NOTES AND COMMENTS

COMPETITION IN DROSOPHILA I: A CASE OF STABILISING SELECTION

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1. Introduction

There are several reports in the literature pointing to the occurrence of stabilising selection for the the number of sternopleural chaetae in *Drosophila melanogaster.* Barnes (1968) found that fitness, as expressed in number of progeny per single pair mating, declined as the parent's number of sternopleural chaetae departed from the mean. An element of competition in the stabilising selection is implied by Kearsey and Barnes' (1970) observation that with flies raised under more crowded conditions the variance of the distribution of number of sternopleural chaetae was lower than with flies raised under less crowded conditions, though the mean number of chaetae was unaltered. Differences in competitive ability that could lead to stabilising selection were observed by Mather and Cooke (see Mather, 1961), the competitive ability of flies with a central number of chaetae being greater than that of flies with a high or a low number of chaetae. Later observations, reported by Mather and Cooke (1962), were however less clear in this respect.

2. Technique

In the present experiments the competitive abilities of flies with different number of sternopleural chaetae, obtained from the F_2 of a cross between the Wellington (W) and Samarkand (S) wild-type lines, were compared using the technique of Mather and Cooke (1962), with however the important difference that the comparisons were not made directly by putting flies of the different chaetae numbers into direct competition in the same culture, but indirectly by assessing the competitive ability of each chaeta class against a common tester stock, 6CL. Individuals of this tester stock are readily distinguished from normal wild-type flies by their high number of sternopleural chaetae, and the individuals emerging from a competitive culture can thus be sorted directly into wild-type and 6CL and their contributions to the total yield of the culture ascertained.

The distribution of sternopleural chaeta numbers observed in 215 flies (105 females + 110 males) from the F_2 of $W \times S$ has a mean of 19·228 and a variance of 6·074. The distribution itself is illustrated in fig. 1. Males and females with 16, 17, 18, 19, 20, and 21 chaetae were collected from the F_2 and held in tubes until sufficient numbers of each sex and phenotype had

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been obtained. 6CL flies were collected simultaneously. The competition cultures were raised in 1″ × 3″ tubes into which unyeasted oatmeal/treacle/agar food had been placed and each of which was divided into two by a removable cardboard partition reaching just into the top of the food cake at one end and up to the bung at the other. A pair of F_2 flies of like chaeta number were placed on one side of the partition and two pairs of 6CL flies on the other. After allowing 24 hours for the flies to recover from etherisation

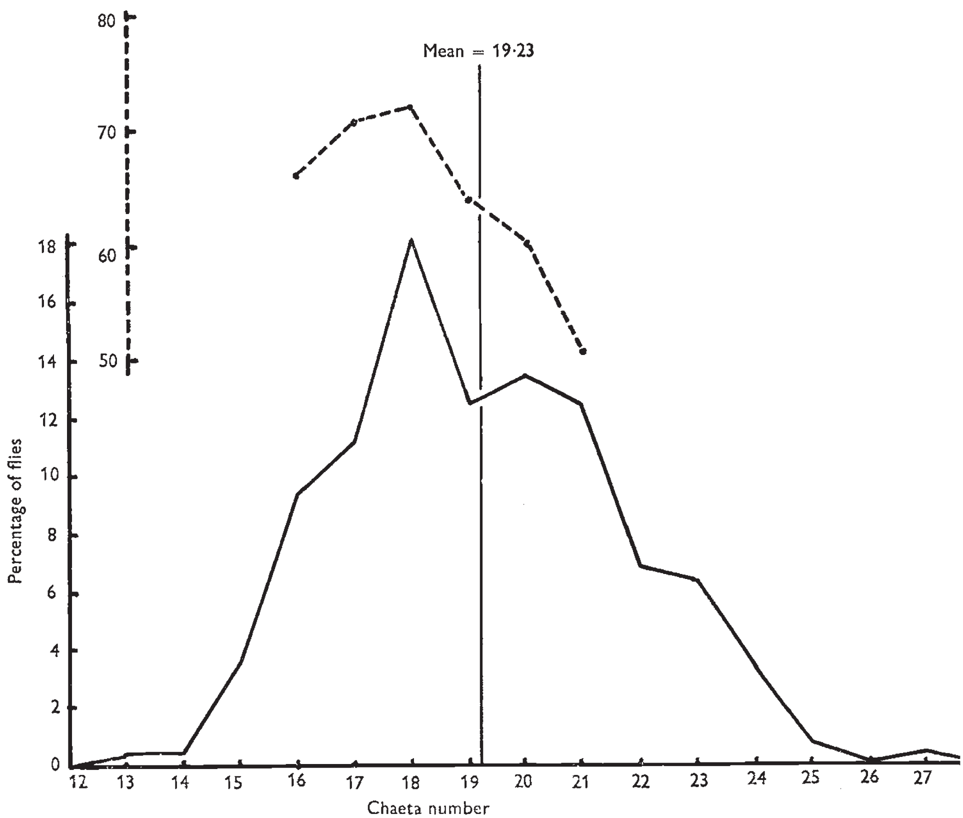

Fig. 1.—The solid line shows the percentage frequencies of flies with the various numbers of sternopleural chaetae among 215 individuals (105 females and 110 males) from the F_2 of Wellington × Samarkand. The broken line shows the competitive abilities as measured by ϕ (see in the text) of the offspring of flies with chaeta numbers from 16 to 21.

the tubes were placed in random order in an incubator at 25° C. The parent flies and the partition were removed from the tubes 3 days later, the larvae of the two kinds, F_3 from W × S and 6CL, being thus brought into competition. Progeny were collected and recorded for type (wild or 6CL) either until no more emerged or up to a maximum of 7 days after the first emergence.

Three experiments were carried out. The six chaeta number classes were represented equally in all three experiments, there being four replicates of each in experiment 1 and experiment 2, but five replicates of each in experiment 3.

3. Results

Four data were recorded from each tube:

(*a*) the yield of 6CL flies;
(*b*) the yield of wild-type (*i.e.* F_3 flies);
(*c*) the total yield (*i.e.* the sum of (*a*) and (*b*)); and
(*d*) the proportion of the yield that were wild-type, transformed into the angle ϕ.

An analysis of variance was carried out on the results from all three experiments for each of the four data. In all four cases there were significant differences between the three experiments and between the chaeta classes, *i.e.* the groups of cultures distinguished by the chaetae numbers of the F_2 parents used in them. There was no evidence of interaction between chaeta classes and experiments except for (*a*), the yield of 6CL flies, where however it was significant at only the 5 per cent. level. The results have, therefore, been pooled over chaeta classes to show the differences between experiments in table 1, and over experiments to show the differences between chaeta classes, in table 2. The overall average yields of the two types of progeny, and their total, from table 2 are plotted against chaeta class in fig. 2; and frequency distribution of chaeta number in the F_2, together with the overall average ϕ in fig. 1. It should be noted that the error variance of ϕ (obtained as the mean square of ϕ between cultures of like chaeta class within experiments and pooled over chaeta classes and experiments) was 56 which materially exceeds $\frac{820 \cdot 7}{65 \cdot 9}$, the value to be expected if it reflected only sampling variation. Evidently circumstances varied sufficiently among replicate tubes to contribute materially to the error variance.

Table 1

Average number of flies and proportions of wild-type (transformed into angles) in each experiment and over all the three experiments

Experiment	Number of replicates	Number of flies: 6CL	Wild-type	Total	ϕ
1	4	13·6	57·4	71·0	63·9
2	4	23·1	62·3	85·5	59·2
3	5	6·2	40·1	46·3	68·1
Overall	13	13·7	52·2	65·9	64·1

Table 2

Average number of flies and the proportions of wild-type (transformed into angles) according to the chaeta classes of the wild-type parents derived from the F_2 of $W \times S$. The averages are taken over all three experiments and hence over 13 replicates

Chaeta class	16	17	18	19	20	21
Number of flies:						
6CL	13·5	8·5	7·6	14·5	18·2	19·9
Wild-type	51·2	61·9	61·6	57·3	49·1	32·3
Total	64·7	70·4	69·2	71·8	67·3	52·2
ϕ	66·2	70·9	72·2	64·4	60·3	50·5

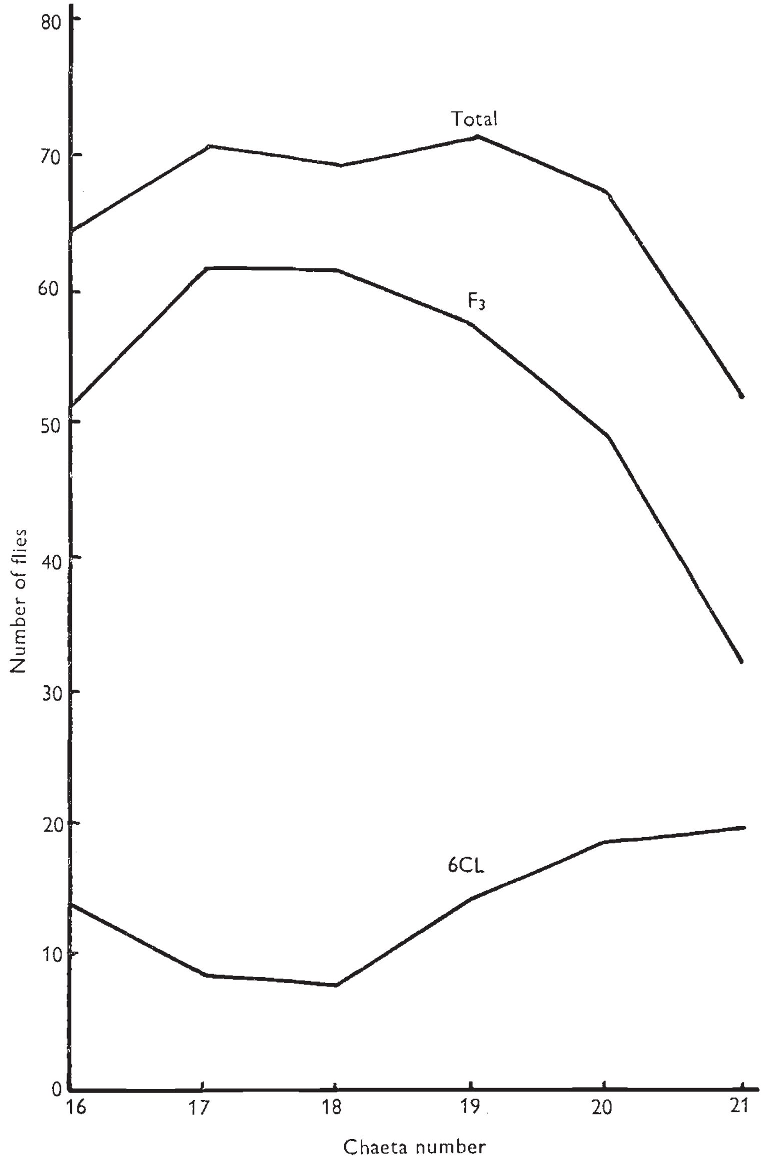

Fig. 2.—The mean yields per culture of F_3 and 6CL flies, and their total, in relation to chaeta number of the F_2 parents. The means have been taken over all three experiments.

Two conclusions emerge from these results. In the first place ϕ, and hence the proportion of wild-type flies, is greatest where the F_2 parents had 18 chaetae and falls away on each side of this chaeta number. The competitive value of the F_2 flies, relative to 6CL, as measured by this technique, is thus greatest for flies from parents with 18 chaetae and falls away on each side of this value. The selection to which these differences in competitive value would be expected to lead will thus have a stabilising component in respect of sternopleural chaeta number. The selection will not, however, be wholly stabilising but contain a directional component too, since the class with the highest competitive ability has a cheatae number just below the mean and the decline in competitive value is more rapid with increase in chaeta number than with decrease. We may observe that Mather (1961) records his low chaeta flies as having a greater competitive ability than his high ones, though both had lower competitive abilities than his flies with middle chaeta numbers. His observations thus accord with the present results, even though his data were from flies from the F_2 of Oregon × Samarkand, competing directly with one another rather than with a standard tester stock such as we have used.

The second conclusion emerges from a comparison of the changes in yield of 6CL and F_3 flies with parental chaeta number. As will be seen from table 2 and fig. 2, the yield of F_3 flies is highest for the central chaeta classes and falls off on each side as would be expected. Equally the yield of 6CL is lowest near the centre and rises on each side, again as would be expected. But the total yield of flies is also highest near the centre, falling away on each side, and this is not obviously to be expected. Evidently individuals of the two kinds, F_3 and 6CL, do not correspond to one another or compensate exactly for one another in relation to whatever agencies are at issue in respect of their relations within the competition cultures; or to put it another way if, for whatever reason may be, an individual of one kind fails to survive it does not prospectively open the way for one and one only of the other kind prospectively to replace it. Indeed, if we calculate the regression of the yield of F_3 individuals on the yield of 6CL over the six chaeta classes we find that the regression coefficient is significant at $-1 \cdot 91$, the three experiments differing no more from one another than can be accounted for by sampling variation. In other words, an increase or decrease of one 6CL individual is compensated by a decrease or increase of $1 \cdot 91$ F_3 individuals. Thus one 6CL fly corresponds in this sense to nearly two F_3 individuals. The reason for this is not obvious as the 6CL flies appear no larger than the F_3s, at least to simple inspection, as might be expected if they made greater demands on the limited supplies of nutriments. A similar relation and regression has been observed in other experiments and the matter will be taken up for further discussion in a later paper.

One last point should be made. It will be seen from table 1 that the average yield of all flies differs from experiment to experiment, and ϕ rises as the yield falls. In other words the superior competitive ability of the F_3 flies (which can be inferred from their yield exceeding that of 6CL despite there being only half as many F_2 parents as 6CL) displays itself even more markedly under the more intensive competition which presumably is associated with lower overall yields of flies, as indeed might be expected.

4. Summary

1. The various phenotypic classes, distinguished by their number of sternopleural chaetae, in an F_2 of the cross between the two wild-type lines Wellington and Samarkand, were compared for the competitive abilities of their offspring by competing each with a standard tester stock 6CL.

2. The results show that offspring of flies with 18 chaetae compete most successfully with 6CL in the conditions of the experiment, competitive

ability falling away as the number of chaetae decreases or increases from this value.

3. These competitive differences will thus lead to stabilising selection for chaeta number, though the results also imply a directional component of selection as well.

4. As a group the wild-type flies appear to have greater competitive ability than 6CL. At the same time it takes nearly two wild-type flies to correspond to or compensate for a single individual 6CL in the sense that a unit change in the yield of 6CL is accompanied by a change, in the opposite direction, of 1·91 wild-type flies.

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5. References

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