# HETEROSIS*

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In accordance whit the theory developed by GEORGE SHULL, EAST, JONES and others, the "degeneration" of strams following inbreeding is due to homozygosis for deleterious recessives. Intercrossing of inbred strains produces an increase in vigor ("hybrid vigor" or heterosis), because deleterious recessives become covered up by favorable dominants. Studies on the genetics of natural populations of Drosophila pseudoobscura support the above theory, in so far as they show that most individuals indeed carry deleterious recessives in heterozygous condition. At the same time, these studies permit formulation of a more general theory of heterosis.

We know that mutations happen from time to time in all organisms, and that a great majority of mutations are deleterious. A dominant or a semi-dominant mutation, if its effects are adaptively negative, is promptly eliminated by natural selection. Not so with deleterious recessive mutations: they accumulate under the protection of the dominant normal alleles until their frequency in the population becomes high enough so that recessive homozygotes are formed. This explains why the dominant alleles of genes found in natural populations are usually favorable and the recessive alleles usually unfavorable to the organism. The degree to which recessive mutants may accumulate in populations, and, hence, the form which the phenomena of heterosis take in different species, will depend upon the population structure of these species. Three typical cases may be distinguished.

(1). Species in which self-fertilization is the only or the predominant method of reproduction, or species with very low

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effective population sizes. In such species dominant as well as recessive deleterious mutants are promptly eliminated by natural selection; only mutant genes with very mild deleterious effects have a finite chance of becoming established. Inbreeding produces no loss of vigor and outbreeding no or very little heterosis. Such forms as the cultivated wheat belong to this group.

(2). Species with intermediate or moderately large effective populations sizes. Accumulation of deleterious recessives in natural populations will take place, and, therefore, the heterosis on crossing inbred strain will be more os less pronounced. Nevertheless, a careful inbreeding with selection will sometimes produce inbred strains equal in vigor to normal crossbred ones. Drosophila pseudoosbscura, and, probably, most of the domesticated animals belong to this group. Possibly, man also belongs, or has belonged until recently, to this group.

(3). Species with very large effective population sizes. Deleterious recessives will accumulate to the full extent determined by their mutations rates (in the case of lethals $q = \sqrt{u}$
...re q is the gene frequency and u the mutation rate). Fur-
...e, since any one chromosome will only very seldom
whe... ...mozygous condition, the viability effects of any one
thermo... ...homozigotes will be largely irrelevant as far as
occur in ho... concerned. Hence, many or even all genes
gene allele in ... ...espect to their effects in homozygotes;
natural selection is ... ...o keep up the adaptive value of on-
may degenerate with ... ...t or all genes will be represen-
natural selection will tend ... ...which would be unfavorable
ly or mainly heterozygotes. Mo... ...nce favorable effects in
ted by a variety of alleles, each of ... ...nomena of hetero-
when homozygous, but which will prod... ...ore no amount
compounds with other alleles. Here the ph... ...qual in vi-
sis will be most sharply pronounced. Furtherm... ...s group
of selection will be able to produce inbred strains ... ...ra-
gor to outbred ones, simply because in species of thi...
homozygosis for any one chromosome will be per se unfavo...
ble. It is suggested that maize belongs here.

Further studies are obviously necessary to test the validity of the theory presented above.