RELATION BETWEEN PERFORMANCE AND HETEROZYGOSITY IN *DROSOPHILA*¹

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A corollary to the hypothesis that performance of crosses increases with an increase in heterozygosity is that it also increases as the parents become more divergent genetically, at least within the limits of barriers to successful physiological function and reproduction. The divergence considered here will include only that which results from the fixation of different alleles or from differences in gene frequencies of the parent populations. Two procedures were employed to test the hypothesis that an increase in heterozygosity leads to a corresponding increase in performance: (1) choosing stocks of diverse ancestry to take advantage of naturally occurring genetic differentiation, and (2) inbreeding which, even from a single ancestral population, leads to genetic differentiation among lines.

MATERIALS AND METHODS

The inbred lines of *D. pseudoobscura* employed in this study originated from stocks obtained by the laboratory at Columbia University from wild populations at Mono Lake, California; Mather, California; and Bryce Canyon National Park, Utah. The Mono, Mather and Bryce strains were developed by mass culture from single fecundated females captured at each location. The laboratory at North Carolina State College further developed inbred lines from each strain by continuous full-sibmating for 20 to 28 generations. Only .002 to .014 of the heterozygosity in the strains would be expected to remain in the absence of such forces as mutation, chance, and natural selection. Mass cultures of two lines from each of two strains from each of the three locations were crossed in all possible combinations. To maintain a manageable experimental procedure, lines from two locations were crossed at one time, as shown in Table 1, for each of three experiments. In the body of Table 1, the symbols are I for inbred lines, II for crosses of lines from the same strain, III for crosses of lines from different strains but the same location and IV for crosses of lines from different locations, each representing a consecutive level of heterozygosity.

Daily egg production was measured for seven days beginning at about ten days of age. Four bottles each containing three females, were measured daily for each of the 36 different entries in one replicate of an experiment. Two replicates were made of each experiment. One experiment, Mather $\times$ Mono, was replicated by making separate crosses of the inbred stocks. The other two experiments were replicated by sampling offspring at successive periods from the same parental crosses.

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TABLE 1

The diallel crossing scheme of one replication of one experiment

		L ₁		S ₁₂		L ₂		S ₂₂	
		S ₁₁	S ₁₁	S ₁₂	S ₁₂	S ₂₁	S ₂₁	S ₂₂	S ₂₂
		l ₁₁₁	l ₁₁₂	l ₁₂₁	l ₁₂₂	l ₂₁₁	l ₂₁₂	l ₂₂₁	l ₂₂₂
	l ₁₁₁	I	II	III	III	IV	IV	IV	IV
S ₁₁	l ₁₁₂	II'	I	III	III	IV	IV	IV	IV
L ₁	l ₁₂₁	III'	III'	I	II	IV	IV	IV	IV
S ₁₂	l ₁₂₂	III'	III'	II'	I	IV	IV	IV	IV
	l ₂₁₁	IV'	IV'	IV'	IV'	I	II	III	III
S ₂₁	l ₂₁₂	IV'	IV'	IV'	IV'	II'	I	III	III
L ₂	l ₂₂₁	IV'	IV'	IV'	IV'	III'	III'	I	II
S ₂₂	l ₂₂₂	IV'	IV'	IV'	IV'	III'	III'	II'	I

RESULTS

The results are summarized graphically in Figure 1 for the three levels of heterozygosity for each location population combined over the two experiments in which the population occurred, and in Figure 2 for the four levels of heterozygosity for each experiment.

A combined analysis of crosses within location populations indicated differences in egg production among levels to be real and to increase with level of heterozygosity. The populations themselves did not differ significantly, nor was the interaction between populations and levels significant. However, from analyses of the three location populations separately, only in Mather were the differences in levels of heterozygosity significant.

From separate analyses of experiments the four levels of heterozygosity were significantly different in the Bryce $\times$ Mather and Mather $\times$ Mono experiments, but not in the Bryce $\times$ Mono experiment. Further elaboration of these results from a combined analysis of experiments yielded no significant differences among levels of heterozygosity, and no significant difference between Bryce $\times$ Mather and Mather $\times$ Mono experiments. However, both of these experiments

FIGURE 1.—Performance of location populations.

were significantly different from Bryce $\times$ Mono, when tested against a significant interaction of levels of heterozygosity with experiments mean square.

In all cases where levels of heterozygosity were significant, there were no significant deviations from linear regression of egg production on equally spaced levels of heterozygosity.

DISCUSSION

In comparing successive levels of heterozygosity two types of errors are involved. One is experimental and the other is sampling of lines. If the lines are homozygous, and presumably they very nearly are, no sampling of gametes from a line is involved. Certainly, the sources and hierarchal classification of the lines is such that an increase in heterozygosity with the numerically designated levels would be obtained for a large sample of lines. Even for the very limited sample of lines utilized, the heterozygosity for any level cannot be less than that of the average of the previous levels. For example, the heterozygosity for Level II can-

FIGURE 2.—Performance of experiments.

not be less than that for Level I, and for Level III cannot be less than that for the average of Levels I and II. Only in the Mono population, Figure 1, and reflected in the experiments involving Mono in Figure 2, are these limits transgressed in that the performance for Level II is less than that for Level I, but this difference is not significant. VETUKHIV (1953, 1954, 1956, 1957) found in general that in crosses between populations of *D. pseudoobscura* from different regions the F_1 's were superior to either parental population for such characters as viability, longevity and fecundity.

Both the performance and heterozygosity depend on the exact lines being crossed as exemplified by the significant interactions of levels with experiments. Nevertheless, it is appropriate to average performance over populations and experiments and relate this average to the level of heterozygosity, since heterozygosity almost certainly increases with consecutively designated levels. Too, the experimental error is reduced. While the relative increments of heterozygosity between consecutive levels are still in doubt, there is little doubt that egg production does increase with the level of heterozygosity, and that it is approximately linear for equally spaced levels.

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SUMMARY AND CONCLUSIONS

Two inbred lines from each of two strains from each of three location populations of *D. pseudoobscura*, and all possible crosses among them, were classified into four levels of expected heterozygosity. Performance, measured as daily egg production for a seven-day period, was related to the expected level of heterozygosity. Separate experiments in time were conducted for each pair of location populations.

While the results varied considerably among experiments and among location populations, the data did suggest that performance increases with an increase in heterozygosity. Whether the relationship is strictly linear requires a more accurate determination of the level of heterozygosity than was possible in this study.

LITERATURE CITED

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