SELECTION FOR A CHARACTER WITH A BOUNDED DISTRIBUTION OF PHENOTYPES IN DROSOPHILA SUBOBSCURA

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INTRODUCTION

A large number of selection experiments on continuously varying characters in Drosophila have been done, but little is known of the effects of selection on characters which have a limited range of phenotypic distribution. Earlier work on such mutant characters affecting bristle number (Macdowell, 1915, 1917, 1920; Payne, 1918, 1920; Sturtevant, 1918) and facet number (Zeleny and Mattoon, 1915; May, 1917; Zeleny, 1922) was mainly done by combining selection with inbreeding. The present experiments on the ocelli-less mutant, which removes the ocelli and some of the macrochaetes from the top of the head, in Drosophila subobscura were designed to study the effects on expression of the mutant of combining selection with outbreeding and inbreeding.

It has been suggested (Robertson and Reeve, 1952; Lerner, 1954; Maynard Smith et al., 1955) that inbreeding tends to reduce the efficiency with which development is "buffered" or "canalised", and, as has been pointed out by Waddington (1942), it is the "wild-type" rather than the mutant phenotype which is canalised. This canalisation should be effective either against disturbances due to changes in the environment, or against disturbing effects of mutant genes. If so, the phenotypic effects due to substituting a mutant for its wild-type allele would be greater on a homozygous than on a heterozygous background. Inbreeding then would tend to counteract the effects of selection for reduced expression. This expectation, which the present experiments were in part designed to test, has not been confirmed.

It has been known that a change of environment may increase the phenotypic variance of a character (Thoday, 1953; Went, 1953), but no serious attempt has been made so far to explore the possibility of utilising this increased phenotypic variance in selection experiments, although work on genetic assimilation (Waddington, 1953, 1956, 1957) has shown that the possibility exists. In these experiments, such an attempt has been made by selecting outbred and inbred population in a changed environment, and comparing the phenotypic changes produced in optimum and changed environments.

The fitness of a selected population may decline for one of two reasons. Firstly, fitness may decline because the character itself is an important component of fitness (Mather and Harrison, 1949; Lerner and Dempster, 1951). Secondly, even if the character does not contribute to the fitness, a decline in fitness may arise due to an
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increase in the level of genetic homozygosity produced by selection. In the present case, changes in the fitness of selected populations have been measured by using productivity and rate of development as criteria.

The results of the present experiments differ in one important respect from earlier studies on continuously varying characters, on which there are no obvious limits to the range of adult phenotypes. In contrast it has been found that for flies homozygous for oc/oc, there is both an upper and lower bound to the range of phenotypes. The existence of these bounds is responsible for many of the peculiarities of this work.

Material and Methods

(a) The initial mutant stock

The initial mutant stock available was homozygous for the mutants oc/oc and fused, the former a sex-linked recessive, and the latter an autosomal recessive causing a fused condition of wing-veins. In order to eliminate the mutant fused, irrelevant for the present investigation, and to obtain the foundation population of oc/oc flies with more potential genetic variability before practising selection on them, females were out-crossed to K and NFS inbred males. Five F2 families were set up, and from these oc/oc flies were selected and crossed in pairs, in a rotational system of mating. The F3 families so obtained, all homozygous for the oc/oc mutant, formed the foundation population (generation = 0) on which selection was practised.

Four cultures of each of the five families of the foundation population, and each of a day's lay of eggs were counted and their phenotypes recorded.

(b) The oc mutant and the procedure of selection

For a better understanding of the expression of the mutant, the ocelli and relevant bristles in a wild-type fly of Drosophila subobscura may be described.

In a wild-type fly (Fig. 1a), the median ocellus is a dorsoventrally compressed structure lying between the ocellar setae, and is smaller than the lateral ocelli. The lateral ocelli are paired roundish structures placed on the lateral sides of the median ocellus, anterior to the post-vertical setae but posterior to the interocellar setae. The ocellar setae are very near the two sides of the anterior ocellus, and are directed forwards. The anterior vertical setae arise close to the inner margin of the compound eyes, and are directed mesially with their terminal ends facing each other along the median line. The postvertical setae, arising on the posterior margin of the head, extend obliquely backwards, converging to cross each other at their hind ends. The posterior pair of vertical setae, which for the sake of convenience have been referred to as the lateral setae, are directed straight backwards from their origins on the posterior and lateral region of the head.

In the foundation population, the flies (Fig. 1) showed a great variety of arrangements of the three ocelli and four pairs of bristles, which appeared to be mainly affected by the mutant.