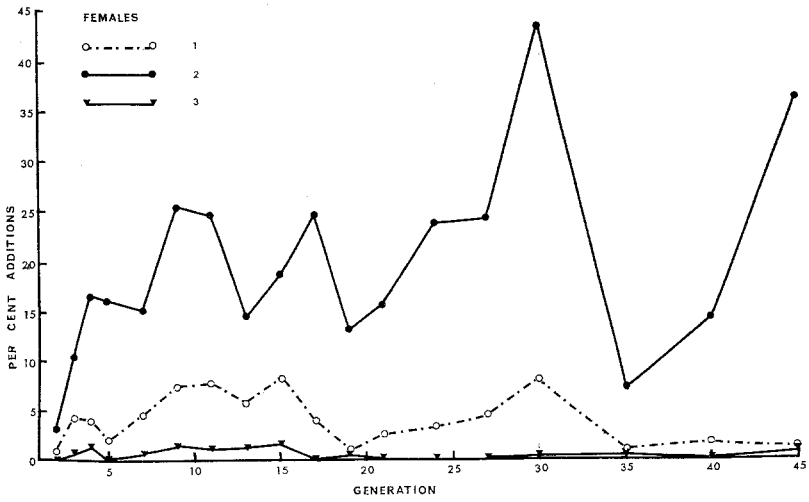


Fig. 1a. The incidence of additional scutellar chaetae in females in strains 1, 2 and 3.

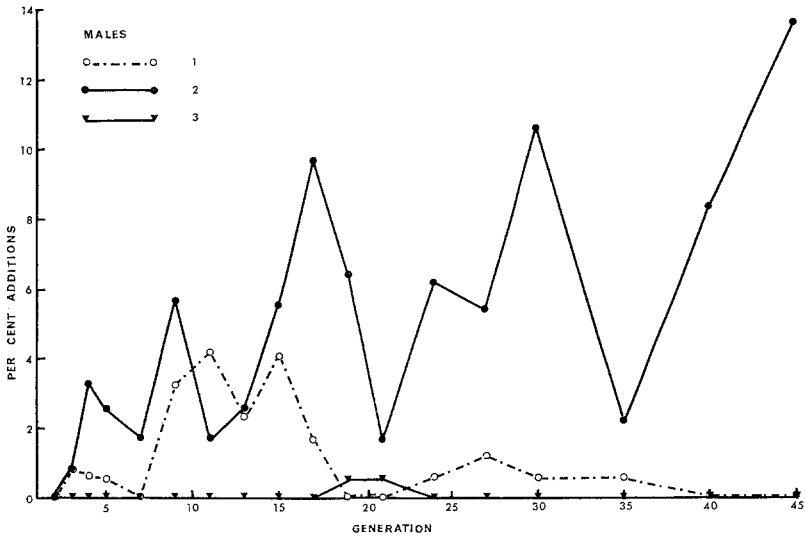


Fig. 1b. The incidence of additional scutellar chaetae in males in strains 1, 2 and 3.

strains are genetic in origin, presumably arising from genetic differences between the three inseminated founder females. This was further investigated by a 3×3 diallel cross set up at the 24th generation from these 3 strains. Two replicates were set up for each strain and hybrid, for which 125 flies were scored per sex. The results, expressed as percentage incidence of flies with additional chaetae are given in Table 1.

The incidence of additional chaetae is far higher in females than males, and this was confirmed by an analysis of variance (Table 2) after applying the angular transformation to the data. The analysis of variance further showed that the nature of the strain of the parents

TABLE 1

PERCENTAGE INCIDENCES OF FLIES WITH ADDITIONAL SCUTELLAR CHAETAETAE IN THE 3×3 DIALLEL CROSS BETWEEN THE THREE STRAINS IN FIG. 1 AT THE 24TH GENERATION

Strain of male parent	Incidence in females			Incidence in males		
	1	2	3	1	2	3
Strain of 1	2.4	9.2	1.2	0	0.8	0
female 2	12.8	31.6	4.4	3.6	7.6	0.8
parent 3	0.8	3.2	0	0.4	0.4	0

The percentages represent the mean of two replicates.

TABLE 2

ANALYSIS OF VARIANCE OF THE PERCENTAGE INCIDENCES OF ADDITIONAL SCUTELLAR CHAETAETAE IN THE 3×3 DIALLEL CROSS

Source of variation	d.f.	M.S.	F	P
Sex classified (1)	1	557.57	56.91	< 0.001
Strain of female parent (2)	2	571.91	58.37	< 0.001
Strain of male parent (3)	2	330.42	33.73	< 0.001
(1) \times (2)	2	59.72	6.10	< 0.01
(1) \times (3)	2	58.92	6.01	0.01
(2) \times (3)	4	32.48	3.32	< 0.05
(1) \times (2) \times (3)	4	2.91	0.30	n.s.
Error	18	9.80		

Percentages were transformed to angles.

of both sexes is highly significant. Smaller but significant first-order interaction terms were found, which are minor compared with the main effects.

The importance of the strains themselves argues for a genetic component in determining the incidence of additional chaetae. To look at this possibility further, the data were analysed according to GRIFFING'S (1956) model for the analysis of diallel crosses which enables the assessment of general and specific combining abilities, and reciprocal effects. The general combining ability is the average performance of a given strain in combination with all the others, and the specific combining ability is the degree to which specific hybrids deviate from the value predicted on the basis of the general combining abilities of their constituent strains. The reciprocal effect is the difference obtained for a given hybrid according to which strain is the female or male parent. The analysis was carried out on the incidence of additional chaetae in the two sexes separately in view of the large differences found between sexes (Table 2), and also because the actual combining abilities for the strains can be estimated; being only meaningful for each sex separately.

In both sexes the results are clear, showing very large significant general combining ability components (Table 3a), and non-significant specific combining ability and reciprocal effect components. From the genetic point of view, this indicates that the strains differ in additive genes which control the incidence of additional scutellar chaetae. The actual general combining abilities of the three strains

TABLE 3

A. ANALYSIS OF VARIANCE OF THE PERCENTAGE INCIDENCES OF ADDITIONAL CHAETAE IN THE 3×3 DIALLEL CROSS USING GRIFFING'S (1956) MODEL

Source of variation	d.f.	Female data		Male data	
		M.S.	F.	M.S.	F.
General combining ability	2	800.97	60.72 *)	190.57	37.29 *)
Specific combining ability	3	29.64	2.25	14.86	2.91
Reciprocal effect	3	6.74	0.51	15.56	3.05
Error	9	13.19		5.11	

*) $P < 0.001$.

Percentages were transformed to angles.

B. GENERAL COMBINING ABILITIES (IN PERCENTAGES)

Strain	Female data	Male data
1	3.65	0.30 *)
2	13.28 **)	2.56 **)
3	0.84 **)	0.09 **)
Mean	4.70	0.65

*) $P < 0.05$; **) $P < 0.001$; for differences between general combining abilities of the strains and the mean.

are given in Table 3b. Relative to the mean, in both sexes strain 2 has positive and strains 1 and 3 negative combining abilities. Although the percentage incidences of additional chaetae are far higher in females than in males, the sequence is the same in both sexes, as would be expected.

The results described so far led directly to the second experiment, where 15 strains set up from single inseminated females collected at the same time, but later than the 3 just described, were studied. The object was to look more generally at the variability between strains. The percentage incidences of additional chaetae, based on two replicates of 100 flies per sex for laboratory generations 2, 3, 5, 7 and 9, are given in Table 4. As before the females show far higher incidences than males, but there is reasonable consistency between the sexes. For example, in both sexes, strains 20, 24 and 26 have the highest incidences of additional chaetae. Similarly those strains having low incidences in females have incidences close to zero in males. These comments apply to the five generations scored, so that there is consistency between generations as found already (Fig. 1). In Table 5, an analysis of variance of the incidences of additional chaetae after applying the angular transformation is presented. There is a highly significant difference between sexes as expected, between strains which is reasonable in view of the comments made above, and between generations which is probably environmental. This last effect can be seen in Table 4, where, for example, most strains have high incidences of additional chaetae in generation 5. The only significant interaction is between sexes and strains. This shows that not all strains have the same relative difference in incidences between the two sexes, perhaps due to differences in sex-linked or sex-limited genes. In conclusion,

TABLE 4

PERCENTAGE INCIDENCES OF FLIES WITH ADDITIONAL SCUTELLAR CHAETAE IN 15 STRAINS

Strain	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Mean
Females.																
gener- ation																
2	6.0	0	5.5	1.0	12.5	0	5.5	1.5	0.5	0.5	3.5	1.5	1.5	1.0	1.0	2.8
3	5.0	0	3.5	5.5	8.0	2.0	7.5	3.0	0	0.5	3.0	3.5	1.0	0.5	0	2.9
5	13.0	0	2.5	4.5	20.0	4.5	13.0	7.5	0	2.0	5.5	4.0	0.5	4.0	1.0	5.5
7	7.0	0.5	3.5	2.5	18.0	8.0	9.0	9.0	1.5	0.5	5.0	2.0	2.5	3.5	1.5	4.9
9	3.5	1.5	3.0	8.0	16.5	5.5	12.0	10.0	1.0	1.0	3.5	2.0	1.5	2.5	2.0	4.9
Mean	6.9	0.4	3.0	4.3	15.0	4.0	9.4	6.2	0.6	0.9	4.1	2.6	1.4	2.3	1.1	4.2
Males.																
gener- ation																
2	2.0	0	0.5	0	0.5	0.5	2.0	0	0	0	0	0.5	0	1.0	0	0.5
3	1.5	0	0	0	0.5	0.5	0.5	0.5	0	0	0	0	0	0	0	0.2
5	2.0	0	0.5	0	3.5	1.0	0.5	1.5	0.5	0	1.5	1.0	0.5	1.5	0	0.9
7	2.0	0	0	0	2.0	0	1.0	1.0	0.5	0	0	0	0	0.5	0	0.5
9	0.5	0.5	0	0.5	3.0	1.0	3.0	0.5	0	0	0	1.0	0	0	0	0.7
Mean	1.6	0.1	0.2	0.1	1.9	0.6	1.4	0.7	0.2	0	0.3	0.5	0.1	0.6	0	0.6

The percentages represent the mean of two replicates.

TABLE 5

ANALYSIS OF VARIANCE OF THE PERCENTAGE INCIDENCES OF ADDITIONAL SCUTELLAR CHAETAE IN 15 STRAINS

	d.f.	M.S.	F	P
Sex classified (1)	1	3916.78	269.78	< 0.001
Strains (2)	14	281.33	19.38	< 0.001
Generations (3)	4	133.19	9.17	< 0.001
(1) × (2)	14	79.0	5.44	< 0.001
(1) × (3)	4	31.88	2.20	n.s.
(2) × (3)	56	15.87	1.09	n.s.
(1) × (2) × (3)	56	11.05	0.76	n.s.
Error	150	14.58		

Percentages were transformed to angles.

this analysis confirms the results described earlier, in showing that the level of incidence of additional scutellar chaetae differs between strains, but is relatively consistent between generations. Furthermore, the differences between strains can be partly attributed to genetic differences between the 15 founder females.

Discussion

The experiments show that populations derived from single inseminated females initially present in the same population may vary significantly from the genetic point of view. Thus in these founder females different genotypes are selected so suggesting genetic drift. However, such differences between strains are maintained for 45 generations, so that the initial founder effect is not lost even after a great number of generations in the uniform environment of the laboratory. Under this uniform environment, some convergence with time might have been expected. It appears as if each strain receives certain genes (and gene complexes) by chance as a founder effect, and is almost completely unable to change these. The variations found between strains mean that when studying morphogenetic variability from samples collected in the wild, the composition of the sample is of the utmost importance. As pointed out in the introduction, this problem has already arisen for mating behaviour in *D. pseudoobscura*.

Some authors (FRASER, 1963) have regarded 4 chaetae on the scutellum as optimal, and the term "genetic leakage" has been introduced to describe the rare aberrant phenotypes of a canalized polygenic system, with special reference to scutellar chaeta variants (classifying any fly with more or less than 4 chaetae, or chaetae in abnormal positions as variants). In strain 2, the degree of "leakage" is extremely high, as the incidence of females with more than 4 chaetae is over 30% in some generations. Furthermore, this high level of additional chaetae is maintained over many generations, and so must be regarded as canalized at this level, especially in view of the evidence for additive genes from the diallel cross. In view of the recent report of MILLER, ERWAY & FRASER (1966), who have found and located genes controlling scutellar chaetae, the possibility of genetically characterising the lines under analysis will eventually arise, as will the possibility of genetically assaying flies caught in the

wild. Such research would be very informative about the extent to which we may regard the number of scutellar chaetae as being canalized at 4.

For many years there has been an immense amount of research on directional selection experiments for many diverse traits, associated with a great deal of work devoted to attempts at predicting responses to selection. Provided that the trait has some genetic basis, there should be a response to selection which at least initially depends on the magnitude of its heritability. After a number of generations of directional selection, extreme phenotypes under the control of extreme genotypes which are likely to be homozygous, will be produced. Thus the response to selection will ultimately diminish so that the population arrives at a plateau. Occasionally after some generations at a plateau, there is a rapid response to selection for a few generations, which is called an "accelerated response to selection", and is likely to be the result of recombination between linked genes controlling the trait giving extreme gametes which will be favoured by selection (see BODMER & PARSONS, 1962 for review).

In spite of quite dramatic responses to selection in *D. melanogaster* for chaeta number for chaetae at various positions, the base population is often very small, both in directional selection experiments (see for example MATHER, 1941; MATHER & HARRISON, 1949; FRASER et al. 1965) and in disruptive selection experiments (THODAY & BOAM, 1959; THODAY & GIBSON, 1962). Some of these experiments were, in fact, begun from stocks derived from single inseminated females (FRASER et al. 1965; THODAY & BOAM, 1959; THODAY & GIBSON, 1962). The results presented in this paper indicate that the nature of the founder female could be very important in determining the exact response to selection, in view of the very great range in the incidence of additional scutellar chaetae found in the various strains. The extreme variability of response occasionally found in different experiments, where selection is carried out on the same trait using identical breeding procedures, may well be partly due to genetic variation between the founder individuals.

This leads to a possible modified procedure which could be used in directional selection experiments. Based on the progenies of the founder individuals, one could carry out an initial selection of favourable strains. Considering selection for increased scutellar chaeta.

number, a procedure may be to take the strains derived from a number of inseminated females, and select only those strains with the highest incidences of additional chaetae. These strains would then be crossed together over two or three generations according to the number of strains chosen, and directional selection then commenced on this heterogeneous background. This procedure should concentrate together a large number of genes for additional chaetae, in view of the evidence for the genetic control of this trait presented in this paper. One might predict that a rapid response to selection would occur more frequently than when using the conventional procedures employed in directional selection experiments. Results confirming this prediction have now been obtained (HOSGOOD & PARSONS, unpublished). Various extensions of this proposed procedure can be envisaged, such as crossing unselected favourable strains with the selection line after some generations of selection, so as to exploit variation which is only expressed at this stage.

We are grateful to Professor M. J. D. WHITE F.R.S. for facilities enjoyed in the Genetics Department, University of Melbourne, where the experimental work was carried out. One of us (S.M.W.H.) wishes to acknowledge a Commonwealth of Australia Postgraduate Award. Some of this work was supported by the Australian Research Grants Committee.

REFERENCES

- BODMER, W. F. & P. A. PARSONS (1962). Linkage and recombination in evolution. *Advances in Genetics* **11**: 1-100.
- FRASER, A. S. (1963). Variation of scutellar bristles in *Drosophila*. I. Genetic leakage. *Genetics* **48**: 497-514.
- FRASER, A. S., W. SCOWCROFT, R. NASSAR, H. ANGELES & G. BRAVO (1965). Variation of scutellar bristles in *Drosophila*. IV. Effects of selection. *Aust. J. Biol. Sci.* **18**: 619-641.
- GRIFFING, J. B. (1956). Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. J. Biol. Sci.* **9**: 463-493.
- LENER, I. M., & E. R. DEMPSTER (1962). Indeterminism in interspecific competition. *Proc. Natl. Acad. Sci., U.S.A.* **48**: 821-826.
- MACBEAN, I. T. & P. A. PARSONS (1966). The genotypic control of the duration of copulation in *Drosophila melanogaster*. *Experientia* **22**: 101-102.
- MATHER, K. (1941). Variation and selection of polygenic characters. *J. Genet.* **41**: 159-193.
- MATHER, K. & B. J. HARRISON (1949). The manifold effect of selection. *Heredity* **3**: 1-52.

- MAYR, E. (1954). Changes of genic environment and evolution. In. Evolution as a process. Eds. HUXLEY, J., A. C. HARDY and E. B. FORD, pp. 157-180.
- MAYR, E. (1963). Animal Species and Evolution. Belknap Press, Harvard.
- MILLER, D., L. ERWAY & A. FRASER (1966). Switch genes and polygenic systems determining number of scutellar bristles. *Genetics* **54**: 348.
- PARK, T. (1954). Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of *Tribolium*. *Physiol. Zool.* **27**: 177-238.
- PARK, T. & M. LLOYD (1955). Natural selection and the outcome of competition. *Amer. Nat.* **89**: 235-240.
- PARSONS, P. A. (1964). A diallel cross for mating speeds in *Drosophila melanogaster*. *Genetica* **35**: 141-151.
- PARSONS, P. A. & D. KAUL (1966). Mating speed and duration of copulation in *Drosophila pseudoobscura*. *Heredity* **21**: 219-225.
- PARSONS, P. A. & D. KAUL (1967). Variability within and between strains for mating behaviour parameters in *Drosophila pseudoobscura*. *Experientia* **23**: 131-132.
- SPIESS, E. B., B. LANGER & L. D. SPIESS (1966). Heterogamic mating control by gene arrangements in *Drosophila pseudoobscura*. *Genetics* **54**: 1139-1149.
- THODAY, J. M. & T. B. BOAM (1959). Effects of disruptive selection. II. Polymorphism and divergence without isolation. *Heredity* **13**: 205-218.
- THODAY, J. M. & J. B. GIBSON (1962). Isolation by disruptive selection. *Nature* **193**: 1164-1166.