

and Poland-China swine. Allen (*Domestic Animals*, pages 26 and 27), writing in 1847, says of cattle: "Every country and almost every district has its peculiar breeds, which by long association have become adapted to the food and circumstances of its position and, when found profitable, they should be exchanged for others, only after the most thorough trial of superior fitness for the particular location, in those proposed to be introduced."

Appreciation of the usefulness of improved breeding stock followed hard on the heels of the pioneering period. Cattle of the Shorthorn, Hereford, and Devon breeds were imported around 1800; although there were yet no herdbooks for those breeds. The new pedigree breeding methods of Britain were followed with interest. The individual pedigrees for the Herefords and for the Devons in those early importations were not permanently preserved, but some of the pedigrees in the early volumes of the American Shorthorn Herdbook trace in part to animals imported as long ago as 1817. Enthusiasm for pedigree breeding sometimes reached the stage of extreme speculation, as with some of the Merino sheep breeding early in the nineteenth century and with the Duchess Shorthorns in the 1870's.

General interest in pedigree breeding was mainly confined to the Shorthorn breed and to certain light horses and to the early sheep breeding in New England until the era of agricultural expansion which began soon after the Civil War. Then purebreeding became fashionable for all kinds of animals. The period from 1870 to around 1890 saw the founding and rapid expansion of breeding societies for almost all kinds of livestock, each with its herdbook, scorecard, etc. Most of the breeds were introduced from Britain; although there were a few from other places, such as the Holstein-Friesians from Holland and the Brown Swiss from Switzerland and draft horses from Belgium and France. Also, there were some native breeds like the cornbelt breeds of swine and the Standardbred and American Saddle Horses. The agricultural colleges, most of which were founded just before or early in this period, promoted the movement toward the general use of purebred sires as one of the quickest ways to improve the quality and efficiency of animal production. Experiments to find or demonstrate the value of the purebred sire in grading up common stock were conducted at some agricultural colleges until well into the 1920's.

The purebreds seemed obviously superior to the common stock in many ways, especially as the country was becoming urbanized and the available markets for animals were becoming similar to the markets for which the British stock had been bred for many animal generations. The initial gulf between the purebreds and the native stock was a wide

one in most cases, since no large group of high grades with which to compare the purebreds had yet been produced. The most urgent need of the times in animal breeding seemed clearly to be a wider use of purebreds.

This expansion in the use of purebred sires made a generally expanding or rising market for the business of producing purebred sires. In turn, that favorable economic situation led to the establishment of still more herds and flocks of purebreds. Of course this rapid expansion in numbers of purebreds could not continue forever. For most breeds it came to a rather abrupt end with the economic depression which began for most agricultural enterprises about 1920. That economic crisis merely hastened the end of the remarkable expansion in purebred numbers which began about 1870. There is still room for promotion of the wider use of purebred sires, and doubtless some expansion in the total number of purebreds will yet be seen; but it will be at a slower percentage rate than was generally true for the half century ending in 1920. There are almost enough purebred flocks and herds to produce as many purebred sires as can be sold at a profitable price for use in commercial flocks and herds.

This end to the long period of expansion in numbers has meant a serious readjustment of the business of those who produce purebreds, and it has also had an effect on the way they regard current breeding problems. There may be nearly enough registered sires to supply all the demand which exists or can be aroused by good salesmanship, but there are not enough highly meritorious registered sires. Much of the emphasis which used to be given to breed expansion is being changed to breed improvement.

A contributory cause to this change of emphasis is that for most breeds large numbers of high grades have already been produced. Some of those are individually more meritorious in a practical way than the average of the purebreds, even though the average of the grades remains below that of the purebreds. Most of the experiments with the use of purebred sires for grading have shown that the averages of grades with more than two crosses of pure blood (that is, with more than 75 per cent pure blood) are very little below the average of the pure breed concerned. When there were no high grades for comparison, the differences between different purebreds seemed small and not worth much emphasis, compared with the gulf which often existed between the introduced purebred and the common native stock. Now the differences between members of the same pure breed are often large compared with the small average differences between purebred and high grade.

The idea of breed improvement is not new in kind—it is merely

receiving more emphasis than formerly. Nearly all of the breed associations included improvement of the breed in their very first statements of the objectives of their association. An excellent example of that was the insistence by many of the early Holstein-Friesian breeders on the adoption of a system of official testing of production before they would merge their two breed associations, one of which lacked this feature. Nearly every breed association, very early in its existence, adopted a scorecard or some other form of official description of the ideal toward which they were working. Occasionally they even went to considerable trouble or expense trying out plans which were intended to improve the breed more rapidly. Often these did not work as expected and had later to be discarded. Examples are the bounties which the Holstein-

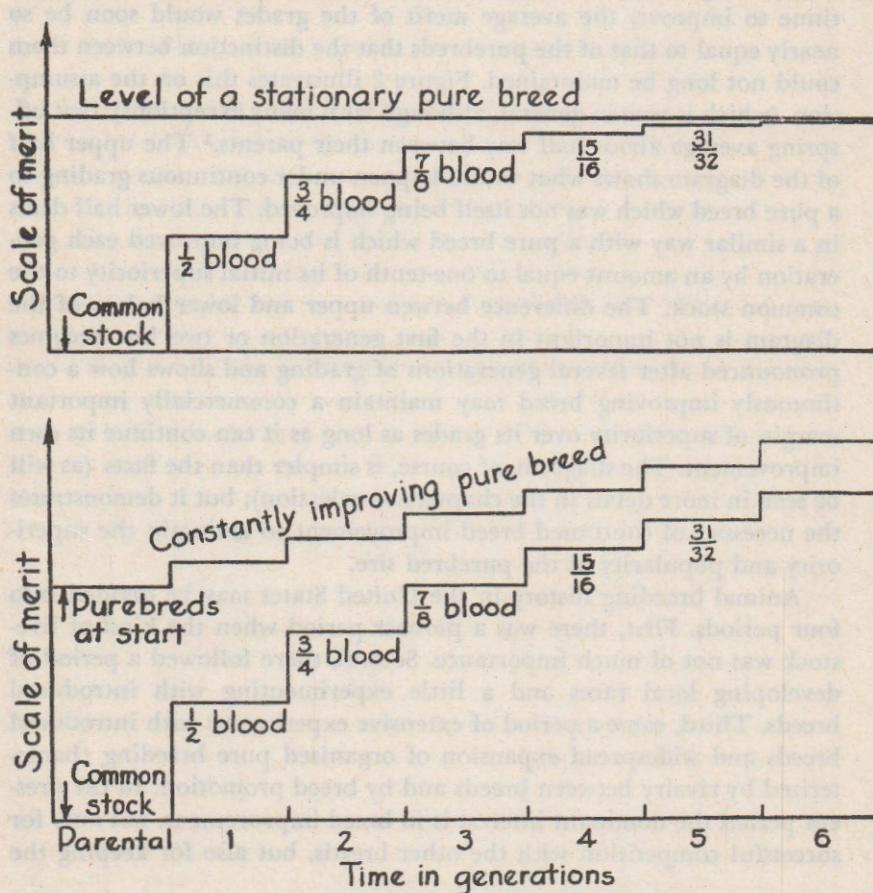


FIG. 2. The contrast between grading to a pure breed which is stationary in merit and grading to a pure breed which is improving its merit by a constant amount each generation.

Friesian association offered in 1889-1891 for butchering or castrating bull calves which would have been eligible for registry, and the ruling of the Hereford association (in effect during 1895-1897) that 10 per cent of all applications for registry of bulls would be refused. The Aberdeen-Angus Association in 1887 had a rule that of every ten bull calves eligible to registry, one must be castrated or two shall be dropped from record. Actually it appears that 70 were castrated and 8 were unrecorded while this was in force.

The very fact that the purebred has generally been found useful in grading up common stock carries with it the necessity for the continued improvement of the purebred itself if the distinction between pure breeds and grades is to be maintained. If the pure breed did not continue to improve, the average merit of the grades would soon be so nearly equal to that of the purebreds that the distinction between them could not long be maintained. Figure 2 illustrates this on the assumption (which is true in general, although with many exceptions) that offspring average about half way between their parents.¹ The upper half of the diagram shows what would happen under continuous grading to a pure breed which was not itself being improved. The lower half deals in a similar way with a pure breed which is being improved each generation by an amount equal to one-tenth of its initial superiority to the common stock. The difference between upper and lower halves of the diagram is not important in the first generation or two but becomes pronounced after several generations of grading and shows how a continuously improving breed may maintain a commercially important margin of superiority over its grades as long as it can continue its own improvement. The diagram, of course, is simpler than the facts (as will be seen in more detail in the chapters on selection); but it demonstrates the necessity of continued breed improvement to maintain the superiority and popularity of the purebred sire.

Animal breeding history in the United States may be divided into four periods. First, there was a pioneer period when the kind of livestock was not of much importance. Second, there followed a period of developing local races and a little experimenting with introduced breeds. Third, came a period of extensive experiments with introduced breeds and widespread expansion of organized pure breeding characterized by rivalry between breeds and by breed promotion. In the present period the dominant interest is in breed improvement, not only for successful competition with the other breeds, but also for keeping the

¹ Allowance for regression toward the mean of the groups from which the parents were chosen needs to be made if the parents were selected individuals. Also *heterosis* sometimes causes the first-cross generation to be better than the diagram indicates.

purebreds distinctly ahead of the grades of the same breed in order to maintain a steady demand for purebred sires. These periods did not begin and end suddenly but merged gradually into each other, and some of the elements which characterize each period were present in lesser degree in all periods. At present it seems likely that plans for breed improvement will go on within the framework of the existing systems of purebreeding, but here and there occurs some experimenting with the combination of more or less blood from two or more breeds, just as was done by some of the breed founders in the days before strictly pure breeding and registration became the standard methods of improved breeding.

CHAPTER 5

The Relation of the Breed Association to Breed Improvement

The activities of the breed associations are intended to maintain the present merit of the breed, to improve the merit of the breed, and to promote the business interests of the members. Some activities serve all three of these purposes, and many serve two of them.

The primary object of breed associations, particularly in countries to which the breed is not native, is to *safeguard the purity* of the breed and to furnish accurate pedigrees to all breeders who desire them. In practically all cases the breed association took over the conduct of the herdbook early in the history of the association. Most of the clerical work in most associations is used for issuing and checking the accuracy of registrations and transfers. Most of the errors discovered in applications for registry or transfer are matters of carelessness or neglect, but close watch is kept for fraud, and occasionally a member is expelled for this reason or his registrations are canceled. Because of the possibility of legal complications and internal dissension, this is not usually done unless the proof is quite conclusive. The accuracy of a pedigree depends mainly upon the honesty and carefulness of the man who signs the application for registry. But the breed association's policy of rejecting or returning applications not accurate in detail and of investigating within reasonable limits cases where fraud is suspected prevents many errors which would come into pedigrees if there were no such supervision. Some associations publish the facts when a member is expelled or registrations are canceled because of fraud. Others keep it quiet to avoid scandal. Probably the first policy is generally the wiser. In either case the news usually spreads fast. Safeguarding the purity of a breed does nothing to *increase* its merit but does act to some extent as a ratchet mechanism to maintain whatever special merit the breed already has and to hold any future improvements which may be made in its average merit. Preserving the present merit of the breed is particularly important if the breed is an introduced one, few in numbers, and surrounded by animals of distinctly different origin.

A breed association tries to *improve* the merit of the breed by guiding the ideals which the breeders use when making their selections and by making official tests or ratings of the productiveness or conformation of individual animals. The ideals of the breeders are influenced by such activities as adopting a score card, or other verbal description of the breed ideal, or a series of "true type" pictures or models. A different approach to the same goal is through control of judging standards at the various fairs. Sometimes that amounts only to advising the fair management upon request whether the breed association considers a certain individual competent to judge that breed. In other cases the breed association prepares a fairly small list of men considered competent, and its contributions of prize money are contingent upon the fair management's selecting its judge from that list. Sometimes the association prints circulars or uses advertisements which serve the double purpose of promoting wider interest in the breed and showing pictures of animals which are considered nearly ideal for that breed. The association sometimes instructs its members as to what is considered important in pedigrees (See example in *Holstein-Friesian World*, 33:300, April 4, 1936).

The general purpose of all these ways of teaching the breeders the official ideals for that breed is that the breeders thus informed shall follow those standards when making their own selections and cullings and will thus move the breed average nearer to the breed ideal. The breed association's efforts end with presenting the lesson to the breeder. Unless he asks for further help from the fieldman or other officer, it is entirely up to him whether he accepts the official ideal and how much or how little he uses it when making his selections and cullings.

Official tests of the speed of individual horses were characteristic of the Thoroughbred and the Standardbred from the very beginning. In the case of the latter, a certain speed was necessary for registration—hence the name of the breed. As long ago as 1832 the preface to the list of Thoroughbred horses in Prussia contained the statement: "Unless herdbooks contain production tests, they will be useless and without interest, since they will contain only names, of which no one knows anything and which mean nothing." (Engeler, 1936). Official testing of dairy cattle began around 1880¹ with the Holstein-Friesian breed in the United States, largely as a result of the work of Solomon Hoxie. (Private production records were being kept at least as long ago as the time of Thomas Bates.) For a number of years there were serious doubts as to whether official testing would become popular enough to be retained.

¹ Pages 15 and 16 of *Holstein-Friesian History*, by Prescott, Price, Wing, and Prescott.

However, it eventually proved so useful, not only for breed improvement but also as an aid in advertising and selling, that no dairy breed association would now try to do without its department of official testing. But such official tests are not yet a prerequisite to registration. Whether the breeder will test or not is still entirely voluntary with him, except as the demands of a considerable portion of his customers put some economic compulsion on him to test.

In the United States, official inspection of whole herds, with a rating of each animal for type, was begun on a voluntary plan in 1929 by one of the dairy breeds and has since been adopted by most of the others. This plan was used by only a few breeders during the depression of the 1930's but now seems to be spreading more rapidly. Type inspection or scoring, sometimes on a compulsory basis, has been practiced much longer in some other countries; for example in The Netherlands or Switzerland.

Many of the swine associations have required the man who registers a litter to report the number of pigs farrowed and raised. Some have published in the herdbooks the number farrowed in each litter. Recently Records of Performance have been established by several of the swine breed associations, the Hampshire having been the first. These are based mostly on weight of litter weaned at 56 days. They are still voluntary and are just beginning to be tried on an extensive scale. They seem to be a sound step forward, but their wide adoption will probably depend on how insistently the breeder's customers ask for such information when they come to buy boars.

Tests for measuring the practical productiveness of beef cattle are being studied at experiment stations,² but these have not been adopted by any of the beef breed associations.

There have been some discussions of a Record of Performance for sheep, particularly for the fine-wool breeds. The shearing records made in New England a century ago were a kind of crude beginning in that direction. No definite plan is in actual operation today.

Although there has been some experimenting with endurance rides for cavalry horses and with pulling tests for draft horses, these have not yet been made an official part of breed association activities.

The associations in the United States do not usually keep official lists of the prizes won by individual animals at the important shows, although some of them do so in an unofficial way. In many cases the breed paper performs that service.

With a very few exceptions—such as the speed requirement for the

² See Montana Agr. Exp. Sta., Bul. 397; also Minnesota Agr. Exp. Sta., Tech. Bul. 94; also *Empire Jour. of Exp. Agriculture*, 8:259-68.

Standardbred horse, the type inspection given to Brahman cattle which are admitted as foundation stock, and the flock inspections which are a part of some plans of poultry improvement—the purely voluntary nature of the production-testing and type-rating done under the auspices of the breed associations in the United States is like that in Britain, but is in marked contrast to the compulsory inspections or testing in some breeds in continental Europe. Those are discussed in more detail in the chapter on selective registration. In considering how far it would be possible or wise for the American associations to go in that direction, there are broad general questions as to how far collective policies and efforts can or should replace or supplement individual freedom to follow whatever breeding policies or use whatever purebred animals one pleases, without regard to whether those would be approved by a majority of one's fellow breeders or by an official inspector of the association. Besides such questions of general principle, there are also some immediately practical questions of expense which might make impossible, in breeds as widely scattered as many of those in the United States, procedures which are feasible in lands where the breed is highly concentrated in one or a few localities. Most directors of the breed associations in the United States are reasonably eager to adopt any new practices or requirements which will increase the merit of their breed faster than at present. They usually demand that the new plan shall be tested in actual operation, however, before they commit their association definitely to it. They have sometimes tried a plausible scheme only to find that it did not work as well as they had felt sure it would, and traces of the confusion and discontent which resulted have remained for years to plague them.

Naturally, many activities of the breed association are directed mainly at promoting the present business interests of the members. Examples are the efforts to expand the breed numbers by getting new breeders to establish herds, the promotion or management of sales and the correspondence which the secretary's office has with would-be purchasers of breeding stock. Most associations prefer to give support and encouragement to sales efforts but not actually to manage the sale themselves lest the dissatisfactions which inevitably arise about some transactions should result in animosity toward the association itself.

The provision of prize money at the more important shows is intended to promote the breed by bringing out larger numbers, thus giving more advertisement to the breed. It is also intended to improve the breed by teaching more people the ideal for that breed.

Many of the larger breeds have one or more papers devoted mainly to promoting the interests of the breed. Most of these breed papers are

privately owned and managed, but some are owned and operated by the association itself. The contact between the association and the breed paper is close and important to both parties, even when the paper is privately owned. Most of the activities of the breed paper are devoted to the immediate business interests of the members—advertisements and news of sales, merchandise for breeder's needs, etc.—but some of these papers carry articles and information helpful in improving the merit of the breed, but not otherwise a matter of financial profit to anyone. Besides the breed papers, most associations print leaflets, buy advertising space in other magazines which reach stockmen, and make occasional use of the radio as part of their regular efforts at breed promotion.

The activities of the fieldmen or breed extension service are in considerable part devoted to expanding the numbers of the breed and helping new breeders get started. The fieldmen work also with boys' and girls' clubs and help established breeders with their problems.

The forms of government of the breed associations vary widely. Usually the policies are determined by an unsalaried board of directors, preferably with overlapping terms and only one-third elected each year to prevent erratic changes in policies. The executive work of carrying out those policies is administered by a paid secretary. Sometimes there is a fixed number of shares of stock, as in most industrial corporations, and one can become a stockholder only by buying a share from someone else. More often the number of shares is not limited but any breeder approved by the board of directors may become a member by paying a fixed (usually small) sum for a non-transferable membership. Sometimes all members present at the annual meeting can vote. In other associations members not present can vote by proxy. Other associations, especially those with large financial reserves, have more or less elaborate systems of delegates or representatives chosen by districts, to ensure proportional representation and to avoid abuse of the proxy system. The form of government is important insofar as it may promote or endanger stability in conducting the association's activities, make it easy or difficult for the board of directors to see that the secretary carries out the general policies they wish, and make it easy or difficult for a minority to seize and hold control. Some of the cases where there are two or more associations for the same breed had their origin in intense dissatisfaction on the part of a group which was not in control, either because it was a minority or because control had been seized by another group which could not be ousted with the existing machinery for governing that association. At one time there were seven separate organizations recording Poland China pedigrees. The number was not finally reduced to one until 1946.

The current problems of the breed associations are numerous. Financial problems have been acute with many associations since 1920. Nearly all of the swine and sheep associations and some of the cattle and horse associations have suspended publication of their herdbooks. What the final substitute for the printed herdbook will be is not yet evident. In some breeds there are still two or more registration associations, with some duplication of operating expenses.

An innovation which is still in the experimental stage in the United States, although it was used by breeders of Thoroughbreds a century ago and advocated by Thomas Bates as a means of overcoming what he thought were defects in the conduct of the Coates Herdbook for Short-horns, is the filing of birth certificates which act as tentative registrations. They keep the date of birth and the records of parentage straight but permit the owner to wait until the animal is mature to complete the registration. This is a common practice in those European associations which require inspection for conformation. Since such inspection must wait until the animal approaches maturity, records of parentage might become lost or incorrect in the interval if this precaution of filing a birth certificate were not taken. The increasing percentages which are incorrect when registration is delayed is illustrated by the following data³ on 19,172 Holstein-Friesian applications received during a six-weeks period.

AGE	PERCENTAGE INCORRECT
Under 2 months	13
2- 6 months	21
6-12 months	25
12-18 months	33
18-24 months	44
Over 24 months	53

The Jersey association has recently experimented with selective registry and a pedigree rating system (the "star bull" plan) for bulls. Several dairy associations are trying plans for calling attention officially to unusually meritorious proved sires; for example, the Ayrshire approved sire plan, and the Holstein-Friesian publication of sire indexes.

Herdbooks, as printed in the past, permit the tracing of pedigrees in only one direction; that is, one can learn from the herdbook what an animal's ancestors were but cannot find what offspring it had. Often a full list of an animal's offspring is more valuable than all that could be learned by studying its pedigree. Most breed associations maintain office records which will permit making such lists (at least from

³ *Holstein-Friesian World*, June 21, 1941, page 708.

females), but those are not published. The nearest approach to published lists of this kind is in the reports of official testing in the dairy breeds where the tested offspring of a given sire or dam may quickly be found. Usually little or nothing is published about the offspring which were not tested officially, although the Ayrshire association attempts to learn what became of each untested daughter of the bulls in its "approved sire plan."

In the United States the breed associations receive no direct financial support from the state or national governments. Correspondingly there is no governmental control or supervision of the associations or their activities, beyond whatever legal regulations apply in general to all nonprofit corporations or associations. However, the representatives of the United States Department of Agriculture and of the state agricultural colleges cooperate in many ways with the breed associations in activities which are expected to improve the practical merits of the breeds or to benefit the buyers of purebred sires. Examples are the supervision of official production tests for the dairy breeds, helping in the management and promotion of livestock shows, conducting purebred sire campaigns, promoting the use of proven sires, etc. In some countries the governments extend considerable financial aid and correspondingly exert some control over association policies. The details of such arrangements vary widely. Examples are Switzerland, The Netherlands, and (especially since 1936) Germany. In other countries, such as Canada and the Union of South Africa, the government cooperates in supervising registration and printing the herdbooks but does not participate in or control other activities of the associations. In yet other countries, such as Denmark and Argentina, the herdbooks are conducted by farmers cooperatives or by a "Rural Society," and the breed association either does not exist or is an advisory and promotional body.

Most of the breed *improvement* has to be done by the breeder himself. The association stands ready to help and advise him, but it does not select the animals he shall use or decide which he shall cull, except in the comparatively few cases where animals are barred from registry because they possess some undesired characteristic. Nor does the association decide which males shall be mated to which females. The actual selections and the choice of a mating system are left almost entirely to the individual breeder to do as he sees fit, provided his animals are purebred and the correctness of their pedigrees is unchallenged. Breed associations must remain more or less responsive to the opinions of the majority of the breeders and therefore cannot be expected to do much pioneering or testing of new and unpopular ideas. This will have to be

done by venturesome breeders or by public research institutions. Practical experience indicates that breed associations are necessary for breed improvement, since practically every breed which has persisted long has soon developed an association to look after its interests. Yet the association's part is on the whole the conservative one of helping hold whatever average merit the breed has already attained and acquainting the beginner and the public with what is considered ideal by most breeders of that breed. Most of the aggressive positive work toward improving the merit of the breed to still higher levels will have to be done by individual breeders who are unusually able, energetic, persevering, or lucky.

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- Early volumes of the herdbooks of the breeds in which you are interested. Read especially the minutes of some of the early business meetings.

CHAPTER 6

The Mendelian Basis of Inheritance

THE PARTICULATE AND DUPLICATE NATURE OF INHERITANCE

The essence of Mendelism is that inheritance is by particles or units (called genes hereafter) and that these genes are present in pairs, one member of each pair having come from each parent. Each gene maintains its identity generation after generation instead of blending with the other genes to form a new kind or blend of hereditary substance, as was thought in pre-Mendelian days. When the individual reproduces, it transmits to each offspring one or the other, but not both, of the genes in each pair it possesses. Thus the parent gives to each offspring only a sample half of its own inheritance. The laws of chance govern this sampling, subject to the restriction that each sample must contain one gene of every pair. This sampling nature of the process of inheritance, scarcely suspected in pre-Mendelian days, allows a parent to transmit different inheritance to different offspring. More precisely, if we let Aa represent a pair of genes in a parent which has two offspring, there is one chance in four (the exact result in individual cases varying, of course, according to the laws of sampling) that both offspring will get A . There is one chance in four that both will get a and there are two chances in four that one will get A and the other will get a . Similar probabilities apply to every other pair of genes. Thus, about half of the genes which two offspring receive from the same parent (i.e., about one-fourth of all the genes they have) are exact duplicates; but the other genes the two get from that parent (another fourth of all the genes they have) were opposite members of the pairs in that parent. In those pairs of genes for which the parent was homozygous it will not matter which gene of the pair is transmitted, for the result will be the same with either. Most parents are heterozygous for many pairs of genes. Here lies the explanation of the fact that identical pedigrees do not mean identical inheritance, although they usually do mean a considerable degree of likeness.¹ That identity of pedigree (as of full bro-

¹ To illustrate the Mendelian basis for the fact that identity of pedigree generally means similarity but not identity of inheritance, let us consider the probable results of a particular mating in a breed heterozygous for many pairs of genes and mating at random with respect to each pair. If the contrasting alleles in each pair are equally frequent in the breed, then the most probable Mendelian formula of mates chosen at

ers) does not mean identical heredity was well known in pre-Mendelian days but either was regarded as one of the unexplained mysteries of heredity or interpreted to mean that a large amount of entirely new inheritance (mutations we would say today) had arisen in each individual.

Since half of the inheritance comes from each parent, except in the case of sex-linked genes, and since in each pair the gene received from the sire and gene received from the dam are equally likely to be transmitted to any one offspring, most of the facts of inheritance when expressed in quantitative form involve the fraction 1/2. It is only a small exaggeration to say that the mathematics of genetics is the algebra of 1/2!

Dominance is not an essential part of Mendelism, although Mendel himself noted it. It is a ready explanation of some cases of "reversion" or "atavism," but not the only explanation for those. The chief part played by dominance is to increase the variability of the population slightly and to make certain genotypes indistinguishable from each other. There is nothing in the mechanism of inheritance which would cause a dominant gene to increase in numbers at the expense of its recessive allele, or the reverse. If q is the proportion of A genes and $1 - q$ is the proportion of a genes in the population and p is the proportion of heterozygotes, then no matter what system of mating prevails, the zygotic ratio will be $(q - p/2)AA:p\ Aa:(1 - q - p/2)aa$. If these have equal opportunity to reproduce (that is, if no selection for or against either of the three genotypes prevails), then the proportion of A genes in the next generation will be $q - p/2$ from the AA individuals plus $p/2$ from the Aa individuals which equals q in the whole

random can be illustrated as below, the mates being alike in some genes and unlike in others. How many different kinds of full sibs could there be from this particular mating? How many different kinds of half sibs could come from this one sire (or dam) mated to all the different kinds of mates which exist in the breed? How many different kinds of individuals can exist in the entire breed? The Mendelian formulae of the parents and the answers to each of these three questions may be indicated as follows:

Formula of sire: $AABbccDdeeFfGGHhIiJjKKllMMNnooPp$

Formula of dam: $AABbCcDDeeffGgHhiiJjKkLLmmNNOoPp$

Kinds of full sibs: $1 \times 3 \times 2 \times 2 \times 1 \times 2 \times 2 \times 3 \times 2 \times 3 \times 2 \times 1 \times 1 \times 2 \times 2 \times 3 = 20,736$

Kinds of paternal half sibs: $2 \times 3 \times 2 \times 3 \times 2 \times 3 \times 2 \times 3 \times 3 \times 2 \times 2 \times 3 \times 2 \times 3 = 1,679,616$

Kinds in breed: $3 \times 3 = 43,046,721$

Since there are more than twenty thousand kinds of full sibs possible from this mating, it is unlikely that two full sibs even from among a large number would happen to be exactly alike. Yet less than one two-thousandth of the total number of kinds of individuals possible in the whole breed are possible at all in this particular set of full sibs. This sire could not possibly sire a twenty-fifth of the kinds possible in the whole breed, no matter what kind of mates he had. This example is schematic in two important respects: first, many more than 16 pairs of genes are doubtless heterozygous in all breeds; and, second, it would be a surprising coincidence if the unlike alleles were equally numerous in more than a few of those pairs.

population, the same as it was in the preceding generation. Without selection the Mendelian mechanism itself does not change gene ratios except, of course, that it permits sampling variations to occur in the segregation process at each generation. Those are slight except in very small populations. There they cause the phenomena of inbreeding.

POST-MENDELIAN ADDITIONS TO THE LAWS OF INHERITANCE

Mendel knew nothing of *chromosomes* or *linkage*. The achievements of genetics in the last third of a century in identifying the chromosomes as the carriers of the genes have not changed the laws which Mendel discovered, except to modify the law of independent assortment so that it is now known to apply only to genes which are on different chromosomes. Cytological investigations of the mammals and birds are unusually difficult because the number of chromosome pairs is large, the chromosomes are small, and the processes of killing, fixing, and staining are apt to cause the chromosomes to "clump" together, so that the observer cannot be sure how many there are.

Because of these difficulties, mammalian and avian chromosomes have not been so well investigated as those of most farm crops and of many lower animals. In several cases investigators do not yet agree in their counts. Some species have been studied by only one investigator. Most of the findings quoted in table 1 are still subject to confirmation.² Work much older than 1920 is quoted only where no subsequent work has been reported, or where this earlier work has been quoted widely. In general the later work is more apt to be correct. On account of the "clumping," the larger numbers are more likely to be correct wherever there is not yet substantial agreement.

Most farm animals have around 20 to 30 pairs of chromosomes; hence two genes chosen at random will nearly always be independent of each other. Yet if one is considering a trait affected by more than six or seven pairs of genes, there is likely to be linkage among some of them.³ On account of linkage, genes which were transmitted to the parent together (i.e., which both came to it from the same one of its parents) will be transmitted together to the offspring more often than if they were independent. Yet in the population as a whole, if crossing-over occurs at all, the "repulsion" and "coupling" phases soon become equally frequent, thus causing linkage to hinder selection (in a hitherto unselected population) in about as many cases as it helps. Hence link-

² For a more complete list and references, see: Oguma, Kan, and Kakino, Sajiro. 1932. A revised check-list of the chromosome number in vertebrates. *Jour. of Genetics*, 26:239-54, and for birds: Miller, R. A. 1938. *Anatomical Record* 70:156-58.

³ The chicken, the mouse, and the rat are the only farm animals for which the construction of linkage maps is yet well along. See *Jour. of Heredity* 31:232-35 and 36:271-73. Some mapping has begun with the silkworm and with cattle.

age does not offer the breeder much chance to get one gene by selecting another closely linked to it. The effects of linkage in causing two genes or characteristics to be together or apart more often than not are conspicuous only in the first few generations after a cross between two unusually homozygous races—a condition which rarely confronts the animal breeder under our present purebreeding systems. The existence

TABLE 1
RECENT REPORTS OF CHROMOSOME NUMBERS IN MAMMALS AND POULTRY

Animal	Number of Pairs of Chromosomes	Heterogametic Sex	Investigator and Date of Publication
Farm animals:			
Horse.....	30	Male	Painter, 1945
	19	Male	Wodsedalek, 1914
	19	Male	Masui, 1919
Ass.....	32	Sokolov, 1937
Mule.....	Unpaired, 51 in all	Wodsedalek, 1916
Camel.....	35	Novikov, 1940
Cattle.....	30	Male	Krallinger, 1931
	19	Male	Wodsedalek, 1920
	30	Male	Makino, 1944
Yak.....	30	Zuitin, 1938
Buffalo.....	30	Pchakadse, 1939
	24	Makino, 1944
Sheep.....	27	Male	Berry, 1941
	30	Male	Several workers, 1931 to 1940
Goat.....	30	Male	Krallinger, 1931
	30	Male	Warwick, 1935
Swine.....	19	Male	Krallinger, 1936
	19	Male	Crew and Koller, 1939
Dog.....	26 ± 39	Male	Painter, 1925
		Male	Ahmed, 1941
Cat.....	19	Male	Minouchi, 1928
	19	Male	Koller, 1941
Farm poultry:			
Chicken.....	33	Female	White, 1932
	39	Female	Yamashima, 1944
	40	Female	Miller, 1938
	16 to 37	Female	Various authors since 1923
Duck.....	38 to 39	Female	Werner, 1927
	39	Female	Sokolov, <i>et al.</i> , 1936
Turkey.....	23 to 39	Female	Various authors, 1929 to 1936

TABLE 1 (*Continued*)

Peacock.....	18 to 29	Female	Tiniakow, 1934
Pigeon.....	31 25 ± 34 ±	Female Female Female	Oguma, 1927 Hance, 1933 Painter and Cole, 1943
Various mammals:			
Man.....	24	Male	Many recent authors
Chimpanzee.....	24	Male ?	Yeager <i>et al.</i> , 1940
Old World monkey..	27	Male	Painter, 1925
New World monkey..	27	Male	Painter, 1925
Nyctereutes (raccoon dog).....	21	Male	Minouchi, 1929
Red fox.....	21	Male	Wodsedalek, 1931
Fox: <i>V. vulpes</i>	17	Andres, 1938 and Wipf, 1942
<i>V. lagopus</i>	26	Andres, 1938
<i>V. fulva</i>	16	Male	Bishop, 1942
Rat.....	21	Male	Many recent authors
Mouse.....	20	Male	Many recent authors
Deer mice (<i>Pero-</i> <i>myscus</i>).....	24 to 29	Cross, 1938
Rabbit.....	22	Male	Painter, 1926
	22	Male	Minouchi and Ohta, 1932
Guinea pig.....	19 31 33	Male Male Male	Harman and Root, 1926 League, 1928 Mols, 1928
Mink.....	14	Male	Schackelford and Wipf, 1947
Hamster, golden....	19	Male	Koller, 1938
" striped....	7	Male	Pontecorvo, 1943
Twelve other species of rodents.....	22 to 43 (only 3 above 27)	Cross, 1931 Krallinger, 1936
Peccary.....	15	
Armadillo.....	30	Painter, 1925
Bat.....	24	Male ?	Painter, 1925
Hedgehog.....	24	Painter, 1925
Opossum.....	11 11	Male Male	Hoy and George, 1929 Painter, 1925
Kangaroo.....	6	Painter, 1925
Eight other genera of marsupials.....	6 to 10	Male	Various authors

of linkage causes the genes to tend to segregate in large groups at any one cell division and hence causes the population to behave as if there were fewer genes than there actually are. But this effect is probably unimportant, since the cross-overs in different cells, even in the same individual, may be at various places on the chromosomes and since genes with opposite effects are as likely to be linked together as are genes with similar effects. Linkage is some hindrance to progress by selection (after the first generation) since it keeps desired and undesired genes from recombining into separate gametes as often as they would if not linked. This lessens slightly the variability among the immediate offspring of selected parents and consequently reduces the amount which can be accomplished by selecting among them.

Mendel did not know of sex-linkage which, in the heterogametic sex, is an exception to the rule that inheritance is in duplicate and comes equally from both parents. Only one pair of chromosomes carries the sex-linked genes. Presumably something like one-twentieth or one-thirtieth of all the genes are sex-linked, although that is only a rough approximation since the sex-chromosomes might carry more or less than their proportionate share of the genes. To ignore sex-linkage will generally lead to but little error; yet there doubtless is some sex-linkage in all farm animals, and probably there are occasional characteristics which are affected by a disproportionately large share of sex-linked genes. The general effect of sex-linkage is to make parent and offspring of opposite sex resemble each other slightly more than parent and offspring of the same sex do. Here and there it has some conspicuous special effect, such as making possible, in some matings, the identification of sex in very young poultry. Partial sex-linkage is known genetically in man and presumably exists in all other mammals in which portions of the X-chromosome cross over with portions of the Y-chromosome. The practical consequences are like those of sex-linkage but even less noticeable.

IS THERE ANY NON-MENDELIAN INHERITANCE?

Each year of genetic research brings added evidence that all inheritance is Mendelian in the broad sense of being in duplicate and particulate, with the particles maintaining their identity. The only well-established exceptions are plastid inheritance, known only from plants, and polyploidy, where inheritance is particulate but present in more than duplicate. Polyploidy seems to be very rare in animals, although it appears to have been important in the evolutionary history of the plant kingdom. On account of the sampling nature of inheritance, polyploidy must be a temporary condition lasting only a few gen-

etc., Savday,

erations until the polyploid individuals either die out or develop a new diploid division among their chromosomes. A few cases of inheritance through the maternal line only have been reported. Most of those have later been found to require some other explanation. Often it is found by further experiment that these were characteristics for which the unfertilized ovum was already organized and the genes which the sperm brought are merely delayed a generation in expressing their effects. Whether the shells of certain snails coil to the left or to the right is an example.

It may never be possible to prove rigorously that all inheritance is Mendelian in this sense, for so long as the inheritance of any characteristic is unknown, an obstinate skeptic might still say: "Perhaps the inheritance of that characteristic conforms to some other rule." It is a fact, however, that many cases of inheritance which were at one time thought not to behave in the Mendelian manner, have been shown by more thorough analysis to behave in that very way except that the number of factors is large or that the interactions between different factors are unusually complicated or that the egg was already so highly organized that the genes in the sperm cell could not show some of their effects until the next generation. Moreover, the ineffectiveness of selection within pure lines seems to be some positive evidence that there can be no appreciable amount of truly "blending" inheritance. (Cf. Fisher, pp. 17-18.)

THE NUMBER OF GENES

There are at least four kinds of evidence which show something about the total number of pairs of genes in certain species. They leave little doubt that the breeder of farm animals must contend with a genetic situation in which the number of different pairs of genes heterozygous in his herd or flock is at least many scores, probably many hundreds, and perhaps even a few thousands.

The first kind of evidence is the number of genes which have actually been found in the organisms studied most. In *Drosophila melanogaster* more than 500 different loci have already been located on the chromosome maps, and many more are known. In *D. pseudoobscura* there are in the third chromosome alone at least 289 loci which can mutate to lethal genes (*Genetics* 26:39). Baur and his co-workers found some 300 genes in the snapdragon, *Antirrhinum majus*. In corn (*Zea mays*) some 400 genes had been catalogued up to 1935 (Rhoades and McClintock). In the wasp, *Habrobracon juglandis*, about 100 mutations at separate loci are known. In *Datura* (the genus which includes the Jimson weed) about 500 genes were known, 77 of them located on the

chromosome map, by 1941. The inheritance of more than 100 characters has been studied in barley (*Genetics* 28:419). In man more than 200 genes have been reported, some 45 of them on the X-chromosome, but the evidence for many of those is scanty because controlled experimental matings are not possible. The number of genes reported for most species of farm animals is only a few dozen,⁴ and many of those are not very certainly established, but only a few thousand farm animals have been observed under such circumstances that genes would have been identified readily.

This kind of evidence has two limitations: First, only genes with effects conspicuous enough to permit their ready identification can be catalogued in the Mendelian manner. Genes with minor effects can only be lumped together in an indefinite background of "modifying factors." Second, the number already found provides scarcely any basis for guessing whether that number is only a tiny fraction or a large fraction of the total number which exists. Certainly the number reported is less than the actual number.

A second kind of evidence comes from cytology. Work (*Journal of Heredity* 33:403-7, 1942.) on the chromosomes in the salivary glands of *Drosophila* shows about 5,000 distinct bands; and the cytogenetics of deletions, inversions, etc., makes it seem plausible that each of these is a gene, although it remains possible that there may be several genes in some bands. Belling in studying the chromosomes of the lily was able to distinguish about 2,200 to 2,500 "chromomeres," or distinct segments of its chromosomes; but the genetics of the lily is not well enough known to show how closely the genes and the chromomeres correspond to each other. Each chromosome in the farm animals surely must carry many genes; but the cytology of mammals and birds is difficult and little except number is known of it so far.

A third kind of evidence comes from some indirect reasoning, based on the number of times certain mutations recurred. The first such estimate was a figure of about 1,800 loci, but it was recognized that the assumptions involved made this lower than the true figure. Gowen and Gay in 1933 reached an estimate of 14,280 loci in *Drosophila*. This estimate had a large sampling error but was thought to have no consistent bias either in the direction of largeness or of smallness. Muller and Prokofyeva in 1935 reached the conclusion that in *Drosophila* the total number of loci ". . . is of the order of a few (ca. 5-10) thousand."

A fourth kind of evidence comes from the experiments on quantita-

⁴ For example, Ibsen in 1933 listed 17 pairs of genes and one multiple allelic series of genes affecting color in cattle. He mentions several other color characteristics, the mode of inheritance of which was not yet clarified. In the fowl 21 genes are already (1940) located in six linkage groups (*Jour. of Heredity* 31:231-35), and other genes are known but not located.

tive inheritance which require for their interpretation a minimum number of genes if those express their effects in the very simplest way (i.e., without dominance or other nonadditive interactions). Sumner's experiments with mice of the genus *Peromyscus* showed that many of the quantitative characteristics in which two varieties or local races differed were each affected by many genes for which neither population was homozygous. "Student" interpreted the Illinois Agricultural Experiment Station's work in selecting corn for high and for low oil content as showing that the oil percentage in the initial stock of corn ". . . was conditioned by the presence, or absence, of a number of genes, at least of the order 20-40, possibly of 200-400, and not at all likely to be of the order 5-10." The Illinois Station's work with the Bowlker herd, which was produced by crossing Guernseys and Holstein-Friesians, has been interpreted (page 123, Annual Report for 1928-29) as requiring more than 10 pairs of genes to explain the breed difference in milk yield and several more pairs of genes to explain the breed difference in the percentage of fat. The Tranekjaer experiments with Jersey and Red Danish cattle in Denmark indicate that at least seven pairs of genes were concerned with the difference in fat percentage between those breeds.⁵ Jull concludes that in the fowl sexual maturity, rate of laying, and persistency of laying are each ". . . affected by a relatively large number of genes, some of which probably influence more than one character." Many other examples might be cited, each yielding figures of from 4 or 5 up to more than 20 as the minimum number of pairs of genes affecting a given quantitative characteristic.

The usual result of an experiment on the genetics of a quantitative characteristic is that the number of genes involved "cannot be less than" a certain number, but might be larger. Usually the longer the genetic investigation continues, the more genes are found. In such experiments the evidence which throws light on gene number usually involves differences between the parental means and between the variabilities of the parental groups, the F_1 or the F_2 or the back-crosses, or it concerns the change produced in the mean and in the variability by a given amount of selection. Often the numbers are small and the sampling errors are high. Those may make the answer obtained either too large or too small. Nearly all other sources of error make the answer smaller than it should be. Thus, this kind of evidence can only show that the number of genes is more than a certain small number which, however, is usually too large to leave any reasonable hope that even the

⁵ Wriedt postulated that one pair of genes would account for the breed difference; but, as Skovsted pointed out, not enough of the parental types reappeared in the back-crosses or in the F_2 to justify that. The figure seven mentioned here is based on comparisons of parental means and F_1 , F_2 and back-cross variabilities.

most thorough study will enable a breeder to know the Mendelian formula for all the important genes in any of his animals.

A fifth line of reasoning, which perhaps scarcely deserves to be called evidence until more is known about the physiology of how the genes produce their effects,⁶ is that the development and functioning of each organ in the animal is so complex and is dependent upon such a delicate interplay of various tissues, hormones, fluids, etc., each acting at the proper time, that it is scarcely conceivable that a small number of genes can initiate and control all of this. The term "unit character" which was freely used in the early days of genetics tends to be avoided now, lest it confuse by implying that one gene by itself is enough to produce the whole characteristic. The gene, not the characteristic, is the unit of Mendelism. In a sense it may be legitimate (and it is often convenient) to refer to *the contrast* between two characteristics—for example, red eye and white eye in *Drosophila*—as a unit character since, in some matings at least, the difference between the two characteristics is caused by a difference in only one pair of genes. Yet it is confusing to speak of *red eye* as a unit character, since more than 40 genes have been found thus far which must all be present if the usual red eye of the wild fly is to develop. If one of them is absent, the eye may be "purple"; if another is absent, it may be "peach"; etc.; but the co-operation of them all (and doubtless of still unknown genes) is required to produce the normal eye. The cooperation of at least 100 genes is necessary to produce normal green chlorophyll color in corn. (*Amer. Nat.* 80:431).

The fact that many distinct abnormalities and defects are caused by a change in only one gene is to be expected if that gene interrupts, at some important stage for which there is no substitute, the long chain of physiologic processes by which the normal characteristic usually develops. For example, in the normal process of horn formation in cattle there may be several stages which, if interrupted, would alter or prevent all the later stages of development; but it is not easy to imagine that any one gene could guide the whole course of horn development, including the growth of the bony core, the blood vessels, nerves, etc. Thus, it may be legitimate to speak of a single gene for hornlessness; but it is not legitimate to infer that the allelic gene to that one is the gene which produces horns. The case is analogous to that of destroying a house by a single act, such as applying a match to it at any one of a number of places. But a house can be built only by the timely co-operation of an enormous number of individual acts. It is scarcely legitimate to speak of refraining from applying the match as an act which builds the house.

⁶ See *Quart. Rev. of Biology* 13:140–68 and *Physiological Reviews* 21:487–527.

The eradication of single-gene defects, such as lethals and semi-lethals, may be an important part of the task of animal breeding; but its practical importance can scarcely approach that of changing the fertility, vitality, growth rates, proportions of conformation, milk production, speed, wool production, etc., which are most of the economic differences between ordinary or moderately inferior and distinctly superior animals. The genetic evidence indicates that these are complex physiological characteristics in which most of the hereditary differences are caused by a large number of genes, each with an individually small effect.

CONSEQUENCES OF THE LARGE NUMBER OF GENES

When only one pair of genes is concerned, two kinds of gametes and three kinds of genotypes are possible. If there are two pairs of genes, each possibility for the one may occur in combination with each possibility of the other, thus permitting four kinds of gametes and nine kinds of genotypes. Three pairs of genes permit 8 kinds of gametes and 27 kinds of genotypes. The general formulae are: the number of kinds of gametes or of homozygous genotypes possible with n pairs of genes is 2^n (which may be written 10^{301n}); the number of different kinds of genotypes possible is 3^n (which may be written 10^{477n}). These numbers become big beyond human comprehension if n is very large. Even if there are only 100 pairs of genes, 31 digits will be needed for writing the number of kinds of gametes possible; and there will be 48 digits in the number of kinds of genotypes possible. The possibilities for hereditary differences under this system are enormous. They may be visualized by comparing them with the number of animals of each species actually alive in the whole world at any one time. During the years around 1926 to 1935 these were as follows for man and for some of the more important farm animals (figures from USDA Yearbooks):

	TENS OF MILLIONS
Human beings	200
Cattle	70
Horses	10
Mules and asses	3
Sheep	69 to 74
Swine	25 to 28
Chickens (in the United States only)	44

Hence, if the number of different genes heterozygous in each species is as large as 40 (and it may well be thousands), the number of different

hereditary combinations possible in each species is millions on millions of times as large as the number of animals which can actually be alive at any one time. It would be a remarkable coincidence if any two living things were exactly alike in all their heredity, except for a few special cases such as identical twins, asexually reproduced organisms, and possibly members of a strain which had been very highly inbred for a long time. Gesell says (*Science* 88:227): "Even in the detailed studies of animal respiration, it has been found that no two dogs breathe exactly alike."

Another comparison to show vividly the enormous number of different kinds of individuals possible is furnished by the physicists' estimate that the number of electrons in the universe is about 10^{80} . In a species in which only 200 pairs of genes are heterozygous there could be 10^{95} different kinds of individuals. This is a million billion times as many as there are electrons in the universe!

In these calculations it was assumed that there are only two allelic genes in each series. In several cases it is already known that there are three or more different kinds of genes in an allelic series (called "multiple alleles" in genetics), and it is possible that all allelic series are potentially multiple.⁷ This increases the number of kinds of gametes and genotypes possible. If m alleles are possible in each of n allelic series, the number of different kinds of gametes possible is m^n and the number of different kinds of genotypes possible is $\left[\frac{m(m+1)}{2}\right]^n$.

Linkage does not affect the number of kinds of gametes which may be produced but does affect their proportions and thereby increases the size of population necessary to permit all kinds of genotypes to be produced. Also, it increases the number of genotypes possible because the multiple heterozygotes will now be different genotypes according to

whether the linkage is in the coupling or repulsion phase. That is, $\frac{AB}{ab}$

and $\frac{Ab}{aB}$ will be different genotypes if linkage exists, whereas both would have been the same genotype, $AaBb$, if there had been no linkage. A triple heterozygote, where all three genes are linked, can exist in four different genotypes, a quadruple heterozygote in eight genotypes, etc.

⁷ Several series have already been found in which there are more than four alleles. The albino series in the rabbit is an example. The maximum number yet reported in any organism is 45 alleles for a self-sterility gene in one of the primroses, *Oenothera organensis*. *Genetics* 26:469. More than 22 alleles are known in the white eye series in *Drosophila melanogaster* and more than 40 at the locus for "bobbed." In man at least four alleles exist to determine the blood types. *A*, *A¹*, *B*, and *O*, and more than a half dozen alleles at the locus for the *rh* blood factor have been reported.

Both these additional complications—multiple alleles and linkage—increase the number of kinds of genotypes possible. Unless the number of heterozygous genes is very small, there is no escaping the conclusion that the number of genetically different kinds of individuals possible in a breed or species is practically infinite. Except in the rare case of identical twins, one can confidently expect to breed cattle, or any other species of farm animal, a lifetime without ever having a second animal exactly like one he produced earlier.

If each gene had a different kind of effect and there was no confusion by environmentally caused variations or by dominance, the number of kinds of animals different in appearance or performance would be the same as the number of kinds of genotypes. If all pairs of genes showed complete dominance, but each pair of genes had a different effect, the number of kinds of animals would be the same as the number of kinds of gametes. But if very many genes are involved, some will produce effects like those of others, some will produce effects only when certain others are present, and some will produce the same effects as variations in environment do. Therefore, if the genetic situation is at all complicated, the outwardly distinguishable kinds of animals grade into each other in an almost continuous series. When we classify a large group of animals on the basis of outward appearance or performance in any one characteristic, even with considerable precision, we are almost certain to include in each class many genetically different kinds of individuals.

THE GENETIC INTERPRETATION OF THE "PURITY" OF PURE BREEDS

In animal breeding usage, purity of breeding refers to ancestry and is not the same as the genetic term "homozygosity," although there is some slight relationship between the two. The purebred animal is one whose ancestors all belonged to that same breed for as far back as is required by the rules governing registration in that breed. Since all breeds are finitely limited in the number of animals alive at any one time, and many breeds were very small in numbers for a long time during their formative period, a certain amount of homozygosity was produced by the resultant inbreeding. This is usually a faint force in purebreeding as practiced today in breeds which have become large and successful, but occasionally was intense during the formative period when the breed was very small. The Shorthorn breed, which has the oldest pedigree record, probably lost through the inbreeding process about 25 or 30 per cent of its initial heterozygosity in the century and a third from its foundation to 1920. Most of this was lost in the formative stage while the ancestry of the future breed was largely included in the

herds of the Colling brothers, who both shaped their breeding operations to an unusual degree around one bull, Favourite. In most breeds yet studied, the breed is now losing something like one-half of one per cent of its heterozygosity per generation. In breeds of cattle and sheep, where the average length of generation is around four or five years, this would mean that in a century the mere fact of absolute purity of breeding would cause a decrease of about 10 per cent in the amount of heterozygosity initially present. This would be partially offset by the occasional registration of a grade through fraud, accident, or official permission, and by the new mutations which might occur and survive during that century. In addition to these three processes of inbreeding, introduction of outside blood, and mutation, selection may have helped either to increase or to decrease the average homozygosity of the breed. Selection, however—in marked contrast to its effectiveness in changing average merit—is a very feeble tool for changing homozygosity, except under the very simplest genetic situations, as we shall see in chapter 11. It is not likely, therefore, that selection has made much change in the average *homozygosity* of the pure breeds since they were first separated from the general population, although it has certainly changed the breed averages distinctly in many cases.

It is sometimes argued that, while the total number of genes may perhaps run into the thousands, yet most breeds (or subgroups of a species in nature) will be homozygous for all but a few of those. This seems improbable, since no genetic mechanism is known by which that condition would be likely to be attained in the first place nor by which it could be maintained very long if it ever were reached. If a breed or species ever became entirely homozygous for a given pair of genes, mutations—even at a very low rate—would cause that homozygosity to be lost bit by bit. Selection is too feeble to restore *complete* homozygosity as rapidly as mutation destroys it, especially if the mutations are usually recessive, although selection is amply powerful to keep consistently undesirable mutant genes from becoming abundant. Inbreeding can be powerful enough to restore that homozygosity, but it is doubtful whether it often is intense enough in nature or in the breeding of large and popular breeds to achieve that end. Wright estimates⁸ that a freely interbreeding species of one million individuals at equilibrium with one new mutation in each 1,000 individuals could support permanently some 30,000 unfixed loci, which is larger than any of the current estimates of total gene number. In other words, few genes in such a species would be entirely homozygous all through the species. Smaller species

⁸ *Genetics*, 16:119–21. See also table 5 in Fisher's *Genetical Theory of Natural Selection*.

would not support so many⁹ unfixed loci. The inbreeding which the pure breeds of livestock undergo comes mostly not from the smallness of the breed in absolute numbers but from the circumstance that many breeders are simultaneously using sons or grandsons of a few currently famous sires.¹⁰ When the pure breeds finally reach equilibrium between the production of heterozygosis by mutations and the loss of heterozygosis because the effective number of animals in the breed is small, it is possible that the pure breed may support only a few scores of unfixed loci. But it is unlikely that the pure breeds have come at all close to that equilibrium point in the comparatively short time (in terms of animal generations) since they were organized. It seems entirely conservative to estimate that the average pure breed is still heterozygous for hundreds of pairs of genes, although, of course, no animal in it is heterozygous for even half of them and probably no one gene is heterozygous in even half of the members of a breed.

MUTATIONS

Mutation is a rare process. The mutation rates observed in the laboratory under otherwise natural conditions are generally around the magnitude of one mutation of each gene in 100,000 or 1,000,000 generations (Stadler, Gowen). The rate is not the same for all genes, however, and can be increased by such extreme environments as exposure to X-rays, radium, ultraviolet light or barely sublethal temperatures. Also a few genes which alter the mutation rates of other genes have been found. Dr. H. D. King observed among 45,000 Norway rats 6 different mutations affecting hair; but the number of genes affecting hair (i.e., the number exposed to mutation) is not known, nor can one be sure how many mutations with small effects occurred but were not observed. White and Ibsen estimate (*Jour. Genetics* 32:47) that in cattle the mutation rate from horned to polled is about one in 20,000. Haldane estimates that the mutation rate to hemophilia in man is about one in 30,000. More typical is the finding of Dobzhansky and Wright (*Genetics* 26:32) that in the third chromosome of *Drosophila pseudoobscura* the mutation rate to lethals must be less than three in 289,000.

If there are 5,000 genes in each individual, then only about one animal in every 20 or 200 would have even one gene which was a new

⁹ The same formula gives nearly 2,560 as the number of unfixed loci in a species of 100,000 individuals, 210 in a species of 10,000 and 16 in a species of only 1,000. Our ignorance of whether the rate postulated for mutation is too high or too low and our ignorance of whether the effective number of breeding individuals is far smaller or only a little smaller than the census number prevent us from using these figures with much confidence.

¹⁰ See Calder's study of the Clydesdale breed of horses. *Proc. Roy. Soc. Edinburgh* 47 Part 2, No. 8:118-40. 1927.

mutation. If the breeder were looking for a mutation in one certain gene, he could expect to find it in only one animal among something like 100,000 to 1,000,000 animals examined.¹¹ Even then, if this mutation produced only a small change in a characteristic also affected by environment and by other genes, the breeder looking for it would have only a small chance of recognizing it when he did see it.

Mutations are not only rare, but they are prevailingly harmful. The larger the change made by a mutation, the less likely is the mutation to be beneficial to the animal. The reasons for this hinge around the facts that mutations seem to be random changes in the genes and that any living animal is already a reasonably successful and highly complicated mechanism. Any random change in its machinery has only a small chance of making it a still more successful mechanism but is very apt to make it operate less well. The bigger the change, the less likely it is to improve the operation of the mechanism.¹² Hence the breeder does not yet have any reason to think that he can help his practical operations by increasing mutation rates.

Because mutations are rare and prevailingly harmful, the only significance they have for the breeder is that a tiny part of his efforts in selection must be spent in keeping these undesired newly mutated genes from becoming too numerous in the breed. Mutations do have great significance in evolution because they provide raw material which can be used by selection and inbreeding or other breeding systems to change the existing kinds of organisms. Even if only 1 in 1,000 new mutations were beneficial, geologic time is so long that such rare beneficial mutations may be important in evolutionary changes. Moreover, mutation serves an important evolutionary purpose by keeping (against the efforts of selection) a certain store of currently undesirable genes available in case the environment should change so as to reverse the direction of selection. For example, suppose a species well adapted to a life in a humid climate were by migration or change of climate forced to become better adapted to arid conditions. If mutation has kept in the species a few genes which make their possessors poorly adapted to a humid climate but better adapted to an arid climate, then

¹¹ When Warren Gammon wished to establish a polled variety of purebred Hereford cattle, he sent about 1,500 letters to breeders inquiring if they knew of such animals. From the replies he learned of 14 purebred Herefords which were polled, but some of these animals may have inherited their polledness from the same original mutation. We can only guess how many horned cattle had been observed by the men who reported these 14 polled ones, or how many of the 1,500 men who received these letters knew of polled cattle but neglected to reply.

¹² See Fisher's *The Genetical Theory of Natural Selection*, pp. 38-41, for more detailed reasoning on this point and for formulae relating the magnitude of a mutation's effect to the probability of its being beneficial.

when the conditions change, some of the newly desirable genes are already present. Selection may begin at once to increase their frequency. If mutation had not kept this store of formerly undesirable genes present, the species might have had to wait for the very slow process of mutation to produce them after the changed conditions arose. Waiting for the mutation might have taken so long that the species would have become extinct first. This consideration may be important in evolution but probably is rarely of any importance to the practical animal breeder, since he is concerned with so much shorter periods of time. Perhaps it might have some slight bearing on such situations as that which occurred in the American breeds of swine between 1910 and 1920, when there was a marked change in ideals and the direction of selection in many particulars was reversed.

GENE FREQUENCY

A gene may be much more abundant than its allele or it may be rarer. Gene frequency will be represented here by the letter q , which can have values between zero and 1.0. It is the fraction of the loci of that allelic series in the whole population which are occupied by the gene in question. Two examples may illustrate q and its variations. In a count of the colors reported for the 6,000 parents of 3,000 Shorthorns chosen at random from the British, Canadian, and American herdbooks, Wright found that 8.6 per cent were white, 43.8 per cent were roan and 47.6 per cent were red. Assuming that the roan is the heterozygote between the red and white (which fits the facts better than any other explanation yet advanced, although there may be some environmental or developmental overlapping between dark roans and reds), and letting q stand for the frequency of the gene for red, it is obvious that 47.6 per cent of the genes in this locus are genes for red in the red animals and that 21.9 per cent of the genes in the population are genes for red in the roan animals, while another 21.9 per cent of the genes in the population are genes for white in the roan animals. The final 8.6 per cent of the genes which occupy this locus are genes for white in the white animals. The frequency, q , of the gene for red in the whole population is, therefore, $.476 + .219 = .695$; while the frequency of the gene for white is $.219 + .086 = .305$. If the population had been mating truly at random, the proportions of red, roan, and white would have been the square of the ratio of the two kinds of genes, or: q^2 reds : $2q(1-q)$ roans : $(1-q)^2$ whites. The actual count shows a slight excess of roans and corresponding slight deficits of reds and whites, as follows:

Color	Actual Percentage	Expected Percentage	Excess of Actual
Red	47.6	48.3	- .7
Roan	43.8	42.4	+1.4
White	8.6	9.3	- .7

The discrepancy, although slight, appears to be significant statistically and is probably to be explained as a result of the practical breeder's preference for roan and his having observed long ago that the proportion of roans was higher from matings of white by red than from any other type of mating. The chief interest in the above example, aside from its illustrating what is meant by q , is that it shows how slight is the departure from random mating, even in a simple one-factor case where there is no dominance to confuse and where ideals are such as to lead to a rather strong effort toward mating unlikes.

Another example of gene frequency may be taken from black breeds of cattle,¹³ such as the Holstein-Friesian or Aberdeen-Angus, in which something like one calf in every 100 to 200 purebreds is born red. The difference between the black and red, in most cases at least, is a single-factor one; and dominance is so nearly complete that no one has yet found how to distinguish the homozygous blacks from the heterozygotes, (i.e., both BB and Bb individuals are black but the bb individuals are red). If we let q represent the frequency of the gene for black, we cannot obtain its value simply by adding the proportion of the homozygotes to half of the proportion of the heterozygotes, as was done in the Shorthorn example, since we cannot identify the heterozygotes. By assuming random mating with respect to this gene (which is reasonable, since all parents are BB or Bb , which cannot be distinguished, and since not much inbreeding is practiced) we can, however, get an estimate of q if we can get a dependable count of the proportion of red calves born. That proportion should be $(1 - q)^2$ where q is the frequency of the gene for black. If the proportion of red

calves born is 1 in 200, then the frequency of the gene for red is $\sqrt{\frac{1}{200}}$ or about 1 in 14 and that of the gene for black is about 13 in 14. Then about 1 in 7 or 8 among the calves born black is heterozygous and the others are homozygous.¹⁴ The accuracy of this estimate depends upon the accuracy of the observation that 1 calf in 200 born is red; and this,

¹³ Wisconsin Agr. Exp. Sta., Bul. 313.

¹⁴ The ratio of homozygous dominants to heterozygotes in a random breeding population will be $\frac{q}{2(1-q)}$.

for obvious reasons, is not very dependable. If the proportion of purebred calves born red is about 1 in 100, then q is about .9 and about one in five or six of the purebred blacks is heterozygous for red. Also the heterozygotes will not be uniformly distributed all through the breed but will be more abundant in those herds where heterozygous sires have been used recently.

Gene frequency will be low for genes against which selection has already been directed for many generations, as is the case with most lethals. There is no *a priori* way of estimating whether it will be high or low for genes which have been the object of selection for only a few generations or for genes affecting the magnitude of a characteristic for which the ideal is genetically an intermediate. In populations which have been very small for a long time or are otherwise intensely inbred, more genes will be fixed, or nearly so (i.e., they will have values at or near zero or 1.0); and fewer genes will have frequencies near one-half than will be the case in large random-bred populations under otherwise similar circumstances.

In the case of multiple alleles, it is usually sufficient to let q represent the frequency of the most desirable gene of the series, grouping all the other alleles together as less desirable and having a total frequency of $1 - q$.

THE BINOMIAL DISTRIBUTION OF ZYGOTES

If mating is random, the proportions in which the zygotes occur will be the square of the gametic ratio, as shown in Table 2. The typical Mendelian F_2 or unselected F_3 ratio is merely a special case of the binomial distribution where q happens to be exactly .5. Even small variations in q affect rather strongly the proportions of AA and of aa . However, the variations in the proportions of AA and aa cancel each other to some extent so that the percentage of heterozygosis changes only a little with variations in q , particularly when q is anywhere near one-half. For instance, it may be seen from Table 2 and Figure 3 that the percentage of heterozygosis varies only from .32 to .50 while q ranges between .2 and .8 which includes 60 per cent of the values which q may have. It is only when q is extremely high or extremely low that changes in it produce much change in the percentage of heterozygosis.¹⁵

The frequency with which each kind of mating occurs depends much on q . Thus, if there are $q^2 AA$ males and $q^2 AA$ females and mat-

¹⁵ If there are multiple alleles, the percentage of heterozygosis will really be a little larger than that shown, since some of those designated here as among the $(1-q)^2$ aa individuals will really be heterozygous for two of the undesired alleles, i.e., will be $A'a$, $A'A''$, $A''a$, etc. Those are homozygous in the sense that neither of the genes is the "desired" one.

TABLE 2
VARIATIONS IN GENE FREQUENCY AS THEY AFFECT THE PROPORTIONS OF THE ZYGOTES
IN A POPULATION MATING AT RANDOM

q	AA	Aa	aa
	q^2	$2q(1-q)$	$(1-q)^2$
.99	.9801	.0198	.0001
.95	.9025	.0950	.0025
.9	.81	.18	.01
.8	.64	.32	.04
.7	.49	.42	.09
.6	.36	.48	.16
.5	.25	.50	.25
.4	.16	.48	.36
.3	.09	.42	.49
.2	.04	.32	.64
.1	.01	.18	.81
.05	.0025	.0950	.9025
.01	.0001	.0198	.9801

ing is at random, the most probable proportion of matings of the type $AA \times AA$ is $q^2 \times q^2$, or q^4 . Extending this to the other five types of matings possible, where there are only two alleles, gives the proportions shown in Figure 4. Matings of the kinds $AA \times AA$ or $aa \times aa$ can constitute anything from none to all of the matings in the population

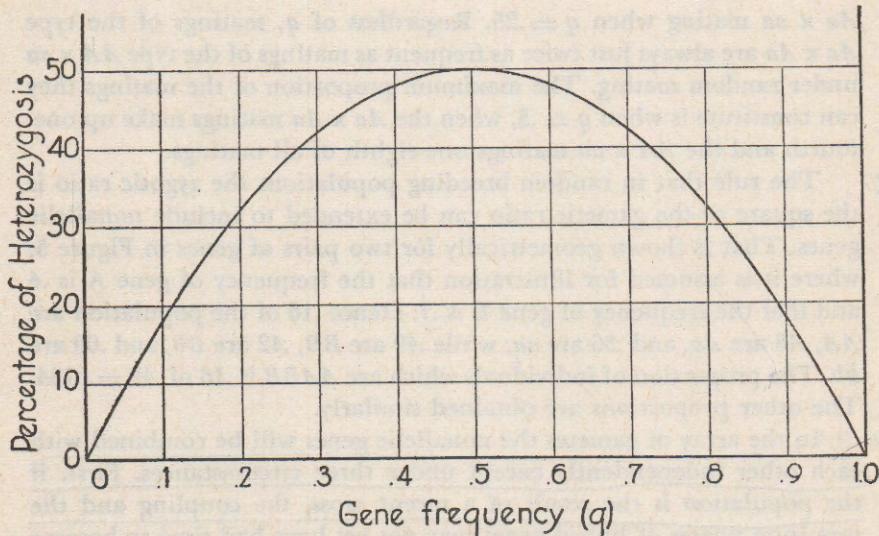


FIG. 3. The percentage of heterozygosity as related to gene frequency in a random breeding population.

according to the value of q . Matings of the kinds $AA \times Aa$ and $AA \times aa$ can constitute from none to 42 per cent of the matings. The maximum figure is reached for the $AA \times Aa$ mating when $q = .75$ and for the

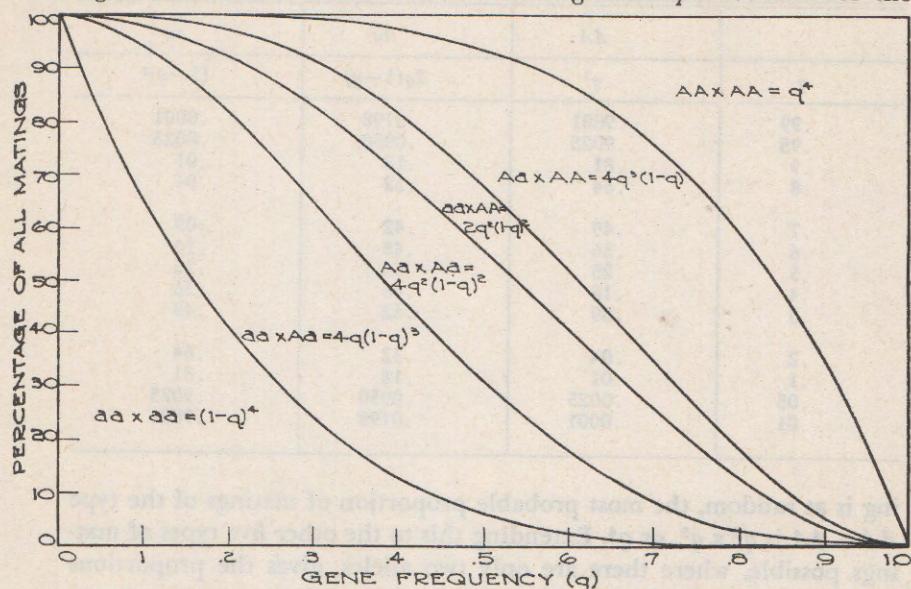


FIG. 4. Showing how the abundance or scarcity of each kind of mating changes with gene frequency in a population mating at random. Vertical distances are in proportion to the frequency of each kind of mating.

$Aa \times aa$ mating when $q = .25$. Regardless of q , matings of the type $Aa \times Aa$ are always just twice as frequent as matings of the type $AA \times aa$ under random mating. The maximum proportion of the matings they can constitute is when $q = .5$, when the $Aa \times Aa$ matings make up one-fourth and the $AA \times aa$ matings one-eighth of all matings.

The rule that in random breeding populations the zygotic ratio is the square of the gametic ratio can be extended to include nonallelic genes. That is shown geometrically for two pairs of genes in Figure 5, where it is assumed for illustration that the frequency of gene A is .4 and that the frequency of gene B is .7. Hence .16 of the population are AA , .48 are Aa , and .36 are aa ; while .49 are BB , .42 are Bb , and .09 are bb . The proportion of individuals which are $AABB$ is .16 of .49 = .0784. The other proportions are obtained similarly.

In the array of gametes the nonallelic genes will be combined with each other independently except under three circumstances. First, if the population is the result of a recent cross, the coupling and the repulsion phases of linked genes may not yet have had time to become equally abundant. Second, if the parents were produced by assortive

Right
through
here

q_A^2 AA	$2q_A(1-q_A)$ Aa	$(1-q_A)^2$ aa	
q_B^2 BB	.0784 AABB	.2352 AaBB	.1764 aaBB
$2q_B(1-q_B)$ Bb	.0672 AABb	.2016 AaBb	.1512 aaBb
$(1-q_B)^2$ bb	.0144 AAbb	.0432 Aabb	.0324 aabb

FIG. 5. Showing how the rarity or abundance of the various genotypes in a random breeding population depends on the frequency of the genes in each pair.

mating (See Chapter 27), genes which produce similar effects will be together in the same gametes more frequently than otherwise. Third, if the parents are a selected group (rather than a random sample or a typical sample of their generation), the gametes they produce will contain slightly fewer extreme combinations and more intermediate combinations than if the same genes were combined entirely at random.

The two-factor F_2 ratio, used in genetics texts to introduce the subject of inheritance where more than one pair of genes is involved, is only the special case in which the frequency of both genes is exactly .5. The zygotic ratio when n genes combine at random can be had by multiplying all the zygotic ratios for each pair of genes together thus:

$$[q_A A + (1 - q_A) a]^2 [q_B B + (1 - q_B) b]^2 [q_C C + (1 - q_C) c]^2 \dots \\ [q_N N + (1 - q_N) n]^2.$$

If the frequency of the desired gene is the same in each of the n pairs, the formula can be written in a simpler form: $[q_A + (1 - q_A)]^{2n}$. This shows why the search for breeding animals homozygous in all desired genes has no prospect for immediate success unless the number of genes desired is very small and the desired gene in each pair already has a high frequency. Table 3 shows the expectation for various values of q and n , figures being shown only where at least 1 in 1,000 is expected to exist.

TABLE 3
PORTION OF RANDOM BRED POPULATION WHICH WILL BE HOMOZYGOUS FOR n DESIRED
GENES = $q_A^2 q_B^2 q_C^2 \dots q_N^2$
Let $q_A = q_B = q_C = \dots = q_N$. Then portion equals q^{2n}

q	n			
	5	10	20	50
.50	.001	.	.	.
.60	.006	.	.	.
.70	.028	.001	.	.
.80	.107	.012	.	.
.90	.349	.122	.015	.
.95	.599	.358	.128	.006
.98	.817	.668	.446	.133
.99	.904	.818	.669	.366

Animals having at least one desirable gene in each pair but not necessarily homozygous for all those pairs are much more frequent. Thus, if q^2 are AA and $2q(1 - q)$ are Aa , those which carry A either in the homozygous or in the heterozygous condition are $q^2 + 2q(1 - q)$, which may be written $q(2 - q)$. Extending this to n pairs of genes gives the figures shown in Table 4. Animals possessing at least one desired gene in each pair are more apt to exist in large enough proportions that it will be finitely possible to find them and to breed from them, discarding all which do not come up to this standard, than is the case with animals homozygous for the desired genes.

In any actual population some of the animals will come nearer than others to having all the desired genes, even though none of them perhaps comes close to that ideal. The practical breeder's simplest reasonable hope is that by selection he can steadily increase the frequency of the desirable genes until sometime—perhaps not until after many gen-

TABLE 4
 PORTION OF RANDOM BRED POPULATION WHICH WILL POSSESS AT LEAST ONE DESIRED
 GENE IN EACH PAIR = $q_A(2 - q_A)q_B(2 - q_B)q_C(2 - q_C) \dots q_N(2 - q_N)$.
 If $q_A = q_B = q_C = \dots = q_N$, then portion equals $[q(2 - q)]^n$.

q	n			
	5	10	20	50
.30	.035	.001
.50	.237	.056	.003	...
.70	.624	.389	.152	.009
.80	.815	.665	.442	.130
.90	.951	.904	.818	.605
.95	.988	.975	.951	.882
.99	.999	.999	.998	.995

erations—they may reach such a high frequency that perfect breeding animals may be born in his herd. But whether or not that goal is actually attained in his lifetime, the increasing frequency of the desired genes will carry the average merit of the population with it, so that he can reap the reward for his efforts in each generation in which there actually is any increase in the frequency of the desirable genes.

In most circumstances the practical breeder is much more interested in average genetic merit than in homozygosity itself. For example, if 10 pairs of genes affect a trait and a breeder is choosing between one animal which is homozygous for five of the desired genes but homozygous for the undesired gene in the other five pairs and another animal which is heterozygous for all 10 pairs, there will be little difference in their breeding usefulness to him. Each has 10 desired genes. On the average each will transmit five desired genes to an offspring, the former to every offspring without exception and the latter sometimes more and sometimes less than five. Probably the wiser choice would be for the more heterozygous animal since the greater variability of its offspring offers more chance for rapid progress by selection among them.

DEVIATIONS FROM RANDOM MATING AS THEY AFFECT THE BINOMIAL DISTRIBUTION OF ZYGOTES

Mating is random when mates are no more and no less like each other than if they were paired by drawing numbers out of a hat. Random mating does not mean promiscuity or carelessness. Deviations from random mating may be of four genetically different kinds: (1) inbreeding, (2) outbreeding, (3) mating like to like on the basis of somatic resemblance, and (4) mating individuals which are somatically unlike each other. There can, of course, be breeding systems which involve combinations or alternations of two or more of these. Sele-

tion, which is deciding that certain individuals shall have many offspring while others shall have few or none, may be practiced along with random mating among those selected to be parents. An illustration is the breeding practiced on large ranches where sires and dams may be highly selected to conform to the owner's standards, but after the selections are made, several sires and many females are turned loose in the same pasture and the matings within that pasture are random, so far as concerns any human control over them. This is selection plus random mating within the group selected to be parents. If the ideals toward which the selections are made differ on different ranches, mating may be random within the limits of each ranch but will not be random with respect to the whole breed, since animals of like types will tend to be on the same ranch and therefore will mate together more often than would be the case if all the sires and dams on all the ranches were in one pasture.

Each of these systems of breeding which is not random will be the subject of a later chapter. Inbreeding tends to make the array of zygotes more like that which would exist if the array of gametes were changed into zygotes by doubling all the genes in each gamete. Inbreeding promotes the formation of families of all kinds, thus adding to the diversity of the population. Outbreeding, which prevails when mates are less closely related to each other than if they were mating at random, is the reverse of inbreeding and cancels many of its effects. It is especially potent in destroying family differences which have been produced by inbreeding, and at producing hybrid vigor or "heterosis." Unless distinct families already exist, outbreeding cannot be carried far. The general effect of mating like to like, within the whole group of parents selected to produce the next generation of the breed, is to make the population more variable by providing more than a random chance for gametes from an extreme individual to meet with gametes from an individual which is extreme in the same direction. The mating of unlikes together makes the population more uniform by making it more likely that gametes from an extreme individual will unite with gametes from an individual extreme in the opposite direction than would be the case under strictly random mating. It is the most potent breeding system for producing immediate uniformity in a population but produces nearly all its effects in the first generation practiced. It is practiced much where the ideal is intermediate and the breeder seeks to mate them so that each will compensate for the defects of its mate.

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CHAPTER 7

The Genetic Basis of Variation

Variation—differences between individuals—is the raw material on which the breeder works. It is not necessary that the animals vary widely enough that the breeder can at the very start find some perfect ones to select, but merely that some of them will be closer to his ideal than others are.

The causes of variation are differences in the heredity with which individuals started life, and differences in the environments, internal and external, known and unknown, to which they were exposed during their development. Except in the case of identical twins, two individuals rarely if ever start with all their genes identical.¹ No two individuals ever develop under absolutely identical environments. Hence in practice an observed difference between two individuals must always be considered as the net result of some differences in their heredity and some differences in their environment. Hereditary and environmental differences may have been far from equal in the size of the effects they produced, but almost always both will have been present. They may have opposed each other or both may have worked in the same direction.

Besides these two main divisions of variation into hereditary and environmental portions, a third portion (necessary for logical completeness) comes from joint effects of heredity and environment which cannot fairly be ascribed to either one alone. Such joint effects may occur either if heredity and environment are correlated or if they interact in some nonadditive way so that the effect of a particular variation in heredity may be larger in one environment than in another or, con-

¹ In organisms which can reproduce asexually, (as many plants can by cuttings, budding, etc.) large groups of individuals with identical heredity can occur. These are called "clones." A highly inbred line either of plants or animals, also approaches the condition in which all individuals in it have the same heredity, but this approach is asymptotic and it is rarely if ever possible to be sure that complete identity of heredity has been reached. The broad term, "isogenic line," which includes identical twins, clones, and completely inbred lines, is convenient where it is desired only to mean that all members of the group have identical heredity, regardless of how that group was produced.