SYSTEMS OF MATING. IV. THE EFFECTS OF SELECTION

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INTRODUCTION

In the systems of mating which have been considered in the previous papers of this series, it has been assumed that all classes in the population reproduce uniformly. The relative frequencies of the various factors within the whole population remain constant, however much change there may be in their combinations. Thus in any of these systems, random mating would in time restore the composition of the original population.

To bring about a permanent change, there must be differences in the rate of reproduction of the classes. Such differences may be due to differential death rate, rate of mating or fecundity. The method of analysis by path coefficients does not appear to be well adapted to the study of such changes except in those cases in which the system of mating itself leads to the breaking up of the population into non-interbreeding lines.

In the latter class of cases, including such systems as the continued mating of brother and sister, of double first cousins, etc., any one of the many possible inbred lines may be selected for further breeding. Random mating may be followed in the selected line without loss of the progress toward homozygosis.

SELECTION WHERE ONE FACTOR IS INVOLVED

The effect of selection of dominants only, in a one-factor case, has been considered by JENNINGS (1916) and by WENTWORTH and REMICK (1916).

If the original population is $\frac{1}{4}AA$, $\frac{1}{2}Aa$, $\frac{1}{4}aa$, the proportion of recessives is reduced according to the series:

$$(\tfrac{1}{4}),\ \tfrac{1}{9},\ \tfrac{1}{16},\ \tfrac{1}{25}\ \ldots\ \frac{1}{(n+2)^2}\ \ldots\ 0$$

The proportion of heterozygotes follows the series:

$$(\tfrac{1}{2}),\ \tfrac{4}{9},\ \tfrac{6}{16},\ \tfrac{8}{25}\ \ldots\ \frac{2\,(n+1)}{(n+2)^2}\ \ldots\ 0$$

Selection of recessives, of course, brings about immediate fixation.

If there is no dominance, selection of either homozygous type means immediate fixation. Selection of heterozygotes leads to no fixation whatever, however long it may be continued. The color of the Blue Andalusian fowl is the classical example of an unfixable characteristic of this kind. The roan color of Shorthorn cattle, the cream color of guinea-pigs and the yellow color of mice are other cases.

SELECTION TOWARD A DEFINITE TYPE

If more than one factor is involved, the problem of the effects of selection is more complicated.

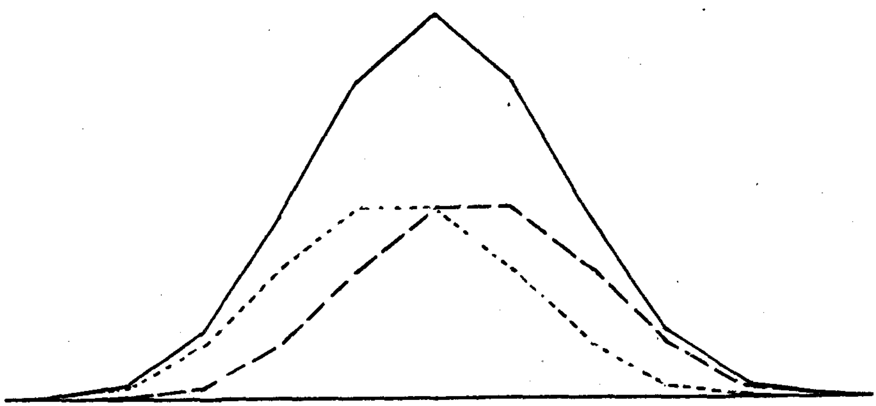

FIGURE 1

Figure 1 represents the distribution curve of individuals in a population as regards a characteristic which depends on n pairs of allelomorphs, the plus and minus factors of each pair being equally numerous, all factors of equal weight and dominance lacking. The number of individuals with each combination of factors can be found from the expansion of $(\frac{1}{2} + \frac{1}{2})^{2n}$.

The standard deviation is $\sqrt{\frac{n}{2}}$. The distribution of the plus factors among the $(2n + 1)$ classes can be found from the expansion of $(\frac{1}{2} + \frac{1}{2})^{2n-1}$ beginning with the first class. The distribution of minus factors is the same, except for a shift of one class range in the entire distribution curve. These points will be clearer from a concrete example. Assume that two pairs of allelomorphs are involved. The following distributions of classes, and of plus and minus factors will be found to be present:

Number of plus factors in individual	0	1	2	3	4	Total
Number of individuals	1	4	6	4	1	16
Plus factors in each class	0	4	12	12	4	32
Minus factors in each class	4	12	12	4	0	32
Total factors	4	16	24	16	4	64

The ratio of plus factors to total factors is, of course, $\frac{1}{2}$ for the middle class. For a deviation of x classes beyond the middle, the ratio (q) is easily shown to be:

$$q = \frac{n + x}{2\,n}$$

If we measure deviation (s) in terms of the standard deviation $\left(\text{in which case } x = s\sqrt{\frac{n}{2}}\right)$, we obtain:

$$q = \tfrac{1}{2}\left(1 + \frac{s}{\sqrt{2n}}\right)$$

For the proportion of heterozygosis produced by random mating, from parents at a given deviation, we have:

$$p = 2\,q\,(1 - q) = \tfrac{1}{2}\left(1 - \frac{s^2}{2\,n}\right)$$

Suppose now that we select for mating only individuals of a certain class. If the middle class is chosen, the proportion of plus factors in all pairs of allelomorphs remains $\frac{1}{2}$. This will remain true after any number of generations of selection. The resulting population, it is true, will show reduced variation. In the two-factor case, the standard deviation becomes $\sqrt{\frac{2}{3}}$ or 81.6 percent of its original value after the first selection and falls to 72.8 percent of its original value after an indefinite number of generations. On the return to random breeding, however, there is a return toward the composition of the original unselected population. Thus symmetrical elimination at the ends of the distribution curve may be carried on indefinitely without any permanent fixation of the intermediate type in our ideal population. In a population of limited size, such selection would, of course, tend to fix some intermediate type, but the inbreeding consequent on small numbers is a necessary condition for this fixation. It should also be said that selection would effect more or less permanent change in a population in which the distribution of the factors is not so regular as in our ideal case.

If selection is directed toward a type between the mean and one of the extremes, the proportion of plus factors in each pair of allelomorphs becomes, as we have seen, $\frac{1}{2}\left(1+\frac{s}{\sqrt{2n}}\right)$ where s is the deviation in terms of the standard deviation and n is the number of factors involved. Almost the full effect of selection is reached in the first generation if the average of the parents is at the desired type. Further selection will merely reduce the variability to some extent. All of this apparent fixation of type is lost on resuming random breeding, except such as follows the change in the proportions of the allelomorphic factors brought about in the first generation.

The end classes deviate from the mean by $\sqrt{2n}\sigma$. If it is possible to breed from one of them exclusively, its type is, of course, fixed immediately. Where there is a large number of factors, however, individuals of the extreme classes are rare in the original population and the homozygous combination of all plus or all minus factors can only be brought about by repeated selection.

INFLUENCE OF ENVIRONMENTAL VARIATION ON SELECTION

In the discussion above, it is assumed that all variation is genetic. This, however, is rarely the case in practice. Let us assume, as in previous cases, that the degree of determination by heredity is h^2.

The distribution curve of our ideal population, including the effects of environmental factors in addition to $2n$ genetic factors, becomes equal to one involving $\frac{2n}{h^2}$ purely genetic factors. The distribution thus follows the expansion $(\frac{1}{2}+\frac{1}{2})^{\frac{2n}{h^2}}$, the standard deviation of which is $\sqrt{\frac{n}{2h^2}}$.

The proportion of plus factors for a deviation of s times the standard deviation is now $\frac{1}{2}\left(1+\frac{sh}{\sqrt{2n}}\right)$. The proportion of heterozygosis in the average pair of allelomorphs:

$$p=\frac{1}{2}\left(1-\frac{s^2h^2}{2n}\right)$$

The result applies, of course, only to the genetic factors. The non-genetic factors continue to vary as much as before. Thus the portion of the standard deviation due to heredity becomes continually less, making the fixation of the characteristic by selection continually more difficult.

SUMMARY

Selection brings about some degree of control over heredity, as long as it is in process, through reduction of variation. The relative proportions of the factors in each set of allelomorphs are modified. There is no permanent increase in homozygosis except such as goes with the change in the proportions of the allelomorphic factors. The two extreme types are the only ones which can be permanently fixed. Even in these cases, the rate of progress continually falls off as the relative importance of external factors on the characteristic becomes greater.

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