SELECTION PROBLEMS IN ANIMAL BREEDING*

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ALTHOUGH ARTIFICIAL SELECTION for the improvement of domestic animals has been practiced from ancient times, there are many problems on which the information available is extremely scanty. As a result, much of the breeding rationale in use is based on purely empirical observations. One of the most important questions which needs further study is that of determining the limits of selection for characters whose variation is controlled by many gene differences with very small individual effects. Experiments on selection have demonstrated that progress may continue beyond the limits anticipated on the basis of a priori assumptions of blending inheritance. Among such experiments are those of Goodale, who selected for increased body weight in mice in one experiment and for the number of white hairs on foreheads in the same species in another.

There are many conditions limiting the progress to be expected under selection. These may be classified in four categories:

1. Difficulties in evaluation of genotypes, which may be considered in terms of:

   a) Incomplete heritability,

   b) Maternal effects,

   c) Non-additive gene interactions, such as dominance and epistatic effects,

   d) Interaction between genotypic and phenotypic variability.

2. Limitations due to the immense number of gene combinations possible, and lack of control over them. These may be discussed in terms of:

   a) Number of gene differences involved,

   b) The frequencies of different alleles at each locus in a given population,

   c) The elimination of alleles through inbreeding, and the consequent imposition of homozygosity.

   d) Restrictions on recombinations due to linkage.

3. The practical necessity of selection for several characters at the same time.

4. The eventual approach to extremes producing possible physiological incompatibilities.

These difficulties can be overcome in some measure by such means as progeny testing, enforced maintenance of heterozygosity, culling on the basis of a properly constructed index, and other breeding techniques. However, it is obvious that in the selection of domestic animals full utilization of the genetic variability in a given population has not been realized. In order to achieve this result, it is necessary to obtain more definite information on many of the points

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mentioned above, as well as to determine, by mathematical investigation, the best ways to use the information obtained.

One factor that may be of considerable practical importance, with respect to which very few data are available, is new genetic variability arising spontaneously through the mutation of genes. How rapidly is variability created in this manner and how can it be used effectively in actual breeding populations? It is entirely possible that mutations affecting economic characters arise continuously with a high frequency but, owing to the very small differentials produced by the individual mutations, they escape detection, and but little advantage is taken of them.

In order to determine whether such mutations do arise and to learn how to utilize them most efficiently, an experiment with rats is being proposed. There
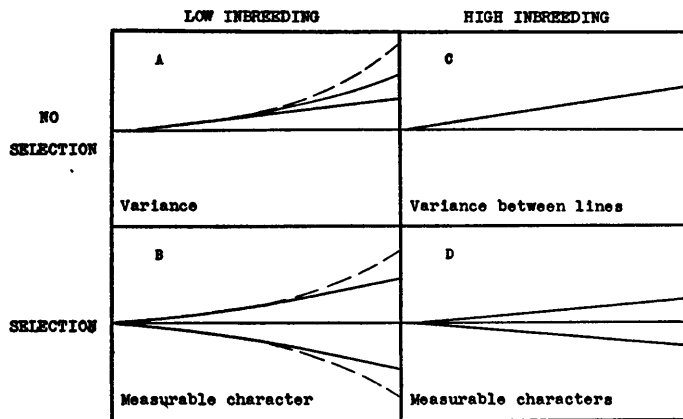
are several ways in which the experiment may be carried out. The purpose of this paper is to present the problem and seek the advice of statisticians with respect to the design of the experiment and its interpretations.

For the present purposes we may consider a design based on the use of highly inbred animals which are presumably genetically homogeneous and homozygous for most loci. The advantage of such a foundation lies in the minimization of variability due to gene differences already present. There are four schemes which can be followed, as illustrated by the four quadrants of the accompanying figure.

A. The foundation stock is to be carried on with random mating (or with restrictions on too closely consanguineous mating) and without selection. Should mutations arise, the variance for a character followed should increase as indicated by the straight line in quadrant A of the figure. If heterozygosity per se is conducive to an increased mutation rate, the variance should increase as indicated by the upper (broken-line) curve. The intermediate curve represents the possible increase in variance produced by changes in relative frequencies of mutant genes. It is questionable whether significant changes in the variance can be efficiently detected under this scheme.

B. Selection in opposite directions in two lines maintained by a system of mating similar to that described above should produce a divergence between the lines with respect to the character studied. The rate of progress here should increase as heterozygosity increases, owing to the accumulation of mutant genes. The curves of quadrant B indicate means of the two lines; the broken-line curves are based on the assumption that mutability increases with heterozygosity. The efficiency of this scheme also needs investigation, since, although detection of mutations may be relatively easy here, quantitative interpretations may present some difficulty.

C. The next alternative lies in carrying on a number of strains each being propagated by brother × sister matings from the common foundation stock. Should different mutations begin to accumulate in the separate strains, it is obvious that an increase in variance between strains will follow the line represented in quadrant C of the figure. Owing to the expectation of equilibrium between the elimination of heterozygosity by continued inbreeding and the origin of new heterozygosity by mutation, this increase in variance between strains may be anticipated to be linear. This scheme will permit the analysis of the magnitude of variation caused by mutation, but will not provide any information on the influence of heterozygosity on mutability.

D. A similar scheme of propagation by brother × sister matings, but accompanied by selection in opposite directions, will produce changes in the means for the character studied as portrayed in quadrant D. The disadvantage of this scheme and, to a lesser degree, also of scheme B lies in the fact that the low heritability to be expected in the foundation stock may prevent rapid separation of the plus and minus strain. An additional problem of interest arising under this scheme is the possible effect of selection toward increased homozygosity.

In order to decide on the most suitable experimental design of the four suggested, it is necessary to formulate mathematical models. The demonstration of the superior efficiency of any one of the schemes over the others requires an extended mathematical analysis. It is hoped that statisticians may express enough interest in this problem to undertake such an investigation.