

SYSTEMS OF MATING. V. GENERAL CONSIDERATIONS

SEWALL WRIGHT

Bureau of Animal Industry, United States Department of Agriculture, Washington, D. C.

Received October 29, 1920

TABLE OF CONTENTS

INTRODUCTION.....	167
Systems of breeding.....	167
Parental and fraternal correlations.....	169
Homozygosis.....	171
The percentage of homozygosis after inbreeding.....	172
Homozygosis under assortative mating.....	174
The effect of selection on homozygosis.....	176
The variability of the population.....	176
SUMMARY.....	177
LITERATURE CITED.....	178

INTRODUCTION

Some of the effects of representative systems of breeding on the composition of a population have been presented in the preceding papers of this series. The purpose of the present paper is to bring together the more important of the results, unencumbered by the mathematics involved in their calculation.

SYSTEMS OF BREEDING

The systems of breeding which have been considered, aside from random mating, are inbreeding of various sorts, assortative and disassortative mating based on somatic resemblance, and selection. With random mating, inbreeding or assortative mating, the relative frequency of the different genetic factors in the original population remains constant. Resumption of random mating leads to a restoration of the composition of the original population. Selection in the sense in which it is here used, which includes any differential rate of reproduction among the classes, whether due to differences in death rate, mating rate, or fecundity, modifies the relative frequencies of the factors and so alone effects a permanent change in the average composition of the population.

These systems of breeding may be combined. Thus the combination of inbreeding with assortative mating has been considered briefly. Most

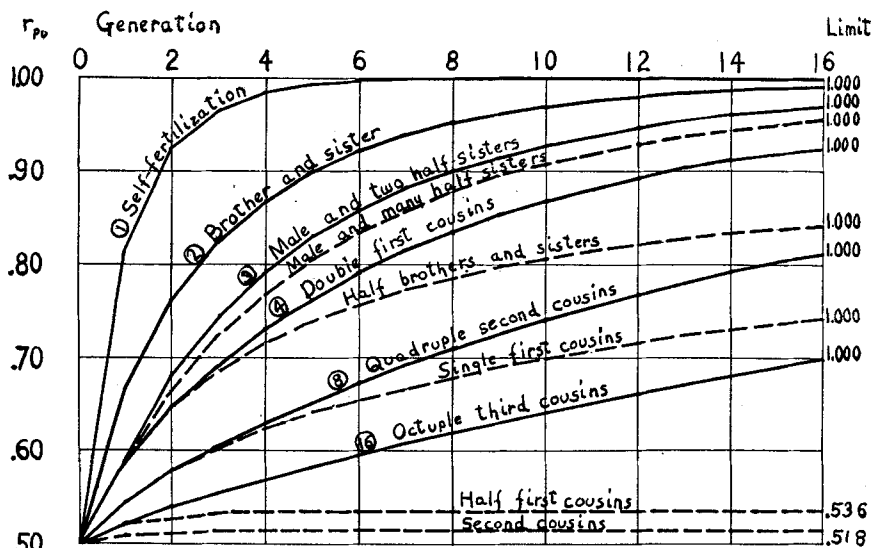


FIGURE 1.—The correlation between parent and offspring in successive generations under various systems of inbreeding for a characteristic determined wholly by heredity and without dominance.

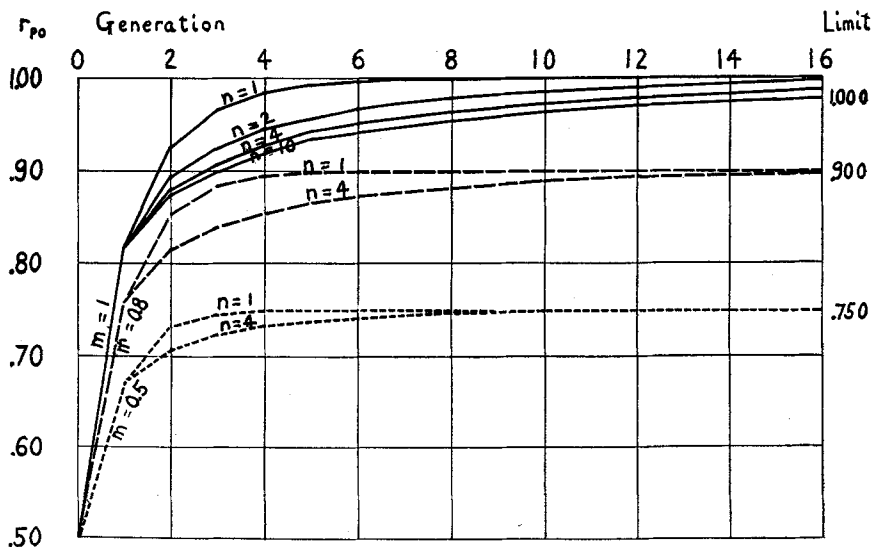


FIGURE 2.—The correlation between parent and offspring in successive generations under different degrees of assortative mating ($r_{pp} = m$) and different numbers of factors (n).

of the systems of inbreeding lead to the breaking up of the population into non-interbreeding lines. The selection of one of these lines, may, of course, be followed by random breeding without restoring the original composition of the population. The combination of all systems, i.e., the selection from among inbred lines, within each of which there has been assortative mating and selection, is, of course, the most effective way of modifying the characteristics of a stock.

In considering the effects of these systems of breeding, the correlation between parent and offspring, that between full brothers, the average percentage of homozygosis, the combinations of the factors which tend to become fixed and the variability of the stock are among the chief points of interest. The complications due to dominance, number of factors, linkage and the degree of determination by heredity should be considered in each case.

PARENTAL AND FRATERNAL CORRELATIONS

In practical breeding, one of the foremost considerations in the mind of the breeder is to obtain such control over the heredity of his stock that the characteristics of the progeny can be predicted from those of the parent. The most direct measure of the success of a system of breeding in this respect would seem to be the correlation between parent and offspring, relative to the general population. As there is a possibility of confusion here, it should be emphasized that in those cases in which the population becomes broken into isolated lines, the correlations between relatives measure the degree of control over heredity only when calculated from data involving a random sample from all possible lines of descent which could have been derived from the original stock. Thus the correlation between members of the same inbred line, from data combining a random group of inbred lines, approaches unity as inbreeding proceeds. The correlation between close relatives within a single line, on the other hand, approaches zero, provided that the characteristic is affected in the slightest degree by non-genetic factors.

Even in using the correlation between parent and offspring, found in the total population, as a measure of control over heredity, allowance must be made for the change in the variation of this population during the course of the inbreeding or assortative mating. A given correlation in a highly variable population means less in the way of control than the same correlation in a less variable population.

The correlations between parent and offspring and among brothers and sisters under various systems of mating are shown in figures 1, 2, 3, and 4.

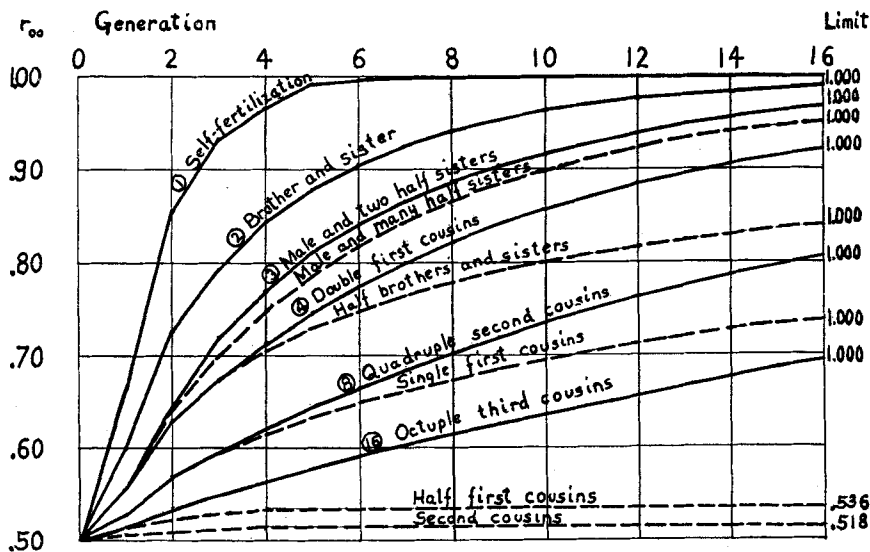


FIGURE 3.—The correlation between brothers in successive generations under various systems of inbreeding, for a characteristic determined wholly by heredity and without dominance. Compare with figures 1 and 4.

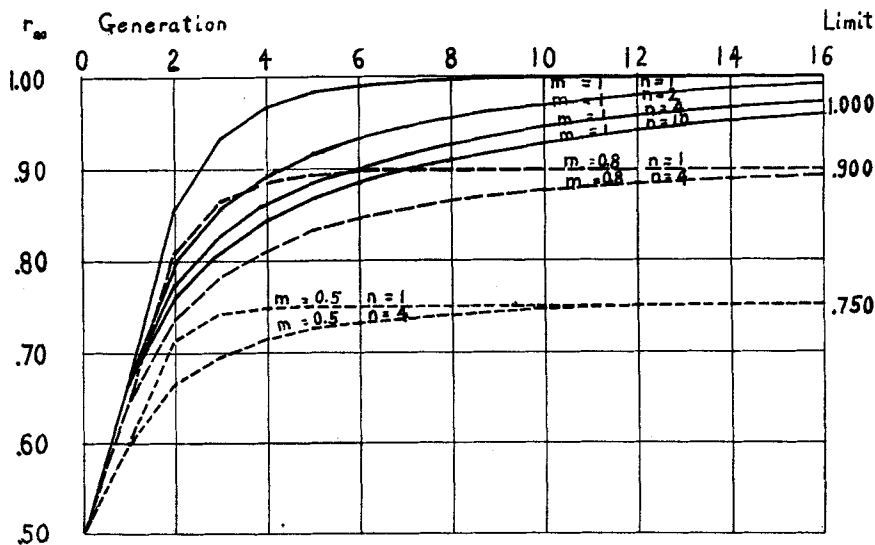


FIGURE 4.—The correlations between brothers in successive generations under different degrees of assortative mating ($r_{pp} = m$) and different numbers of factors (n). Compare with figures 6 and 2.

Figures 2 and 4 seem to indicate a high degree of control over heredity through assortative mating even for characters affected by many factors. This control, however, is relative to the greatly increased diversification of the total population under such a system of mating and means little as to actual reduction of variation among the progeny of given parents. The writer hopes to deal directly with the changes in the variation among brothers and sisters in a later paper. For the present, the percentage of homozygosis gives the best single measure of the effects of different systems.

HOMOZYGOSIS

The average percentage of homozygosis is important in a number of ways. It measures the permanency of the change effected by the system of mating. Thus, no matter how high the correlation between parent and offspring, random mating among the descendants of even a carefully selected group will be followed by the loss of the uniformity which has been gained unless the group consists of individuals homozygous in the same factors.

The percentage of homozygosis of an individual is also important as one element in the very important quality of prepotency. Prepotency, as used by livestock breeders, means the power of an individual to exert a predominating influence on the character of his progeny. With our present knowledge of genetics, it seems clear that prepotency depends largely on homozygosis in dominant factors; the number of factors involved and linkage, being it may be added, important elements in the transmission of prepotency. Fixation of heredity and prepotency are generally desired in practical breeding. Unfortunately, a high percentage of homozygosis is also apt to go with a reduction in fecundity, growth and vigor. These effects appear to be due to the greater frequency with which mutations are recessive than dominant, and to the greater likelihood that any mutation will be harmful than advantageous. Thus dominant factors seem to be, as a rule, more conducive to vigor than recessive ones. With a given proportion of dominant and recessive factors in a stock, the proportion of individuals showing each dominant factor varies with the amount of heterozygosis. Moreover, as JONES (1917) has pointed out, the likelihood that certain of the factors conducive to vigor will be linked with injurious factors reduces the chance of obtaining vigorous homozygous lines even by selection.

THE PERCENTAGE OF HOMOZYGOSIS AFTER INBREEDING

Figure 5 shows the increase in homozygosis in successive generations of various systems of inbreeding. These results are independent of the degree of determination by heredity, dominance, the number of factors or linkage.

The solid lines show a series of systems in which the population breaks up into non-interbreeding lines in which there is a limited number of individuals in each generation. Self-fertilization (one individual in each

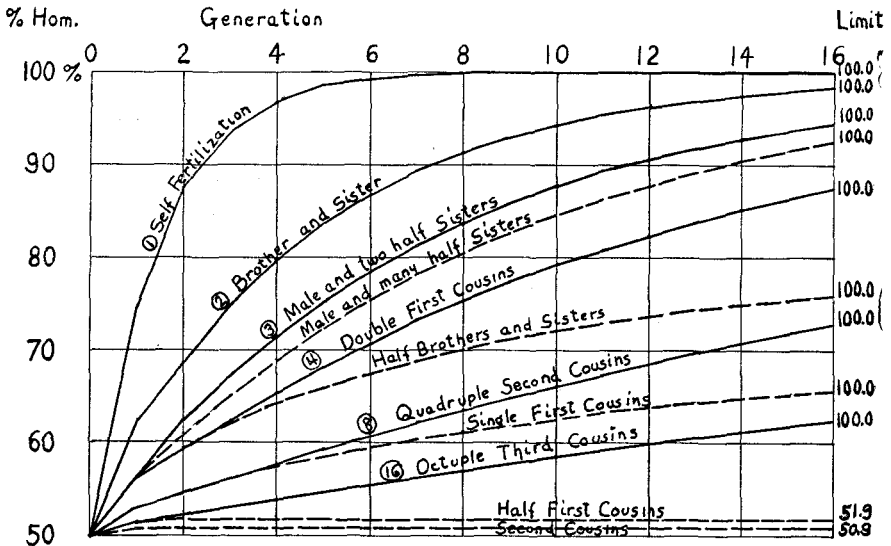


FIGURE 5.—The percentage of homozygosis in successive generations under various systems of inbreeding. Systems in which the population breaks up into separate lines containing a constant number of individuals are represented by solid lines, the number of individuals being indicated. The percentage of homozygosis after an indefinite number of generations, is given at the right for each system.

generation in each line) leads to a very rapid increase in homozygosis, 90 percent being passed in the third generation and 95 percent in the fourth. Continued brother-sister mating (two individuals in each generation) passed 90 percent homozygosis before the eighth generation and 95 percent before the eleventh. The system in which one male in each line is mated with two half-sisters, full sisters of each other (three individuals in each generation), passes 90 percent homozygosis in the twelfth generation. Continued mating of double first cousins (four individuals in each generation) does not pass 90 percent homozygosis until about the seventeenth or eighteenth generation. The rates of increase in the cases of

quadruple second cousins (eight individuals in a generation) and octuple third cousins (sixteen individuals in a generation) are naturally slower.

These systems of mating are of interest as representing the least possible inbreeding within lines containing a constant number of individuals. In all of them, there is a continuous approach toward perfect homozygosis. The general formula obtained for systems of this kind shows that this is true in all cases of this kind. Thus there can be no equilibrium in a population of limited size, until perfect genetic uniformity is reached provided that there is no differential reproductive rate among the classes. The familiar formula for a Mendelian population in equilibrium, $x^2 AA + 2xy Aa + y^2 aa$, applies strictly only to a population of infinite size. However, the rate of increase in homozygosis in populations of more than sixteen is so slow, where inbreeding is avoided, that it is ordinarily of little significance.

The system in which one male is mated with half-sisters, which are half-sisters of each other, breaks the population into distinct lines, but lines whose size is limited only by the number of females which can be used with one male. This system is the highest shown in dotted lines in figure 1. There is a fairly rapid increase in homozygosis, 90 percent being passed before the eleventh generation and 95 percent about the eighteenth. This system is of interest as being probably the most practical method of fixing a character in a herd of live-stock. If a man breeds wholly within his herd, saving one male in each generation, the typical mating will be between half-brother and sister, and most of the females will be half-sisters of each other. The system is economical in the use of males, permitting careful selection of the herd sire, and results in the simultaneous fixation of the same characteristics throughout the herd. With the other systems considered, nearly as many males must be saved as females and the herd can not be held together easily, tending to break into sub-groups in each generation, within which different characters tend to become fixed.

In all but the last system, described above, the number of ancestors in each generation (back of a certain point) is constant. Theoretically, in the last system, the number of ancestors of an individual increases by one in each generation. Practically, of course, it would be impossible to carry out the system strictly in this way. The occasional use of females which were full sisters of each other would, however, have very little effect on the rate of increase in homozygosis, as may be seen by comparing the curve for the system in question with that immediately above it in figure 5.

The second broken line shows the effects of the system in which each male is mated with two half-sisters and each female with two half-brothers.

This gives a network of descent in which the number of ancestors of any individual increases by one with each generation back. The continued mating of first cousins produces a somewhat similar type of pedigree, the number of ancestors increasing by two in each generation. In both of these cases, there is a continuous approach toward perfect homozygosis but at a rather slow rate. The percentage of homozygosis rises only from 50 to 75 percent after fourteen generations of the system of mating half-brothers and sisters described above, and only to 65 percent in the same number of generations of first-cousin mating.

It might be thought that any system of inbreeding if followed consistently would lead ultimately to perfect homozygosis. It appears, however, that this is not the case for matings more remote than between single first cousins within a population which can be considered indefinitely large. The continued mating of half-first cousins causes a rise from 50 percent to 52 percent homozygosis after an infinite number of generations. This is about the same change as is to be expected after fifteen generations of mating in a population of 100 in which inbreeding is avoided as far as possible. The continued mating of second cousins only causes a rise in homozygosis from 50 percent to 51 percent.

As already noted, it seems most probable that the general effects of inbreeding—fixation of characteristics, decline in fertility, size and vigor—are due to increasing homozygosis. On this view, matings more remote than between first cousins are of virtually no significance as inbreeding. The limitation of the breeding population to less than 100 in a generation is of more significance even within fifteen generations.

It should be pointed out, however, that where a character depends on a single recessive factor, rare in the general population, but known to be present in a particular family, the mating of half-first cousins, second cousins, or even more remote relatives may mean sufficient chance of recurrence of the character to be given consideration.

HOMOZYGOSIS UNDER ASSORTATIVE MATING

The degree of homozygosis following assortative mating based on somatic characteristics depends not merely on the closeness of the assortative mating, but also on the degree of determination by heredity, the number of factors, linkage and dominance. There is an approach toward perfect homozygosis as a limit only if there is perfect assortative mating and complete determination by heredity. Even under these conditions, as shown in figure 6, the approach is rather slow where the characteristic depends

on as many as four equivalent factors. Dominance also greatly reduces the rate of increase in homozygosis. With linkage, the effect would be that of a smaller number of factors than actually present.

Complete determination by heredity is not common in practice. If there is any variation due to environment or irregularity in development, the percentage of homozygosis approaches an equilibrium point which falls far short of unity even where such variation is not great.

Imperfect assortative mating reduces also the level at which the percentage of homozygosis reaches equilibrium. This is illustrated in figure 6.

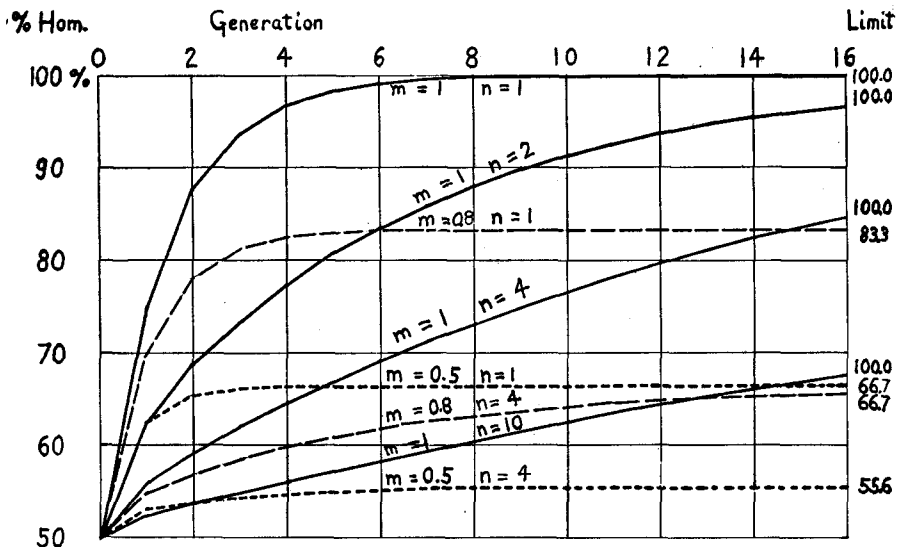


FIGURE 6.—The percentage of homozygosis in successive generations under different degrees of assortative mating ($r_{pp} = m = 1.00, 0.80, \text{ or } 0.50$) and different numbers of factors ($n = 1, 2, 4 \text{ or } 10$). It is assumed that all variation is genetic and that there is no dominance. The limiting percentages are given to the right.

In most actual cases there will be a certain amount of non-genetic variation and perfect assortative mating is not likely to be attained. Taking also into account that most characteristics seem to depend on a considerable number of factors and that there is likely to be some dominance, it may be concluded that assortative mating based on somatic characteristics is seldom of much value as a means of increasing homozygosis and hence of permanently fixing characteristics or of bringing about prepotency.

Combinations of inbreeding with assortative mating bring about an increase in homozygosis which is only slightly less than the sum of the separate effects as long as these are small. The combined effect is, of

course, always somewhere between the larger single effect and unity. Random breeding in a group of close relatives from an inbred line causes no substantial loss in homozygosis, however long it is continued.

THE EFFECT OF SELECTION ON HOMOZYGOSIS

Continued selection toward a given type, from a stock in which there has not been inbreeding, causes an immediate change in the relative frequencies of the favorable and unfavorable genes in each set of allelomorphs. This in itself brings about some increase in homozygosis. Thus, a change from 50 percent *A*, 50 percent *a*, to 75 per cent *A*, 25 per cent *a*, means a change from 50 percent homozygosis to 62.5 percent. Further selection toward the average reached by the first generation, however, produces no increase in homozygosis. There is continuous progress toward perfect homozygosis only when selection is directed toward an extreme type. Even in this case the rate of progress continually falls off unless mutations occur frequently. Straight selection unaccompanied by close breeding is thus not an effective method for permanently fixing characteristics.

THE VARIABILITY OF THE POPULATION

Either close inbreeding or assortative mating, unaccompanied by selection, leads to increased variability in the population as a whole. The distribution curves under certain conditions are shown in figure 7. Any system of inbreeding which leads to complete homozygosis in all lines, brings about a doubling of the squared standard deviation of the whole population in so far as the variability is genetic. The same result follows assortative mating of + 0.50 if an indefinitely large number of factors is involved. The effect is somewhat less for small numbers of factors. With closer assortative mating there is still greater diversification of the population until under perfect assortative mating, the population reaches equilibrium only when concentrated at the two extremes.

Disassortative mating, on the other hand, naturally holds the population together better than random mating. Perfect disassortative mating halves the squared standard deviation, giving a population in which there is no correlation between parent and offspring and none between brothers if environmental factors and dominance are absent.

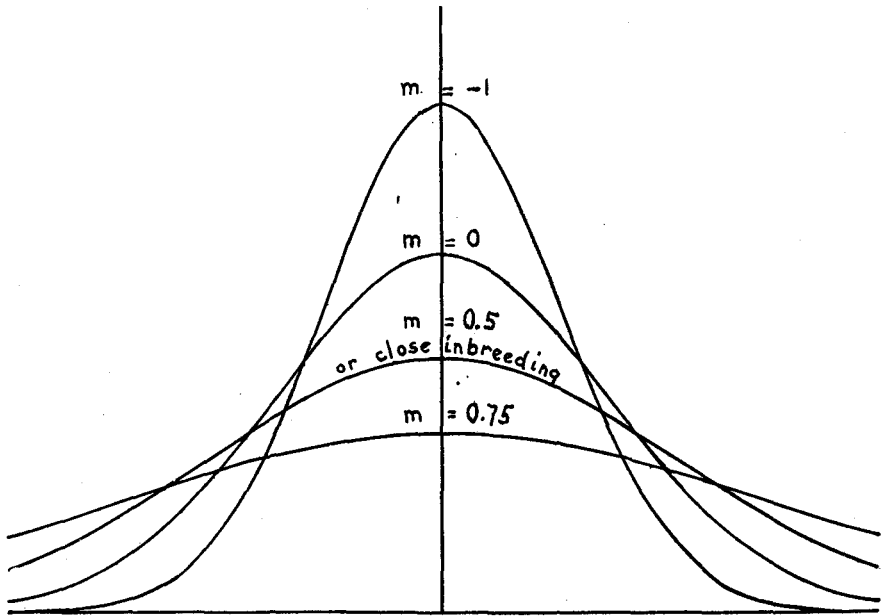


FIGURE 7.—The distribution curves of populations in which variation is wholly genetic and due to a large number of factors, after reaching equilibrium, following an indefinitely large number of generations of perfect disassortative mating ($m = -1.00$), imperfect assortative mating ($m = 0.50$ or 0.75), or any system of close inbreeding (leading to 100 percent homozygosis), compared with that in the original random-bred stock ($m = 0$). Perfect assortative mating ($m = 1.00$) leads to concentration of the population at the two extremes of the range.

SUMMARY

It will be seen that all of the systems of mating have their advantages and disadvantages. Close inbreeding automatically brings about fixation of type and prepotency. Intermediate types are fixed as readily as extremes. It is the only method of bringing to light hereditary differences in characters which are determined largely by factors other than heredity. On the other hand, close inbreeding is likely to lead toward reduced fertility, size and vigor.

Matings between relatives more remote than first cousins have little significance as inbreeding, except in so far as there is continued breeding within a population of small size.

Assortative mating and selection can lead to fixation of extreme types only and are not very efficient in this respect. Selection, however, is the only means of permanently changing the relative proportions of the various genes present in the original stock. It is an essential adjunct of the other systems as means of improvement.

Assortative mating leads to the greatest diversification of the population as a whole, and thus is practically always accompanied by selection either in nature or in live-stock breeding. Under conditions such that all progeny are to be saved for breeding, this diversification of the population is a disadvantage. Disassortative mating is the method which best holds the whole population together, pending the fixation of the average type by close inbreeding.

LITERATURE CITED

- JONES, D. F., 1917 Dominance of linked factors as a means of accounting for heterosis. *Genetics* 2: 466-479.
- WRIGHT, S., 1921 a Systems of mating. I. The biometric relations between parent and offspring. *Genetics* 6: 111-123.
- 1921 b Systems of mating. II. The effects of inbreeding on the genetic composition of a population. *Genetics* 6: 124-143.
- 1921 c Systems of mating. III. Assortative mating based on somatic resemblance. *Genetics* 6: 144-161.
- 1921 d Systems of mating. IV. The effects of selection. *Genetics* 6: 162-166.