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Modifying the sternopleural hair pattern in *Drosophila* by selection

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Two apparently very similar quantitative characters, the numbers of hairs on the sternopleural region and on the abdominal sternites of *Drosophila melanogaster*, show unexpected differences in their genetic behaviour. In particular, the amount of left-right asymmetry of the sternopleurals (i.e. the mean absolute difference in numbers of hairs on the two sides of the fly) tends to decline when inbred lines are intercrossed, and can be both increased and decreased by straightforward selection; the corresponding index for the sternite hairs—the uncorrelated variance between two sternites, or the mean absolute difference between the numbers of hairs on each—appears, on the other hand, to be susceptible neither to selection nor to change when inbred lines are crossed (Mather, 1953; Reeve & Robertson, 1954; Reeve, 1959).

In discussing these differences, Reeve (1959) suggested that they might partly be explained by anatomical differences between the two characters, in that the region covered by the sternite hairs is strictly delimited by the extent of the sternites which they cover, while the sternopleural hairs cover a much more indefinite region with no obvious boundaries. The pattern of the sternopleurals is also less restricted than that of the sternite hairs, which give a fairly even coverage of a definite sclerotized area. Variation in sternopleural asymmetry might thus result from variation in the precision with which the sternopleural region is defined, or in the precision with which the general pattern of the sternopleural hairs is determined, two factors which do not seem likely to affect the sternite hairs.

In order to throw some light on this problem, a selection experiment has been carried out to test how far the sternopleural hair pattern is modifiable genetically without the intervention of major mutations. Typically the sternopleural hairs form a variable dorso-ventral row, with two much larger and more stable bristles, one at each side near its dorsal end, and additional hairs occurring sporadically near them. An imaginary straight line drawn through the bases of the two large bristles divides the hairs into

two groups, a dorsal (D) with usually 1–2 hairs and a ventral (V) with some 6–7 hairs. Selection was carried out to reduce the number ($V - D$) and make it negative if possible, thus piling up hairs on the dorsal side of the line and reducing the extent of the ventral region. This seemed to be the simplest way of altering the hair pattern.

The results of an experiment with the Pacific wild stock, selecting the most extreme 20–25 parents of each sex out of 60–70, and mass-mating them each generation, are shown in Table 1. Here V and D are the sums of the numbers of ventral and dorsal hairs on the two sides of the fly, while left-right asymmetry is measured in the usual way as the mean difference in the number of hairs on the two sides, regardless of sign.

Table 1. *Effects of selection for sternopleural pattern*

Stage of selection	Sternopleural indices		
	$V - D$	$V + D$	$ L - R $
Generation 0	9.00	15.20	1.14
23–26	1.33	16.43	1.21
% change	-85	+8.1	+6.1

There is no doubt that the sternopleural hair pattern is genetically modifiable, since the excess of ventral hairs has been reduced during twenty-three generations of selection from 9.0 to 1.3, or by 85%, and individuals with 1–3 more dorsal than ventral hairs now turn up quite frequently in the selected population.

The changes in the other indices shown in the table are of equal interest. Since V is initially much larger than D , one would expect that selection to reduce ($V - D$) would reduce the total number of hairs ($V + D$). This actually occurred for the first few generations, but since then ($V + D$) has gradually risen until it is now some 8% larger than its initial value. This clearly shows that we have brought about a genuine change in the distribution of the hairs, and have not simply cut off the tail of the ventral group by reducing the region within which they can be produced. Some effect of this kind has probably also occurred. During the course of the experiment no obvious change has been noticed in the size or position of the two large bristles, and it is clear from inspection of the flies that our results have not been produced by moving the two large bristles ventrally.

Mean asymmetry, $|L - R|$, has only risen by about 6% during the experiment, a change which must be attributed entirely to scale effects, since the asymmetry and the total hair count have risen in almost exactly the same proportion. Now twenty generations of artificial selection with restricted population size must have brought about a marked deterioration in the adapted gene-pool of the population, with a consequent reduction in the general level of developmental homeostasis; but this clearly has not been reflected in any increase in the level of asymmetry. Our experimental results do not, therefore, support the theory put forward by Mather (1953) and Thoday (1958) that asymmetry is a measure of developmental homeostasis. This theory has been criticized by Reeve (1959) on the basis of other experimental data.

Our experiment has demonstrated clearly that the sternopleural hair pattern can be quite strikingly modified genetically, but without changing the level of asymmetry. It does not, therefore, explain the difference in genetic behaviour between the two quantitative characters based on hair count. It seems likely, however, that crossing inbred lines, or selecting directly for asymmetry, brings into play other genetic differences which do actually alter the degree of precision with which the sternopleural hair pattern is determined, and so affect asymmetry. Evidently the whole problem of the genetic control of sternopleural hair number, pattern and asymmetry is more complex than might be supposed, and needs further analysis.

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