

## Disruptive selection on sternopleural chaeta number in *Drosophila melanogaster*

BY W. SCHARLOO

*Genetisch Instituut, Rijksuniversiteit, Groningen,*

M. DEN BOER AND M. S. HOOGMOED,

*Genetisch Laboratorium, Rijksuniversiteit, Leiden, The Netherlands*

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### 1. INTRODUCTION

It is generally accepted that reproductive isolation leading to the irreversible division of a Mendelian population into two species must be initiated during a period of geographical isolation (see Mayr, 1963). Thoday & Gibson (1962, Gibson & Thoday, 1963) obtained partial isolation within a population of *Drosophila melanogaster* by artificial disruptive selection for the number of sternopleural chaetae. This occurred in two experiments from the same base population after seven and twelve generations respectively. On the strength of these results they concluded that speciation does not require geographical isolation and that sympatric speciation by disruptive selection in a heterogeneous habitat is at least a theoretical possibility.

For several reasons it seems important to repeat Thoday's experiments on different base populations. (1) It is important to have facts about the occurrence of genetical variability which could lead to sexual isolation in a number of populations. (2) Thoday and Gibson's base population was founded with four inseminated ♀♀ caught in a dustbin. Therefore, these females do not necessarily come from a single population, and genetical differences causing a considerable degree of isolation could have been present already at the start of the experiment. If this were so, the disruptive selection had not built up the sexual isolation. (3) It is not known whether lines selected from Thoday and Gibson's base population for respectively high and low chaeta number show isolation. So nothing is known about a possible relation between the character selected for and the isolation. It would be important to know whether disruptive selection on any other character would also produce isolation.

### 2. MATERIAL AND METHODS

Two experiments were started from different base populations which were offshoots of the Pacific cage population (see Robertson, 1960) and the Kaduna cage population (see Clayton, Morris & Robertson, 1957). These populations have been maintained for many years in the laboratory and it is known from several selection experiments that a large amount of genetic variability was present. The same character and the same selection method were used as in Thoday and Gibson's experiments.

The experiments were started by counting the number of sternopleural chaetae on twenty ♀♀ and twenty ♂♂ from each of four bottle cultures. From each sex the eight flies with the highest and the eight flies with the lowest chaeta number were chosen

(irrespective of the culture from which they came) as parents of the next generation. The thirty-two selected flies were allowed to mate for a period of 24 hours in one bottle. The bristles of the ♀♀ were recounted and the ♂♂ were discarded. The eight low females were divided at random into two groups of four and transferred to two bottles (the low part). The high females were separated in a similar way to give the high part of the population. This procedure was repeated in every generation.

This selection system is in the first generation comparable with an experiment in which divergent directional selection is practised in ♀♀ with an intensity of eight out of eighty individuals. In ♂♂ extremes are selected in the same way as in ♀♀ but the low (l) and high (h) ♂♂ contribute to both parts of the line. So no directional selection is practised in ♂♂ and they do not contribute to the divergence of the two parts. But the selection of extreme ♂♂ increases the probability that extreme low individuals appear in the low part of the experiment and extreme high individuals in the high part of the experiment. If mating occurs at random and all matings contribute equally to the next generation one-quarter of the progeny of the total selection line will descend from l×l matings and one-quarter descend from h×h matings. When low individuals are selected from generation 1 (g 1) the majority will descend from l×l matings and the majority of the selected high individuals will descend from the h×h matings. This tendency will increase when divergence between the two parts of the line increases.

When all selected low individuals come from the l×l matings, the selection is made from, on the average, twenty individuals descending from these matings in the total sample of eighty flies which are scored in every generation. But in the next generation on the average one-half of the descendants of the ♀♀ which form the low part of the line are hybrids descending from l×h matings and will not contribute to the divergence. Therefore, the divergence of the low part from the mean of the original population will be only half the divergence which could be expected if the selection intensity was eight out of twenty in an experiment with normal directional selection. The same argument can be applied to the high part of the disruptive line.

With such a low selection pressure only a slow divergence between the low and high parts can be expected.

However, this kind of selection will confer a premium on individuals with a tendency to mate with flies having a similar bristle number. But it will be obvious that in this case selection is practised for two characters simultaneously, i.e. bristle number and tendency to isolation. This is in contrast with the experiments of Knight *et al.* (1956) and Wallace (1954) in which selection acted against hybridization only. Unless both characters have a positive genetic correlation by pleiotropy or linkage, rapid progress in any of the characters cannot be expected.

But if sexual isolation is obtained the possibilities for divergence in bristle number become far better. Selection is then strictly comparable with divergent directional selection. From the total number of flies on which bristles are counted then forty descend from l×l matings. Because no hybrids are formed, the same selection pressure applies to ♀♀ and ♂♂. If genetic variability for bristle number is still present, such a selection intensity would cause a rapid divergence.

### 3. RESULTS

The results of our experiments are shown in Fig. 1. The upper graph shows the mean number in the low and the high parts of the two experiments plotted against generation number. In both experiments an immediate response to selection occurs in the first generation when the selection intensity is relatively high.

The difference between the high and low parts (plotted in the lower graph) is approximately three bristles in the first generation. After this, when the selection intensity for

divergence is small, the difference rises to five to six bristles in some generations but is only slightly higher at the end of the experiment in generation 15 than in generation 1. Linear regressions of this difference on generations 1–15 are  $0.05 \pm 0.08$  and  $0.12 \pm 0.04$  for the Pacific and Kaduna experiments respectively. So after the first generation the divergence increases significantly only in the Kaduna line. This is reflected in the percentage overlap of the frequency distributions of the low and the high parts (Fig. 1, middle graph). This was computed as the percentage of their total area the distributions of the low and the high parts had in common. In both experiments the percentage of overlap dropped between generations 5 and 11 but rose afterwards to its original level of 40–50%. In spite of the low percentage of overlap in generation 8 of the Kaduna experiment no lasting separation of the frequency distributions is obtained. This is in

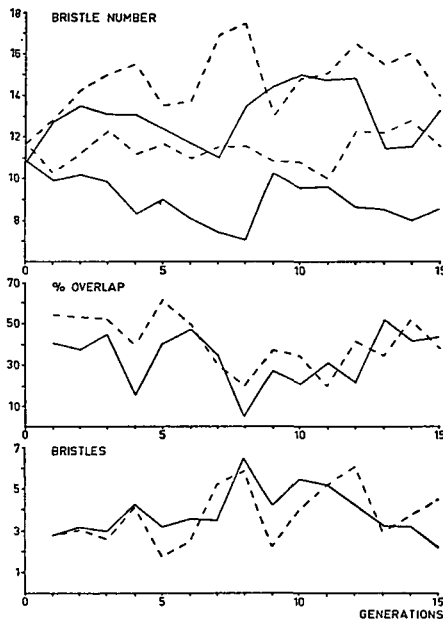


Fig. 1. Top: mean values of high and low parts of the experiments. Middle: percentage overlap of the frequency distributions of the low and high parts. Bottom: the difference between the low and the high parts. The full line represents the Kaduna selection, the broken line the Pacific population.

contrast with Thoday and Gibson's experiments where a complete separation of the frequency distributions of the low and high parts occurred. Forced hybrids showed a frequency distribution intermediate between those of the low and the high parts. On this evidence they concluded that either the hybrids were not found in their selection line or they were far inferior in competitive ability. They produced some evidence that both processes were involved (Thoday, 1963).

In our experiments there is no reason to suppose that isolation played a role. The frequency distributions have still a considerable area of overlap at the end of the experiment and the divergence between the low and high parts of the line after generation 1 was only significant in the Kaduna selection.

Moreover, in the Pacific selection 'migration' occurred between the low and the high parts of the experiment. In the fourteen generations of this experiment only in generations 2, 8, 10 and 11 was there no progeny of low ♀♀ among the flies selected for high

bristle number and no progeny of high ♀♀ among the flies selected for low bristle number. In generations 2–4 and 8–11 all low flies were selected from low bottles and in generations 2, 7, 10, 11, 13 and 14 all high flies came from high bottles. But the high part of the line was partly bred from flies selected from the low part in six generations and the low part from flies selected out of the high part in six generations. Probably these flies descend from  $h \times l$  and  $l \times h$  matings respectively. But in the opposite part of the experiment also 50% of the flies are hybrids and will probably contribute to the selected flies, enhancing the gene exchange between the two parts.

In the Kaduna selection migration occurred only occasionally; only in generations 1 and 13 one of the low ♂♂ descended from high ♀♀. This is perhaps the reason that significant divergence occurred in the Kaduna experiment only.

#### 4. CONCLUSION

It seems worthwhile to make a deeper analysis of the consequences of this type of selection. In view of our experiments and the considerations given above it may be provisionally concluded that Thoday and Gibson's results were the consequence of a special situation in which there was perhaps a genetic correlation between bristle number and isolation tendency. This would explain the fact that in two independent experiments from the same base population isolation was obtained rapidly. But our experiments were performed on base populations held in artificial homogeneous environments for several years. So the possibility remains that natural populations submitted to natural selection in a heterogeneous habitat possess just the genetical differences which can be used as building stones for isolating mechanisms but which are not present any more in cage populations.

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