Livestock Breeding at the Crossroads

A Foreword on the General Results of the Survey of Germ Plasm in Beef Cattle, Dual-Purpose Cattle, Sheep, Swine, and Horses

In the belief that the time is ripe for a thorough reexamination of present methods and results in livestock breeding, this introductory article endeavors to present a summary of the general situation. Even though they are presented with a due realization of their tentative nature, some of the conclusions will be considered debatable. It is hoped, however, that they will arouse active and thoughtful interest among those most vitally concerned, scientifically and economically, in the vast livestock industry.

During 1935, in cooperation with the State agricultural experiment stations, the Department carried on surveys of germ plasm in all of the important classes of livestock and field crops. The details of the livestock surveys, both as to the information requested and the results obtained, are given in the articles on the various classes of farm animals which follow this general discussion. Specific data were requested so that any resulting catalog of superior germ plasm that might be developed would be scientifically correct.

The survey for these classes of farm livestock, however, revealed the striking but negative fact that the State agricultural experiment stations and the Department of Agriculture are interested in the art and practice of animal breeding, but that insufficient consideration is given to the subject of heredity insofar as it concerns the characters of economic value in these animals. In other words, no catalog of superior germ plasm in these classes of livestock resulted from the survey. Lack of yardsticks for measuring genetic variation in the most important economic characters, and hence lack of records of value for judging superiority, eliminated the possibility of cataloging superior material at this time.

Neither within nor between the State agricultural experiment stations and the Department of Agriculture has there been a systematic effort to develop, isolate, perpetuate, or catalog superior germ plasm. Purebreds have been firmly identified in the public mind with animals of superior merit. In the common use of the term,

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1 Many workers in the Department have contributed to this article, and much valuable historical and genetic material was supplied by J. L. Lush, head of the animal breeding subsection, Iowa State College.
however, as applied to the classes of livestock here considered, a purebred is an animal registered or eligible for registry in the official records of the association for its breed. The rules governing eligibility for registration differ somewhat for different classes and breeds of livestock. A great deal of attention has been given registered animals as such, and especially blue-ribbon winners, but there has been no corresponding amount of attention, in the case of most of the classes of livestock dealt with in this article, to finding out whether these animals really carried superior germ plasm or whether, so far as functional abilities are concerned, their germ plasm might be actually inferior to that of other animals.

Naturally, breeders and farmers look to the scientist for leadership in the development of both basic information and methods of improvement. The contributions in this direction have been very modest, and there has been little change for the better in the situation since the survey of animal-breeding projects at the State agricultural experiment stations was made by the animal-breeding committee of the National Research Council in 1927.

Are We at a Turning Point in Livestock Breeding?

THE art and practice of animal breeding is older than recorded history. The dog was domesticated far back in the Old Stone Age. Oxen, sheep, and swine were already domesticated when the New Stone Age began in Europe. Horses were being ridden at least as far back as the early Bronze Age in Europe (stirrups and bridle bits have been found in Bronze Age deposits) and perhaps much earlier in Asia. The practice of animal breeding goes back hundreds and perhaps thousands of times as far as complete written records of it.

Since the founding of the present breeds, progress has consisted largely in increasing the number of purebreds. There is evidence that this period of rapid expansion is nearing its end. What is to be the next step? Since little or no genetic effort has been made to improve the breeds themselves, progress now seems to be slow, in marked contrast with the situation in plant breeding, where efforts at improvement, as well as the spread of superior material, have been continuous and have brought notable results.

There are indications, however, that livestock breeding may be at a turning point in its long history. He would be a wise man who could say exactly what direction it will take, but at any rate there is a growing feeling that something is basically wrong in the present situation.

One thing would be agreed on by a considerable number of forward-looking breeders and experimenters—that while the methods and practices of the past have accomplished a great deal, giving us the fine breeds of livestock we have today, yet these methods and practices have taken us about as far as they can. The most we can expect to do, if we continue to follow them, is to hold the gains that have been made. Breeding in these five classes of livestock, in other words, is likely to become a frozen and static art, satisfied to stay where it is, or at best to make extremely slow progress.
It may be that this is what must happen in animal breeding. The fundamental difficulties in the way of further advance are real and great, and it may prove to be true that we have gone as far as we can genetically, at least for a long time to come, barring some unexpected development as epoch making as the discoveries of Mendel. Further progress in the livestock field may depend on other factors, such as improvements in feeding or greater knowledge of the functioning of endocrine glands in the animal organism. Too confident predictions cannot be made one way or the other. But if a blueprint for future progress cannot be made at present, there is no question about the need for a fresh appraisal and analysis. Out of such an analysis, it should be possible to develop or discover some of the conditions that will be necessary if there is to be further progress.

WHAT RETARDS PROGRESS?

The present situation in livestock breeding is the product of a complex of forces or conditions that have acted to paralyze movement toward any practical goal. They might be summed up under four general headings:

1. The domination of standards that are incomplete and in some cases inaccurate.

2. Lack of real yardsticks to supplement or revise existing standards.

3. Large gaps in the knowledge of animal genetics.

4. Certain factors that stand in the way of experimenting, including the expense of new experimentation.

Confusion Caused by Questionable Standards

Generally speaking, the questionable standards are of two kinds—esthetic or show points, and pedigrees as these are commonly used.

In the case of most of the classes of animals here dealt with, breeds have become well established through generations of effort, almost entirely on the part of private breeders, many of whom were geniuses when it came to dealing with animals. The registered animals that constitute these breeds are equivalent to trade-marked articles. They are produced in accordance with specifications as to type, conformation, color, and what not. Many of these specifications are equivalent to trade marks, and the trade marks may or may not stand for real values in a given case.

Almost every breed, for example, has an official description of its ideal, which is not primarily based on biological values applicable to a breed-improvement program. Insofar as such direct attention and effort to something that has no scientific basis, they may be called artificial devices. There is no question about the value of the show ring for bringing livestock men together in a common meeting place to discuss their problems and interests; but by descriptions and pictures, farmers and breeders are easily led to believe that some practices have a scientific basis that does not exist.

It is not that esthetic show points are wrong in themselves. In the case of Pomeranian dogs, for example, they are useful because the sole object is to produce an animal with a certain special and characteristic appearance valued by fanciers. A beef steer or a hog, however, is not the same kind of animal as a dog, and when the
breeder of farm livestock concentrates effort on fancy points, and exaggerates their importance, he multiplies the goals he desires to attain and they become so complex, and there are so many things to take into account, that really fundamental considerations get scant attention. As a result, improvement is retarded or stopped.

Emphasis on show points, of course, has not by any means been confined to livestock men. In 1918 Erwin Ilopt, writing in the annual report of the Nebraska Corn Improvers’ Association, had this to say about some practices of the earlier corn shows:

No point seemed to be too finespun in judging corn. Judges looking grave and wise as owls stood ponderingly over exhibits of corn, setting such momentous questions as to whether this exhibit containing two ears with somewhat “pinched in” butts was or was not superior to another exhibit in which was an ear with an exposure of cob at the tip of exactly three sixty-fourths of an inch. Meanwhile, wondering crowds of awe-stricken people stood open-mouthed, watching the judges make their epoch-making decisions. I am afraid that * * * I have been one of the pious frauds who were presumed to know by some delicate process of divination just which ear or exhibit was better than another. The whole thing would have been ludicrous if it had not been so pathetic. * * *

[A] notice * * * should be displayed in a prominent place over the corn show [reading] something like this: “This is all a joke, folks. Don’t take the thing too seriously. It should be distinctly understood by all visitors that this is just a little game we boys have gotten up among ourselves. It has no relation to utility. Our prize-winning exhibits, upon which we so pride ourselves, mean nothing. They will not yield any more than other ears * * *

“In other words, it would not be so bad if we took the public into our confidence and would frankly acknowledge that we had deliberately set up an arbitrary and artificial standard of beauty and that all this hurrah and hullabaloo had little or no relation to what farmers are really interested in, namely, bushels of shelled corn per acre, profitably raised.”

In the case of some classes of livestock, these show points have developed out of the emphasis on the show ring as almost the only place provided for measuring merit.

The idea of pure breeding is ancient, as may be seen from the extravagant claims about their own purity of descent embodied in the racial mythology of so many tribes and peoples. Casual references imply that this idea was extended to their livestock. 2

In the country of their origin, the pure breeds were but slightly set apart from the common stock of their districts, but when they were first introduced into a foreign country they were usually so distinctly different from the native stock that the gap between purebred and other stock was wide. Hence the emphasis on purity of breeding has naturally been greater in most importing lands than in most exporting lands, except that, as a breed developed an important export market, the demands of the customers—as of American and Argentine buyers of Shorthorns from Britain—often widened the gap between registered and nonpedigree or short-pedigree stock, even in their native lands. In a day of expanding numbers of registered animals and more emphasis on the difference between them and other stock than on the differences between various recognized breeds, efforts at improving the average merit of the registered animals were usually less immediately important than efforts at breed promotion and still further extolling the merits of the breeds as such.

2 However, the practice of cross-breeding was also explicitly recommended at times, and in the absence of complete pedigrees, some outcrossing doubtless took place even where the ideal was pure breeding. It is probably correct to say that the general picture of animal-breeding systems among ancient peoples was pure breeding with occasional crosses of distinct races. Yet there must also have been periods when the cross-breeding was so frequent that it more than counteracted the tendency of pure breeding to create uniform local races distinct from each other.

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Breeds Developed for the Same Purpose are Arbitrary Division Fences

But the fact is that in many cases the outstanding points of difference between many breeds of meat-producing animals are extremely superficial. For instance, a Hereford and a Shorthorn steer are easily identified on foot for a well-known reason, but he would be a rare individual who would care to stake his reputation on telling them apart as they hang in the cooler as well-finished sides of beef. They may have come from equally fertile strains; they may have made equally efficient gains, and the carcasses may be indistinguishable. Yet the pedigrees of these two steers are separate and their ancestors have lived for over a century in an animal society where mixing of the two germ plasms constitutes a breach of etiquette punishable by

![Figure 1](image-url)

FIGURE 1.—Third-cross calves from the well-known grading-up demonstration with Shorthorn cattle at Sn-ta-Bar Farms, Grain Valley, Mo. Results there indicate that after the third or fourth cross of registered sires on grade cows, only exceptional sires can bring about further improvement.

condemnation to the butcher's block. A similar situation exists among swine, where in many cases it is impossible to identify the breed once the head and bristles are off. Have breeders accumulated these combinations of hereditary material under the banners of the various breed societies without realizing the underlying similarities of the breeds? Whether they have or not, it is clear from our knowledge of history and our realization of the present situation that in the biological field the breeds, particularly those developed for the same purpose, are often arbitrary division fences maintained to please certain groups of breeders.

The situation is somewhat more complex than this picture indicates. There are other factors that interfere with any steady progress toward livestock improvement. For one thing, ideals change from time to time for the same class of animals and from one locality to another.
Again, confusion arises from the fact that the current show-ring ideal is not necessarily the same as that followed by the breeder for a number of reasons, the most important of which is probably economic pressure. There may be almost a right-about-face in ideals at different periods, as when the show ring called for small Poland China swine during the first decade of this century and later swung to the other extreme of size and length, while the farmer's ideal remained somewhat intermediate. Doubtless there is some justification at times for such discrepancies, but they are often carried too far merely to justify breed peculiarities and thus actually impede progress by decreasing the intensity of selection for really important traits.

Another example of divergence between show-ring and farmer ideals was the show-ring demand for a ton horse in the draft breeds at a time when the market demand was for a horse weighing around 1,600 pounds. The reason for this difference was the belief that with the kind and size of mares the farmers possessed, it would take a ton stallion to sire 1,600-pound mares or geldings. In many cases, too, the shortcomings of show-ring ideals concern important characters such as the length of wool on sheep, which cannot be accurately evaluated when the degree of trimming and the date of the previous shearing are unknown to the judge.

The net result of all this has been a tendency to lead livestock breeders farther away from a scientific approach than they were when modern animal-breeding practices took general form in Great Britain in the late 1700's and early 1800's.

Pedigrees Give a False Sense of Security

The second point mentioned under questionable standards concerns pedigrees. Actually, this is not the second but the first requisite in the case of registered animals. Unless an animal has a pedigree that entitles it to registration in the records of the breed association, it cannot be used by the leading breeders. Pedigreed animals are considered the bluebloods among livestock.
Of course, the pedigree is nothing new. Some use of pedigrees began long ago, as witnessed by ancient proverbs in nearly every language, and by human genealogies such as those in Genesis or in ancient Hindu writings. However, these may have been used more to settle legal questions, such as the inheritance of property, than for biological reasons. The Arabs used pedigrees extensively in their horse breeding, but there seems to be no definite record of what they did with them in actually deciding how to mate horses. The systematic recording of complete pedigrees for a whole breed is a comparatively modern development, the first herdbook of that kind having been published in 1822 for Shorthorns in Great Britain.

When the breeds were small in numbers and the breeders few, only private herdbooks were in use. Indeed, some early breeders objected to telling a customer the pedigree of an animal, believing that the method of breeding was a trade secret which would lose its cash value if others learned it and imitated it. However, in the case of breeds whose numbers became so large that no breeder could know the pedigrees even of all the sires, the breeders felt the need of centralized records. This was especially the case when there was a strong export market. In such cases, before a herdbook society had been formed to record pedigrees, unscrupulous dealers often sold for export any animals they could persuade the customer to take and gave whatever pedigrees would best please him.

It was largely to remedy this situation and to preserve for breeders whatever monopoly value there might be in the possession of the limited number of animals eligible for registry that the first herdbook, The Coates Herdbook for Shorthorn Cattle, was organized. There had been one earlier herdbook, The General Stud Book for Thoroughbred Horses, but it was planned mainly to record the pedigrees of the winners of races each year; it was a kind of advanced registry for special performers rather than a list of the pedigrees of an entire breed. Other breeders, especially those who had much export trade, organized herdbooks somewhat after the Shorthorn model, slowly at first—only a few herdbooks were in existence before 1870—but rapidly in the decades just before 1900.

Again, as in the case of esthetic standards, there is nothing wrong with pedigrees in themselves. They are an indispensable tool of the breeder, since the real concern of breeding is the passing on of heritable factors from one generation to the next. The trouble with pedigrees in the case of registered animals is that they have remained a heritage from the past, inadequate from the modern scientific standpoint; but at the same time they gave a false sense of security. Very often the usual type of pedigree contains little but the names and identification numbers of ancestors, and not even that much about collateral relatives. In such cases it is only a meaningless genealogical jumble. Before it can even begin to be adequate as part of the basis for breeding, it is necessary to find out from other sources how superior or inferior these ancestors were. Again, it is often the case that the items recorded about each ancestor are only the more favorable ones, selected to impress the reader. Usually he cannot guess very closely how much bias was thus introduced. Yet these pedigrees are used as though they were solid indications of merit.
Lack of Real Yardsticks

Little attention was given to improving farm animals in the United States during the pioneering stage, since other things incident to subduing a strange land were naturally more important. The first animals brought over usually were stock that came from the same localities as the colonists themselves, but no definite record of individual pedigrees was kept. When the pioneering stage ended, attention was given to improving the animals both through developing new local breeds and through importing breeds already developed in other lands. Local breeds were developed in regions where the conditions demanded new types that could not be found elsewhere.

Thus were developed the Morgan horse for general utility on the small farms in the hilly areas inland from the Atlantic coast; the American saddle horse for riding in the hilly areas of the Middle States, from Virginia to Missouri; the Standardbred horse for rapid transportation of light loads in areas where roads were improved enough for light vehicles; the Vermont Merino in the hilly parts of New England, when the premium on fineness of wool was high and Australia had not yet come to the front as an important source of fine wools; the Corn Belt breeds of swine as a means of turning unprecedented surpluses of grain into a more marketable form; the adaptation of the Hereford breed from the original imported type to one better suited to utilize scanty and often highly seasonal forage resources.

It is evident, then, that the breeds did not actually originate as fancy animals but were developed out of practical needs. In the early days in England, for instance, the ideal steer at first was an animal big enough and powerful enough to make a good draft ox.
With the passing of draft oxen, this ideal changed. What was needed then was a smaller animal that would utilize feed more economically, lay on meat of better quality, and dress with less waste in the slaughterhouse. That ideal in turn was met. In each case, the breed developed was a useful animal of better-than-average merit, or it would not have survived.

But in general each breed had certain easily identified characteristics of color or form or both, and men naturally associated these characteristics with merit and sought animals that would conform to them as closely as possible. This point is well illustrated by the preference frequently shown by some Hereford breeders for a certain shade of color merely because an outstanding sire possessed that shade, though there is no satisfactory evidence as yet that this color in Herefords has any association with other qualities. There is naturally a tendency to remember the color of an exceptional sire and to forget the poor sires that had the same color. Similarly, if a man has good luck on a day when he happens to be carrying a rabbit’s foot in his pocket, he may associate the good luck with the rabbit’s foot and insist on carrying one forever after. He forgets the days when he was unlucky in spite of the rabbit’s foot, and he has no accurate way of measuring and standardizing conditions that might bring him good luck with more certainty.

Thus the more superficial standards have hung on stubbornly, and better ones have not been developed to replace them. Criteria

THE methods and practices of the past have accomplished a great deal, giving us the fine breeds of livestock we have today, but these methods and practices have taken us about so far as they can, and the most we can expect to do if we continue to follow them, is to hold the gains that have been made. Breeding in these classes of livestock, in other words, is likely to become a frozen and static art. This is in marked contrast with the situation in plant breeding. There are indications, however, that livestock breeding may be at a turning point in its long history. He would be a wise man who would say exactly what direction it will take, but there is a growing feeling that something is basically wrong in the present situation. If a blueprint for future progress cannot be made at present, there is no question about the need for a fresh appraisal and analysis, out of which it should be possible to develop the main outlines of a program for further improvement.
are lacking both for livestock products and for the animals themselves. We do not, for example, have accurate standards for judging the quality of meats, though progress is being made in that direction. We do not know how to tell with any accuracy whether an animal is an efficient producer of high-quality meat except by the slow and expensive individual feeding test. Otherwise, about the best we can do is to make a rough guess based on conformation. How accurate this guess is likely to be may be judged from a single example in another field. Dr. Gowen, of the Maine Agricultural Experiment Station, found that a 7-day test was about twice as accurate an indication of a cow's productive capacity for the year as scoring by the most expert judges, drawing on the garnered wisdom of the ages to tell from the cow's looks what she would produce.

It is obvious that this lack of accurate yardsticks is a major handicap in breeding.

FIGURE 4.—Yearling Southdown ewes in the Government's flock at the National Agricultural Research Center, Beltsville, Md. These ewes show remarkable uniformity and are distinguishable from one another only by the closest observation. They are closely related on their dam's side and six of the group are by the same sire.

Gaps in Genetic Knowledge

For many reasons, not as much is known about genetics in the case of animals as in the case of plants. It is generally considered that the animal is a more complex organism than the plant. With the larger animals, the rate of reproduction is much less rapid than with plants; the numbers the geneticist has to work with are much smaller; the effects of environment are more difficult to separate from the effects of inheritance; and self-fertilization, which simplifies the work in the case of many plants, is out of the picture.

A few characters have been pinned to definite factors, but they are almost exclusively characters that have no practical significance from the standpoint of performance—coat colors in horses and cattle, for example, and plumage colors in poultry. (In the case of fur-bearing animals, however, coat colors are characters of great economic importance.) Even though there is little experimental evidence connecting any definite genetic factors with productiveness, fertility, rate and economy of gain, or physical vigor, it has been demonstrated that these characters are affected by inheritance and subject to manipulation by breeding methods.

Productiveness, fertility, and vigor are characters of profound biological significance, affected by many things in the make-up and
the environment of an animal. Moreover, they are almost certainly the result of many genetic factors closely interacting, and this makes the problem of analysis extremely complex even when the factors are known, which is rarely if ever the case. Suppose, for example, that there are 10 dominant factors, $A, B, C, D, E, F, G, H, I,$ and $J$—to take an imaginary case—that affect production favorably, while the 10 contrasting factors, $a, b, c, d, e,$ etc., affect it unfavorably. These 10 pairs of factors can come together in nearly 60,000 different combinations. The breeder would have a very difficult time indeed finding out what had happened in a given instance. This emphasizes the need of casting off all useless procedures and false standards that might make it harder to reach the goal of superiority in livestock breeding.

The lack of genetic knowledge puts the scientist in much the same position as an aviator in a fog who knows exactly where he wants to go, but has inadequate instruments to guide him. Just as every improvement in instruments makes the way through the fog a little easier and safer for any make of airplane, so will advance in our understanding of animal inheritance enable the breeder of any breed to proceed more safely and efficiently.

**Hesitation in Experimenting**

The chief obstacles in the way of extensive experimenting that might bring results in the livestock field are usually considered to be the high cost per unit and the slow rate of reproduction of the larger animals. The professional breeder hesitates to take chances by departing from known methods when he feels that results are by no means certain, and that he runs the risk of losing everything he has gained. In plant breeding there is greater readiness to experiment because new strains can be tried out in a small way, results are known fairly quickly, and there need be no great loss in case of failure. Readiness to experiment is in itself one of the chief factors making for progress in scientific work.

Yet so far as the scientist is concerned, these are perhaps not the decisive reasons why practically no research has been conducted on the role of inheritance in the expression of such things as meat characters, for example. It is the indefiniteness of the characters themselves, changes in popular demand, and the inability of the investigator to control the forces affecting development that have prevented experimentation. The slowness of reproduction and the high cost of cattle did not stand in the way of determining the mode of inheritance of red and black coat colors in Aberdeen-Angus cattle so definitely that control by the breeder is as nearly absolute as it can be for any inherited character.

**A BRIEF EXCURSION INTO GENETIC HISTORY**

These are some of the factors, then, that have tended to make breeding what it is in the case of certain classes of livestock. Yet even the negative aspects of the situation give some ground for optimism. The lack of knowledge at many points at least makes it impossible to predict certain failure for a given line of experimenting. But the lack of knowledge is by no means complete. Breeders are in a far

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3 The number of genotypes in the $F_2$ generation, where $n$ is the number of pairs of factors involved. In this case, $3^{10}=59,049.$
better position than were the pioneers who founded the dominant breeds of today. The latter could proceed only by trial and error, and the results they secured were more or less a complete mystery.

The chief contributions so far made by genetic science to animal breeding are explanations of facts or processes that were already known but were puzzling. Showing how an apparent chaos of contradictions was really the natural result of orderly laws is an intangible contribution, but it has been important in dispelling superstition and enabling breeders to concentrate with more success on effective methods. The laws of heredity are now well enough known so that new breeding practices more effective than the older empirical ones have begun to be used. This is particularly true with some of the refinements of progeny testing and some of the combinations of selection with inbreeding systems.

Mendel’s big service was in explaining why identical pedigrees need not mean identical heredity—a thing that hitherto had been puzzling. Also, his discoveries freed the breeder from the belief—so strongly held by Darwin—that any genuinely new inheritance would be lost if it were not at once firmly seized by selection. It is no longer considered necessary, as Darwin and all other believers in “blending” inheritance thought it was, to pay much attention to genuinely new inheritance in the form of mutations or sudden changes in germ plasm. Mutations do occur, but so far as is now known they are exceedingly rare and frequently harmful, so that they constitute only a very minor obstacle against which the breeder must struggle. Rarely, mutations which are advantageous from the very start occur, but these usually have only small effects. The mechanism discovered by Mendel is one that preserves an almost infinite store of individual variability within any large interbreeding population but has no inherent tendency to change the averages of the population unless selection in one direction is also practiced, or unless the population is so small—as in inbreeding systems—that the laws of chance permit the population average to wander over a wide range.

Around the beginning of the present century a number of scientists, among whom the most prominent were Weismann in pre-Mendelian days and Johanssen after Mendelism was rediscovered, made fairly clear the distinction between an animal’s outward appearance or performance and its real heredity or breeding value—its “germ plasm” in the philosophical language of Weismann, or its “genotype” in the more precisely mechanistic writings of Johanssen. This, too, was not a new idea to practical breeders, but it began to explain in terms of scientific law commonly observed facts that hitherto had appeared capricious and chaotically unrelated.

The solution of the inbreeding problem is probably the major contribution of the second decade of genetics to the practical art of plant and animal improvement. A number of geneticists, mostly American, have had a part in clarifying the principles and consequences of inbreeding. Among them should be mentioned Shull, East, Jennings, King, Jones, and Wright. The work of explaining inbreeding was fairly well completed in 1921, and new practical methods of plant breeding—especially of corn breeding—based on that knowledge were already in operation. Wright has widely generalized the knowledge of inbreeding since then, especially irregular inbreeding, which is usually the only kind encountered in livestock pedigrees. Some practical applications to animal breeding are
already beginning to come, and these are discussed in the articles dealing with separate classes of livestock.

The consequences of breeding systems that involve some combination of selection with inbreeding and outbreeding and assortative mating are beginning to be understood, largely as a result of the studies of Wright, Fisher, and Haldane. These studies have explained many hitherto puzzling observations of breeders—for example, the usual effectiveness of selection in getting a herd average to approach an ideal, especially when first practiced, but its usual ineffectiveness—unless accompanied by inbreeding—in genuinely fixing that ideal.

HOW CAN WE BREAK THE JAM?

The knowledge of breeding systems has gone far enough so that a fair beginning can now be made at drawing practically useful measures and working plans for breed improvement beyond what was possible with the former empirical rules, though a considerable amount of further study and experimenting is necessary to clarify the details.

The geneticist is not able to map the factors or genes of an animal, as many of the genes in the pomace fly have been mapped, for example; but knowing in considerable detail how inheritance operates he is able in some cases to act as if he knew the genes themselves. This acting as if we knew is one of the most fruitful methods of science. Corn breeders do not know the factors that control yield, date of maturity, height of stalk, disease resistance, and similar important economic characters. But they do not hesitate to act as if they knew what the factors were, and thereby they have developed strains valuable in these respects. Undoubtedly these strains do carry the factors, whatever they may be. The corn breeder does not say that he has to wait until they are cataloged before he can use them.

Thus it seems possible to lay down the broad outlines of a program that might break the jam. This program would have four main points, corresponding to the four factors that now prevent further progress.

Point 1. Getting Rid of Standards Based on False Methods of Evaluating Merit

Everything that is known about genetics indicates that it is vital to concentrate on as small a number of objectives as possible. The indispensable objectives in livestock breeding are production, reproduction, and vigor in the broadest sense. They are sufficiently difficult to attain without adding others that have no bearing on fundamental values. Every unnecessary factor introduced for color, conformation, or what not makes the problem that much harder. For example, four genes can combine in the F2 or segregating generation in enough different ways to produce 81 genetically different offspring (genotypes), and ordinarily the number of individuals that would have to be examined to work out the mode of inheritance would be at least 1,000. It is evident, then, that breeding for unnecessary details adds not only to the difficulty of the work but to its cost.

Point 2. Developing Practical Yardsticks

The process of getting down to essentials can be only partial, however, until we develop better criteria for measuring and evaluating
animals from the standpoint of efficiency of feed utilization and apply them on a much wider scale than at present. Then must follow—notably in the case of meats and of wool—the development of quicker and more certain methods for analyzing the product itself. Scientists have not been idle in this field, and research here must continue.

Testing for advanced registry in the case of dairy cows is an example of the use of practical criteria in judging animals. Another example is the use of speed records in breeding horses. In both cases, the use of these practical yardsticks has apparently brought results. The progeny test, discussed later in this article and in each of the articles dealing with a specific class of livestock, should be included among the indispensable procedures wherever it is practicable. This applies also to sound pedigree records. For example, no direct measure of the egg-production value of a cock is possible, but his value can be judged from the production records of his progeny.

Point 3. Carrying on Breeding Experiments

Without extensive experimentation, all discussion of breeding policies must remain theoretical. The scientist can readily formulate theories, but unless they are put to practical test, they have only an academic value. It has already been pointed out that, in the case of the larger animals, breeding experiments are likely to be costly and to consume a great deal of time. In addition, they demand scientific training and ability, and the economic results are by no means certain. For all these reasons, it seems unlikely that adequate experimenting will be done by private breeders who are compelled to stick closely to operations that are profitable. A few wealthy men might undertake this kind of work, but accidents happen to private fortunes, men change their minds, and successors may not have the same ideals, and, under these conditions, there is no assurance of continuity. It looks as if this function must be performed by governmental agencies, or by foundations or institutions of one kind or another, for the good of the livestock industry as a whole.

Point 4. Continuing Genetic Research

Study of genetic factors in animals must of course be continued, in combination with research in animal physiology and embryology. Real progress in livestock breeding may depend on getting greater genetic knowledge than we now have more than on any other one thing. There is an interaction, however, between practical experimenting and basic research—each complements and contributes to the other. If, for example, genes are to be studied, they must be taken up one by one; and this can best be done as part of a program of practical experimenting.

In other words, the problem of livestock breeding cannot well be separated into watertight compartments of theory and practice. It must be considered as a whole. But for that matter, breeding itself is not a watertight compartment. It is only part of the whole biology of the animal organism.
The Real Purpose of Inbreeding

The third point above, carrying on breeding experiments, calls for further discussion. No detailed experimental program can be laid down here, but present knowledge indicates that it should be based on inbreeding as the first step to develop distinct strains or families whose characteristics may be accurately known and studied.

In recent years, some workers have taken an experimental approach toward inbreeding, especially in the case of swine, and have secured some extremely interesting results. These efforts are discussed in the articles on the different classes of livestock.

Inbreeding is the surest and quickest way to produce homozygous combinations of genes, that is, factors that are the same from both parents so that the offspring gets a double dose of the same thing—an $ABC$ from the mother and an $ABC$ from the father, for example, not an $ABC$ from one and an $abc$ from the other. It need hardly be said that some of the genes thus concentrated may be factors for either desirable or undesirable traits. Suppose—again to take an imaginary example—that $A$, $B$, and $C$ are all desirable, while $a$, $b$, and $c$ are undesirable. By inbreeding, we isolate a family with the combination $aaBBCC$. The double dose of $a$ might show up as lack of fertility, for instance, whereas if the progeny had had an $A$ from one parent and an $a$ from the other—that is, a heterozygous combination—the $A$ might mask or dominate the $a$ and the lack of fertility would not show up. This fixing of some unfortunate combinations of genes, in fact, often happens when cross-fertilized organisms are intensely inbred. An actual instance is given in the record of Bates’ Duchesses. These were closely inbred, and “a low level of fertility seems to have become fixed and to have doomed the efforts to maintain a ‘pure’ Duchess strain after Bates’ death.” The low fertility, however, was considered to be an advantage. It made the stock scarcer and therefore higher priced.

It was one thing to avoid inbreeding, however, when the causes of the evil results were unknown. Today the causes are well enough understood so that there is a possibility of controlling results or discovering and avoiding the danger line.

One method of control is the use of selection. It is true that intense inbreeding may bring defects to light so fast that selection cannot discard all the defectives. In that case it may be necessary to modify the intensity of the inbreeding, which means proceeding more slowly. But on the other hand, one of the major uses of inbreeding is to bring defects to light rapidly in whole families. By such segregation, it is possible to study the defects and perhaps discover their inheritance. More important from the practical standpoint, however, is the fact that selection can then get at the defects in whole families as well as in individuals and throw out the families that carry them. So long as selection is practiced only between indi-

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4 The intensity of steady inbreeding systems can be measured closely enough for most practical purposes by Wright’s formula (1931) that in a population of limited size closed to outside blood and containing many more breeding females than breeding males, the fraction of the existing heterozygosity lost per generation because of the inbreeding inevitable from the limited size of the population is about one-eighth $M$, when $M$ is the effective number of breeding males used each generation. The “effective number” will be smaller than the actual number if the sires are not used equally and if very unequal portions of the descendants of the different sires are saved. Application of this formula gives the following percentages of the genes heterozygous in each generation which will probably become homozygous the next generation in populations of various sizes closed to outside blood: 50 percent under self-fertilization (impossible in farm animals, of course); 19 percent under steady brother-sister mating (uneconomic with farm animals on account of the large number of males required); 11 percent in a one-sire herd; 6 percent in a two-sire herd; 4 percent in a three-sire herd; 3 percent in a four-sire herd; 2½ percent in a five-sire herd; and 2 percent in a six-sire herd.
individuals, there is no guarantee that a fine animal may not, in his heredity, carry undesirable genes whose effects will appear unexpectedly in future generations. In this sense, inbreeding may be considered as a sort of truth detector, or a sounding apparatus to discover what is under the surface.

But selection, and modifications in intensity, are not the only means of controlling the undesirable characters brought to light by inbreeding. Lines that were undesirable would not matter to the plant breeder. He would merely throw them away. The animal breeder is forced to be more saving of his material. When an inbred line goes bad, he resorts to occasional outbreeding to correct the defects, or to bring in other desirable characters. If two inbred families with different defects are crossed, it frequently happens that the immediate result in the offspring is an increase in the intensity of desirable traits, such as vigor and productiveness, not only above that of the parents, but above the average of populations of exceptional merit not affected by inbreeding. Thus at one stroke previous losses are wiped out and

there is a net gain besides. The nature of the mechanism that brings this about is now well understood, even though the genes involved cannot be identified; essentially it consists in breaking up undesirable gene combinations that have become fixed and introducing compensating or modifying factors from another family, though that family itself may have undesirable characteristics.

The full effect of such outbreeding is apparent in the first or at most the second generation. Thereafter the inbreeding should be continued again, to act as a ratchet mechanism and hold the gains made—until another shot of outside genes is necessary.

Inbreeding may be thought of as a means to encourage distinct families to wander from the breed average, some becoming superior and others inferior in many different ways. Outbreeding is a tool for suddenly leveling and destroying these family differences and starting over again with what amounts to a new family. The two in combination are at the heart of modern plant breeding. In this field they have been, and continue to be, the most effective means yet dis-

Figure 5.—The guinea pig has played an important role in animal breeding, especially in relation to the hereditary basis for such complex traits as fecundity, rate of gain, body size, resistance to disease, and certain anatomical abnormalities. Much time and expense have been saved through use of these little animals as material for investigating breeding problems of far-reaching importance to livestock.
covered for achieving results and attaining the maximum certainty of control. Geneticists are well aware that theoretically they should give comparable results in the case of animals.

Admittedly, the more intensive forms of inbreeding, in the case of animals, require facilities and a procedure that make them unsuitable for general use, at least until much more is known about possibilities, limitations, and necessary precautions; though in the modified form known as line breeding, inbreeding is used in practical operations, combined with outbreeding.

Bakewell used inbreeding as a valuable tool. When his success encouraged others to establish flocks and herds of his breeding, the larger numbers available within each breed reduced to an almost negligible level the inbreeding consequent upon pure breeding. The very popularity of a breed, therefore, usually brought the inbreeding almost to an end, leaving selection as the only method by which the breed was improved or changed after the formative period when it existed in only one or a very few herds.

This in general has been the breeding history of most pure breeds, especially those of British origin. Many of Bakewell's followers used his methods on the native stock of their own regions. What proportion of them failed we have no way of knowing. Those who succeeded went through a formative period of selecting and inbreeding animals while their numbers were small enough so that the inbreeding was a force of some magnitude. As the new breeds became recognized as successful and were expanded in numbers, the inbreeding was generally dropped, except here and there when some stubborn individuals sought to breed a "pure family" within a breed, as in the case of the Bates-bred "pure Duchess" family of Shorthorns already mentioned, or the "straight Scotch" Shorthorns, or the "straight bred" Anxiety 4th Herefords of more recent years.

There are cases in practical breeding history where the occasional use of parent-offspring matings for one or two generations has been conspicuously successful. The extensive use of the Shorthorn bull, Favorite, on his daughters in the Colling herds in the early history of the breed is probably the most conspicuous, but there are many others less extensive, such as the use of the Aberdeen-Angus bull, Earl Marshall, on several of his daughters. Breeders have been particularly apt to resort to the method when the parent appeared to be of such extraordinary merit that it would be years before an animal equally good could be found to replace it.\(^5\)

Inbreeding Experiments with Guinea Pigs

Wright's work in inbreeding guinea pigs at the National Agricultural Research Center at Beltsville, Md., is now a classic example, and as already indicated, some work has also been done with larger animals. The Beltsville experiment has been carried on by the Bureau of Animal Industry for 25 years and has involved records of over 100,000 guinea pigs. These include the records of 23 separate families, each descended from an original pair exclusively by matings of brother with sister, without selection; a control stock in which inbreeding has been carefully avoided; and crosses among the inbred

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\(^5\) Inbreeding less intense than brother × sister and parent × offspring matings is slight in effect. Thus, when sire and dam have two grandparents in common—as human first cousins do—the offspring will probably have lost about one-sixteenth of the heterozygosis which the grandparents had. If the mates have only one grandparent in common, the corresponding fraction is about one thirty-second.
families. Some of the inbred families have been carried through 35 generations of continuous brother $\times$ sister matings. It should be kept in mind, however, that the experiments with guinea pigs differ from practical procedure with large animals in that one male was mated to one female instead of to many females.

On the average there has been a decline in all elements of vigor, but at the same time a conspicuous differentiation among the families. Although the most obvious differentiation concerns such characteristics as color, number of toes, and a tendency toward production of particular types of abnormalities, there are also significant family differences in all the elements of vigor and reproductive ability. These elements of vigor have proved to be inherited independently of each other, and each family has come to be characterized by a particular combination of traits, usually involving strength in some respects and weakness in others. Crosses between different inbred families have resulted in a marked improvement of both parental stocks in every respect. A certain portion of the increase in vigor of the first cross between the inbred families is maintained on resuming random mating, the proportion depending on the number of lines involved in crossing.

The relation of this experiment to a livestock-breeding program is summarized in Department Bulletin 1121, entitled "The Effects of Inbreeding and Cross-breeding on Guinea Pigs." In this bulletin, it is pointed out that, because of the large and confusing effect of environment on traits of economic importance—

progress by ordinary selection of individuals would be very slow or nil. A single unfortunate selection of a sire, good as an individual, but inferior in heredity, is likely at any time to undo all past progress. On the other hand, by starting a large number of inbred lines, important hereditary differences in these respects are brought clearly to light and fixed. Crosses among these lines ought to give a full recovery of whatever vigor has been lost by inbreeding, and particular crosses may safely be expected to show a combination of desired characters distinctly superior to the original stock. Thus a cross-bred stock can be developed which can be maintained at a higher level than the original stock, a level which could not have been reached by selection alone. Further improvement is to be sought in a repetition of the process—the isolation of new inbred strains from the improved cross-bred stock, followed ultimately by crossing and selection of the best crosses for the foundation of the new stock.

On the whole, however, experimental work of this sort with large animals has been tentative, halting, and partial, due to the practical drawbacks previously mentioned—cost, numbers, time, lack of knowledge, and uncertainty as to results.

As the situation now stands, however, more extensive work on this line by experimenters seems to be a logical step. This is not to say that the homozygosis or "purity" for certain characters achieved by inbreeding should be confused with merit and made an end in itself. Homozygosis is not the final goal. Merit is the goal, and getting animals pure or homozygous for certain important characters is one of the methods for achieving it. Theoretical genetics shows why it is a potent means, and practical plant breeding shows how it works out in that field.

**Crossing of Unrelated Inbred Strains**

This is a method used in plant breeding, and in certain respects in practical livestock operations on the farm. Essentially, it consists in maintaining distinct, widely divergent lines of known composition
as breeding stock, then crossing these lines and using the progeny or F₁ generation for market or for production. As breeders have long known, the first generation of crosses between certain breeds has marked hybrid vigor or heterosis. Too little effort has been made to use this hybrid vigor as part of a regular breeding system in the livestock field, with the notable exception of mules and some work with sheep and swine. Logically, the method should have considerable value, and its possibilities should be systematically explored. When the relation between homozygosis and merit in animals is better understood, it may be that the real goal will turn out to be controlled heterosis.

**Figure 6.—Duroc-Jersey-Yorkshire cross-bred litter, produced in Indiana.** The litter weighed 4,080 pounds, or more than 2 tons, at 6 months. Ten-litter contests sponsored by many States produced some surprising results. An Indiana sow in four consecutive litters farrowed a total of 54 pigs and raised 53 of them. Six gilts from her first litter raised a total of 63 pigs for their first litters.

### Ways of Improving the Inheritance of Farm Animals

**QUITE** aside from the question of research and experiment, the livestock man, whether producer or breeder, is interested in methods immediately applicable to the improvement of his own animals. This subject is discussed in books on practical genetics, in Federal and State bulletins, in technical journals, in courses in the agricultural schools and colleges, and in farm gatherings. Nevertheless it may be well to repeat here some of the preliminary considerations that must be kept in mind in practical livestock breeding, if only for the reason that progress does not lie entirely in the hands of the experimenter and the professional. The farmer whose production is confined to plant crops may have little direct concern with breeding; he may buy all his seed from others who specialize in seed production. But the livestock farmer, in most cases, is very directly concerned in animal breeding, since it is the necessary first step in production. Any advance in livestock breeding, then, must rest on a broader base than in the case of plants. It must be understood, accepted, and used by large numbers of farmers as part of their everyday routine. Incidentally, in carrying on breeding operations intelligently, the farmer may make definite contributions and achieve worth-while results even though he does not have theoretical knowledge. This is exactly what was done by the early breeders.
The methods now available for improving the inheritance of farm animals are fundamentally the same as those in use before there was any science of genetics, but they are better understood and can be used to better advantage. A beginning has been made at measuring what each breeding method will do under certain circumstances, and more experience with such quantitative measures may work as much change in breeding methods as the use of definite weights did in transforming ancient alchemy and household chemistry into modern scientific and industrial chemistry.

Fundamentally, the various practical ways of improving the inheritance of a race or breed include selection, which means that some parents are deliberately caused to have many offspring, others few or none at all; inbreeding, or mating closely related animals, and its opposite, outbreeding; mating like to like regardless of pedigree; and mating unlike individuals regardless of pedigree. Usually in a breeding program, selection is combined with one or more of the other possibilities.

Three facts must be kept always in mind, and due allowance made for them.

(1) Hereditary factors are sorted out by chance before being passed on to offspring.

Suppose there are seven slips of cardboard, each one painted a different color on each side—one black on one side, white on the other; one gray and brown; one green and red; one yellow and blue; one orange and purple; one pink and lavender; one crimson and scarlet. They are thrown into the air. They come down on a whirling disk, each slip with one side uppermost. As the disk whirls, the colors appear as a single tone. This tone is the character of the animal. If a single slip had happened to fall with the other side up, the animal's character might be entirely different.

This is something like what happens in inheritance.

(2) Environment has an effect. Examined in daylight, the disk looks different than it does under the yellow light of an electric bulb, though the slips are exactly the same.

(3) The observer may make mistakes. If he has to match or grade several disks, for example, in accordance with the amount of a certain color, he would not do a good job if he were color-blind for that color.

In general, it may be said that the details of a breeding program may be complicated, but the main outlines are clear and simple. When these main steps have been taken, there is not much freedom of choice left among the details. Thus a breeder will rarely need to solve a complicated problem in order to make an important decision.

**PRODUCTION TESTS**

The first thing is to have an ideal in mind toward which to work, though this does not mean that the ideal has to be a fixed one; it may have to be flexible to meet changing economic conditions. The definition of each character should be as exact as possible. A decision should be made as to the importance of each deviation from a desired character. Deviations should be measured as accurately as possible.

The desirability of keeping out nonessentials and sticking to essentials has already been stressed. To cull a productive cow because she is not quite the right color, for example, makes it that much more
difficult to breed productive cows. The ideal should be as simple and practical as possible. Historically, tests for practical productiveness have always been important and have not been stressed nearly enough. Elsewhere in these articles on livestock breeding, the necessity for developing yardsticks for the measurement of valuable characters, particularly in the meat animals, is discussed. Tradition has it that Bakewell made many measurements and notes on the cuts of beef and mutton from his animals and even preserved some of the choicer cuts pickled in jars as a sort of museum to record his progress in improving his breeds for the butcher.

A surprising number of the early British breeders of cattle and sheep had had some years of experience as butchers before they became breeders. Thomas Bates a century ago paid attention to the feed records, milk records, and occasional churn tests of his Shorthorn cows. In North America, shearing contests attracted wide attention and were important in the development of the Vermont Merino. Speed at the trot or pace was the main element in the standard around which the American Standardbred horse was developed.

Production tests supervised by the dairy breed associations were an American innovation, largely the work of Solomon Hoxie and his friends. They had a doubtful struggle until near the turn of the century, when their success was assured by laboratory discoveries which produced reasonably simple and usefully accurate tests for the fat percentage of milk.

The importance of simplification may be shown numerically. Other things being equal, progress in selecting for one trait, when selection is based on that trait alone, will be the square root of \( n \) times as fast as when selection is for a number of traits equal to \( n \). Suppose we are selecting for four traits. Then \( n = 4 \). The square root of 4 is 2. Thus progress in selecting for one trait alone would be twice as fast as in selecting for it equally along with three others; it would be three times as fast as in selecting for nine traits, since the square root of 9 is 3. If the traits are positively correlated with each other, progress will not be slowed quite so much, but such correlations make only a little difference unless they are high; moreover, correlation may be negative and make progress a little slower than the simple formula indicates.

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FIGURE 7.—A contrast in inheritance for meat-producing carcass: A, Southdown; B, Rambouillet. They were suckling lambs when slaughtered. The Southdown dressed 51 percent; the Rambouillet, 43 percent. The Southdown had no grain; the Rambouillet received grain in addition to grass and mother's milk. Tendency toward early maturity and ready fattening also plays a part in this contrast. Tradition often influences consumer judgment fully as much as does the actual palatability of the meat.
Some of the swine-breed organizations have always required that the breeder state the number of pigs farrowed and the number raised, but there has been no requirement that disinterested witnesses attest the record. Experiments with the Danish plan for testing the feeding ability and killing quality of swine were begun by the United States Department of Agriculture and the agricultural experiment stations of Iowa, Minnesota, Wisconsin, and West Virginia in or soon after 1926. At least one swine-breed association—the Hampshire—has started an advanced registry with admission based on performance of offspring in official feeding or slaughter tests, or on winnings of offspring at recognized shows, or on inspection and farm performance. Late in the 1920's some attempts were made in Michigan, Utah, and California to organize an advanced registry for Rambouillet sheep based on yield and quality of clean wool. Pulling tests for draft horses using a dynamometer developed at the Iowa Station were begun early in the 1920's and are an attraction at many livestock fairs today, although they have not yet developed into a test commonly applied to brood mares or stallions. The Hereford breed has established a Register of Merit based on the show winnings of offspring. The articles on the different classes of livestock give additional information on these production tests.

LOCAL IDEALS AND INTERMEDIATES BETWEEN EXTREMES

Some traits are consistently desirable or undesirable in all localities and under all circumstances—resistance or susceptibility to disease; efficiency or inefficiency in the use of feed; high or low fertility. Other things are desirable under some circumstances but undesirable under others.

Generally speaking, extremely large size and weight are more likely to be desirable in regions where pasture and feed are always good than in regions where there are frequent periods of scarcity, as in much of the range country, or in the common management of cattle in the Cotton Belt.

It is also important that each breeder consider his own feed resources and market outlets and make his ideal correspond closely with what will usually be most profitable in his locality and for his type of farming. If this were carried very far, it might lead to a different ideal in every type-of-farming area, although the breeder would be restrained by the general market demand from going as far as local conditions might otherwise dictate. Livestock breeders have probably not gone as far in this direction as they could with profit.

The ideal is often an intermediate rather than either extreme, or demands a certain balance among characteristics rather than that each one should have a certain degree of expression. Livestock breeding in North America is full of examples of this. In Poland China swine there are at least two extreme types—chuffy, fat animals and long, rangy animals. In cattle there are the extreme beef-type and the extreme dairy-type breeds, and in sheep those especially noted for wool and those especially notable for mutton. In poultry there are the early maturing, high-producing egg breeds like the Leghorn, and the slow-maturing, meaty breeds like the Brahma. In horses there are the heavy draft animals and the light, fast race horses or trotters. Each extreme has a specific field of usefulness, but in each case the most widely useful type is likely to be an intermediate between extremes.
Breeding evidence indicates that the intermediate type is not always easy to maintain or improve. There is a tendency for it to split and go toward the extremes. It may never be possible, in other words, to get an intermediate as perfect in its way as the extreme type. The problem, however, is a challenge to breeders, and plant breeding indicates that it is not impossible to solve. Plant breeders regularly combine several economically important characters, such as high yield, high quality, and high disease resistance, in a single variety. Though even in plants this has not been easy, large numbers and skillful technique being necessary to get positive results, nevertheless these results indicate that, where there are no physiological hindrances, it should be possible in the case of animals to hold the gains made in the development of intermediate types and perhaps to bring about improvements as yet hardly dreamed of, developing intermediate breeds superior, for example, to the present Rhode Island Red in poultry, the Milking Shorthorn in cattle, the Morgan horse, the Hampshire hog.

In this connection, it should be noted that in the United States, reliance has been placed mainly on importing breeds already regarded as highly improved in their native lands. Partly this was a natural desire to save time by starting where other breeders left off rather than starting at the beginning and ignoring the improvements already made; but in many cases it is likely that something was lost by ignoring the adaptability to American conditions already attained by the local stock. In retrospect, it looks as if American farm animals might now have been even better suited to the needs of American agriculture if more of the breeds had been built on a foundation of native stock blended with the excellence of the imported breeds—as the American Saddle horse was built on a native foundation but with extensive use of Thoroughbred stallions—rather than going over completely to pure-breeding the imported race, as was done in most cases.

Importations began almost as soon as there was any recognition of improvement in the native lands of the breeds. Merino sheep and jack stock from Spain came before 1800, and Shorthorns and Herefords at about the same time. From then until the Civil War small importations came from widely scattered sources—as cattle from Great Britain, the Netherlands, and India; Angora goats from Turkey; sheep from France and Great Britain; swine from China, Italy, and Great Britain; and horses from many lands. Even camels were imported between the Mexican and Civil Wars in one extensive attempt to adapt them to the needs of army transport in the Southwestern States. The high tide of importation came in the era of agricultural expansion which began at the close of the Civil War. Many of the major breed associations were organized in the late seventies and in the eighties of the last century. The agricultural depression of the nineties checked much of the importation.

As a protection to the health of livestock in the United States, importations of breeding stock from certain countries in which dangerous diseases exist are restricted by Federal quarantine regulations. Such restrictions have had the effect of preventing importations of certain classes and breeds of livestock common to such countries.

Recently the Department has brought into this country breeding stock of Danish Landrace swine, Hungarian Puli dogs, Hungarian
Nonius horses, and Red Danish cattle—animals that have reputations for superiority in Europe and that may be useful in breeding experiments.

**LOCATING THE BEST ANIMALS**

It is not an easy matter to estimate whether an animal has the hereditary factors that will enable it to approach the desired ideal in a given environment. A mere record of purity of breeding is not enough. Pedigree, individual performance, and progeny tests must all be taken into account. Each has value if it is of the right type, but each also has limitations. All three of these methods should be used in practical breeding, but no single formula for the amount of attention to give to each can be generally valid. Sometimes it may be necessary to cross two or more breeds in order to get into a herd all the kinds of genes it is desired to combine in the ideal. In practical breeding this is usually done as a last resort if there is no way to find all the desired inheritance within one breed, and only when the breeder and his associates are prepared to maintain a flock or herd large enough to have at least three to five sires in use at all times.

Pedigree comes first in time and is cheapest. But even though certain factors are known to be present in the parents, it is impossible to tell just what combinations will turn up in a given individual among the offspring, as we have seen in the analogy of the colored cards; but it is possible to tell what combinations will turn up on the average in a large number of offspring considered as a group.

**More Data Needed in Pedigrees**

Too often, as already noted, pedigrees are not of the right type and thus have little or no practical value. The most valuable pedigree is one that gives the full performance record—bad points as well as good points. A desirable breeding animal is one that is directly descended from proved individuals on both sides of the pedigree. To rely on remote ancestors or relatives is to increase the element of guesswork.

The extreme limit that can be approached by the study of pedigree would be reached if one knew the exact heredity of both sire and dam. Yet even with that extreme knowledge, the chance or sampling nature of Mendelian inheritance would insure that some offspring would be above and some below the average of the parents in each respect in which the parents were not both genetically pure. Except for genes so abundant that most members of a class or a breed are already genetically pure for them, one or the other or both parents will in more than half of the cases be genetically impure for any particular pair of genes. This gives plenty of room for one offspring to vary far from the average of its parents, but such variations, being random, tend to cancel each other in the averages of large numbers of offspring.

**The Performance of the Individual**

Individual performance is second in time and cheapness to pedigree analysis, and is usually most accurate in a population not previously selected on either basis. It cannot be used for one of the sexes in sex-limited traits like litter size, egg production, milk production,
or some temperamental traits such as the working disposition of a gelding; and it cannot be used for either parent in the case of traits that can be measured only when the animal is dead, such as yield and quality of meat.

Besides being a basis for direct selection, individual performance is, of course, used in pedigree selection and progeny tests. Pedigrees are weighted averages of the individuality and performance of ancestors and collateral relatives, while progeny tests are averages of the individuality and performance of offspring.

Individual performance, however, is not an accurate indication of the ability of an animal uniformly to pass on desirable traits to its progeny. Other things that interfere with using this as a guide to breeding value are:

1. Mistaking the effects of environment for the effects of heredity.
2. Incompleteness and errors in the methods of measuring merit.
3. Dominance, which sometimes makes an animal that has inherited something from only one parent just as meritorious an individual as another that has inherited it from both parents.
4. Complex gene interactions, which may be confusing in all sorts of ways. For example, if an animal has four genes of a combination of five which together would produce a desirable result but separately produce no effects or undesirable ones, such an animal's own performance or appearance would cause it to be rated as no better or worse than one that had none of the five genes; yet it might be valuable as a breeder to transmit the desirable genes. Not much is known definitely from actual experiment or observation about the general importance of complex gene interactions as a source of error in domestic animals; but from the nature of the case it is to be expected that they would quite often be unimportant in a population which is first being turned by selection in a new direction, but might often be quite important in a population which has been under intense selection toward a certain goal for several generations.

The first and second of these sources of error—environment and mistaken judgment—are almost certain to be the more serious ones in the case of economic traits, since these are generally much influenced by environment and, because of their physiological complexity, by many genes. Dominance is not a very important source of error except for rare recessive genes—such as lethals, that is, factors so deadly that their presence in the homozygous condition does not permit the animal to survive—which individually have a large effect. The above statement does not hold true, however, for a group of animals that has already undergone considerable preliminary culling. In this case, dominance may be responsible for a rather large portion of the remaining discrepancies between breeding value and individual appearance or performance.

Theoretically the breeder may reduce the error arising from environmental effects and imperfect measurements of merit by (1) analyzing the factors in the environment and correcting the record to bring it in line with what it would have been under standardized conditions—though it may be impractical to correct for more than a few of the most important factors; and (2) using lifetime averages
instead of single records or ratings. Prominent among traits for which this last might be helpful are annual milk and butterfat production by dairy cattle, wool production by sheep, strength or speed of horses, fertility of swine, and the more plastic details of type or conformation or action. Under practical conditions, however, there are so many factors that interfere with getting significant lifetime averages that they are not greatly used. They would be even less useful for egg production of poultry in cases where only a minority of the females are kept for more than 1 year. For certain other traits that can be measured only once, a lifetime average has no meaning. Examples would be early maturity, growth rates, longevity, dressing percentage or other characteristics observable only at slaughter time, and—under practical conditions—efficiency of the use of feed for growth or fattening.

Errors in selection arising from dominance or from complex gene interaction can be corrected only by study of the pedigree or resort to progeny tests—which means getting away from the individual animal and trying to see its genetic possibilities through its ancestors and descendants. Usually such errors can be only partly corrected in this way. In some cases—for example, red color in black breeds of cattle—where pure recessive tester stocks are available and can be used economically, the progeny test can effectively overcome the errors introduced by dominance. Such a test is necessary to determine which progeny of a sire or dam are carrying red if a red calf has been dropped, since to produce a red calf both parents must carry the recessive character.

The Progeny Test

The third basis for selection, the progeny test, discussed at some length in the other livestock articles, goes back perhaps 2,000 years. Varro had recommended that the excellence of rams and boars be judged by the excellence of their get, and there is no reason to think the idea was original with him.

The progeny test, however, often comes so late that it finds its chief usefulness as a part of pedigree records. In the case of the larger animals, too, sometimes only a few of the offspring can be tested, whereas to be fully useful, the progeny test should be extensive enough to overcome the statistical errors of Mendelian sampling in the transmission of factors from the parent to the offspring. Sire indexes, discussed in the article on dairy cattle, are helpful in overcoming other difficulties such as differences in the merit of the mothers of the progeny.

\[ \frac{1}{1 - r + \frac{r}{n}} \]

In the general case the portion of an animal's apparent difference from its herd average, which is most probably the real difference where the animal's own record is an average of a unselected single records, is

\[ \frac{1}{1 - r + \frac{r}{n}} \]

of its apparent difference, where \( n \) is the number of unselected records and \( r \) is the average degree of resemblance (coefficient of correlation) between different unselected records of the same animal within that herd. Where \( r \) is nearly perfect—that is, where an animal's different records are nearly always alike, as in the case of coat color or many skeletal differences—there is little need to use lifetime averages. But much is gained in traits where one record of an animal differs widely from the next without apparent cause. For example, in annual butterfat records of dairy cattle, the correlation between records of the same cow in different years in the same herd seems usually to be somewhere around 0.33 to 0.50. With the smaller figure—that is, where environmental forces are less well controlled or corrected—one would make the least mistake by valuing the animal at 0.33, 0.50, 0.60, or 0.66 of its apparent superiority over the herd average, according to whether its record were the average of 1, 2, 3, or 4 years of records. Where environmental forces are sufficiently well controlled or corrected so that the correlation is 0.50, the corresponding figure would be 0.50, 0.66, 0.75, and 0.80. The use of lifetime averages costs very little if records of production or type at certain intervals are already available.
AN ANALYSIS OF TWO METHODS OF MATING

Inbreeding, outbreeding, and cross-breeding have been discussed earlier in this article, at least in their bearing on a possible program for further progress. For a more detailed discussion, centering on practical operations, the reader should consult Federal or State bulletins, or a good textbook. Mating like to like and mating unlikes have not been touched on, however, and something about the effects of these two methods will be given here.

Mating like to like was perhaps the first method used by animal breeders, since it is the most obvious. It apparently increases the likeness between parent and offspring, or among sibs, and therefore seems to give the breeder increased control over heredity. This, however, is deceptive. Actually, mating like to like increases the variability within the breed, and much of the resemblance between the parent and offspring is merely by contrast with this greater variability. There is very little effect on homozygosity or genuine fixation of type. Nor is there much effect on traits that are considerably influenced by environment, since the effects of environment would in themselves seem to make animals alike when they really were not, and therefore would tend to prevent the mates from being very much like each other in their heredity, even though they might have been chosen to be very much like each other individually. By contrast, inbreeding has a large effect on such traits, because animals are mated to each other purely on the basis of their being closely related by inheritance, and inherited traits that tend to make them react in the same way to a given environment become concentrated.

Most of the effects of mating like to like are realized in the first or second generation. If it is continued after that, it merely holds the condition of increased variability. All in all, the practical usefulness of the tool, as genetics is understood today, is largely confined to increasing variability, and to bringing about a rapid change to extreme types. It may be useful to a breeder whose ideal is different from that of most of his fellow breeders.

When there is agreement on the ideal for a breed, such mating of like to like as can be practiced increases the variability of the breed, and therefore should make selection more effective. Something of that kind happens where breeders are agreed on the ideal but some, because of superior skill or more money, can purchase more nearly ideal groups of males and females than others can. This leads to a greater diversity in the breed than if every herd were truly a random sample of the males and females of the breed. From the principles involved, it seems doubtful that the process can go very far in breeds in which there is substantial agreement about ideals, but actual data to verify this are practically nonexistent. Even in cases where there is a diversity of ideals and a breed is split in two directions, as in the case of Poland China swine 20 to 30 years ago, when extreme “hot bloods” and extreme “big types” each had ardent advocates, and the American type and the island type in Jersey cattle, the separation brought about by mating like to like is rarely anywhere near complete unless there is also considerable separation by pedigrees.

Mating like to like, regardless of pedigree, is easily confused with selection. Many of the statements about it in print do include
something about the effects of selection. The difference may be shown by an illustration. If a cattleman has bought two bulls to be used equally on his herd of cows, he can practice no further selection so far as those bulls are concerned until their calves come. His power to select them was exercised when he chose them rather than other available bulls, and when he decided that these two were to be used equally on his herd. He can, however, still practice the mating of like to like by dividing up his cows so that each shall be mated to the bull more like her, or he can practice the mating of unlikes by mating each cow to the bull less like her.

Mating unlikes is frequently practiced where the ideal of the breeder is an intermediate. An animal too extreme in one direction is mated to another which is too extreme in the opposite direction. In the process of selection also, the breeder uses this method because he cannot find perfect animals. If his females are unusually good in some respects but below average in others, he will usually be careful to select for his next sire an animal especially strong where the females are weak, but since he cannot get a sire perfect in all points, he compromises by accepting one a little weak where most of his females are strong.

Mating unlikes is the most powerful tool for immediately producing uniformity in a breed, but it exerts nearly its full effect in the first generation. Inbreeding, if carried to the limit and accompanied by selection which would discard all but one inbred line, would produce
much greater uniformity, but it would require more time, and because of its other consequences it is not often used for this purpose in practical operations.

Contrary to widespread opinion, the mating of unlikes has almost no effect on homozygosis. Unless one starts with a group of inbred lines, he need not fear any material loss in genuine fixity of inheritance when he practices this method of mating. For the practical breeder the mating of unlikes is a very useful means of keeping the breed in the middle of the road and discouraging extremes. This is especially advantageous where the ideal is some kind of an intermediate. The breed tends to return almost at once to its original condition when the mating of unlikes is discontinued.

Future Progress in Livestock Breeding Demands
the Cooperation of Four Partners

LIVESTOCK improvement is a matter that concerns a vast number of people. At one end is the consuming public and such groups as the meat packers; at the other end, scientific workers, professional breeders, and farmer-producers. Each group has its own interests and attitudes, but all of the groups—public, scientists, breeders, and producers—have a stake in the future of livestock breeding, and cooperation is necessary if there is to be progress.

THE FUNCTION OF THE SCIENTIST

The situation of the scientific experimenter has already been discussed. He finds himself faced by problems that in some cases are so complex as to be seemingly insoluble. The influences of heredity, food, and environment in the development of an animal are often extremely difficult to isolate. Most of the characters with which the animal geneticist deals show a wide range in expression, and they are affected by an undetermined number of genes, probably large. Practically nothing has been done toward identifying specific economic characters with definite genes, and there is even good reason to doubt that much can be done in this direction for traits of genuine economic importance, without using larger numbers of animals and more money than would ever be available for the work, not to mention unlimited time. Cattle cannot be handled experimentally by the millions like pomace flies; and even in the case of pomace flies, though they are extraordinarily favorable material, the genes that have so far been definitely mapped correspond for the most part to such characters in animals as coat color or the presence or absence of horns.

Moreover, there is always the fundamental difficulty inherent in the chance sampling between pairs of genes that is nature’s method of passing on inheritance. Of course it will never be possible to pick desirable genes for an animal as items can be picked from a catalog to make up a combination order. Still, by a system of inbreeding, by carrying on the work for several generations, and by wise selection, it

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should not be impossible to develop strains of livestock that carry many desirable genes and are valuable breeding animals.

In other words, to offset the case against the possibility of progress, which is not difficult to make, there is the record of achievements already made; the great advance in our knowledge of how heredity operates, which makes it possible to formulate experimental procedures and breeding practices based on something better than guesswork; and the real and steady advance in plant breeding—a science that also, at one time, had to start from scratch. The amount of experimental work in genetics with animals is extremely limited, even in the case of such small animals as the rat and the guinea pig, compared with experimental work in nutrition, for example, or in plant genetics. As long as there is still so much undone and untried, and so many problems are pressing for attention, the situation cannot be considered hopeless.

The scientist alone is equipped to explore this field of experiment and research. His part may not be dramatic and his progress may be slow, but he should be able to progress provided he adheres to certain principles. He may have to concentrate on character analysis as a prelude to further character synthesis. He must refuse to be too much influenced by the immediate pressure of economic considerations. It may be quite as useful, for instance, to isolate a strain of low-producing dairy cows, with a view to discovering what is responsible for low production, as to concentrate eternally on trying to get high producers. The scientist may have to forget some preconceived notions of the roles played by genetics, endocrinology, and anatomy. He must avoid having his judgment warped by traditional breed standards. He should be free to work on a sufficiently large scale and over a long period.

THE INTEREST OF THE PROFESSIONAL BREEDER

The point of view of the breeder of animals used largely as breeding stock rather than for the market is that his operations must yield a profit, and the breed standards must be maintained. Professional breeders have been concerned for generations with the incorporation of desirable qualities into their stock and they have believed that these qualities could be maintained and improved through pure-breeding practices. They make almost constant use of selection, although in many cases the effectiveness of the selection is relatively slight. Ever since livestock exhibitions began, the professional breeder has followed show-ring standards rather closely, and the breeder who could win consistently at the shows soon became the leading breeder of registered stock in his community. Through the application of this system, the meat breeds of livestock have changed, but to what extent the homozygosity of the breeds has changed is open to question. Show-ring standards are arbitrary at best and they are superficial genetically.

In many cases the power of selection for meat characters amounts to practically nothing when based on present standards of measurement. The breeder makes frequent mistakes and by a single unfortunate selection of a sire he may easily lose all he has gained. He is

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10Several breed studies have shown that current pure-breeding practice tends to fix something like 0.33 to 0.50 percent of the unfixed inheritance per generation, plus or minus whatever amount—probably small—is changed by selection, and minus whatever is lost through accidental or fraudulent registration of grades. There are thus no very valid theoretical reasons for expecting a recognized breed to be very much more homozygous today than it was when it left the hands of its founders, in whose small herds the limited size of the population and the deliberate line-breeding to a few choice animals were forces powerful enough to increase homozygosity noticeably.
greatly in need of new measures of excellence that will enable him to make further progress in unifying his stock for those characteristics for which they are valuable.

If we ever reach the stage where it will be possible to judge meat animals in the show ring on the basis of ability to transmit economy of gain, superiority of meat quality, and high fertility, then the breeder will be in a position to know with certainty where the strains of superior breeding worth are located. This will be true particularly if there comes a time when data of this kind can be recorded for large numbers of animals within each of the meat breeds.

The professional breeder has a heavy stake in the existing situation, and he cannot be expected to make radical changes that would jeopardize his gains. Yet he must keep an open mind and be ready to meet changing conditions. It is true that he is influenced by the producer’s needs, but he in turn influences the producer by setting up ideals, so that he has a great responsibility in the animal industry. While cost and other factors would probably prevent the breeder from initiating large-scale experiments involving any great departure from existing methods, he should be the first to recognize the need for these experiments, to cooperate in them fully, and to put them to practical use as soon as they show good results.

THE INTEREST OF THE FARMER PRODUCER

As for the farmer—he is relatively free to change his system of breeding, the blood lines used, and his general procedure whenever he believes this is necessary to increase the profitableness of his stock. The limitations set by the current show-ring standards for pure breeds seldom carry much weight with him. His interest lies primarily in the cost of feed per hundred pounds of gain, uniformity of growth, and a product that will sell well. Because of the constant changes in market demand, he is frequently called upon to bring about rather drastic changes in the characteristics of his animals. It is important, therefore, that he maintain stock which is sufficiently flexible so that he may be able to make these changes without too much difficulty. At the same time, it is important for him to possess
breeding stock that will uniformly pass on economically important characters to the offspring.

The farmer is greatly interested in the development of strains that are more economical to raise and that will produce a high-quality product commanding a premium on the market. On the other hand, the scientist, the professional breeder, and others interested in livestock improvement have not given enough attention analytically to these practical considerations. At the same time, if the price of improved strains is too high, the farmer may not be able to sell the offspring on the market at a sufficient premium to justify the use of the improved stock. This is one reason why so many grade sires are in use. As long as there are grade animals equal in performance to many of the registered ones, it is certain that the farmer will continue to use them in preference to registered animals. In future developments, it must be kept in mind that the farmer is interested primarily in profits and only secondarily in some of the things that the show-ring and breed associations have fostered.

Farmers who are interested in meat or wool production for profit do not have a fixed ideal, because ideals change with changing economic conditions. The breeder who is dealing with a class of livestock possessing sufficient flexibility so that its course may be varied in step with changing economic conditions is in a particularly favorable position to maintain satisfactory, long-time average profits. A good example of the need for such flexibility is furnished by the lard breeds of swine which were developed to be a help in marketing a varying and unpredictable corn crop, turning large surpluses into heavy hogs with high yields of lard, while small corn crops went to market as lighter and leaner hogs. In recent years a shrinking export market and low lard prices have made it likely that the ideal for swine breeders will tend toward a hog with more lean and just enough lard to make it sell well. But this situation in turn may change.

It takes at least one animal generation to effect any change and may well require two or three generations to make significant progress on the road toward a new ideal. In the meantime, the ideal may have changed again, owing to changing economic conditions. Thus the ideal itself is largely dependent upon economic factors that can change more rapidly than a breed average can be changed by the breeders. At the present time a certain amount of flexibility and variation is a part of the ideal for those characters largely affected by economic conditions. From the standpoint of the experimenter or the scientific worker in animal husbandry, this situation is a challenge to know more of the inherent make-up of the various breeds of animals, so that when a change in economic conditions does occur, breeders can more surely and more quickly effect the necessary modifications in their stock.

Not all characters, of course, are affected by economic changes. High reproductive power and disease resistance are desirable under any circumstances, especially in view of the competition in animal husbandry today. Examples of low fertility or even of sterility in farm animals having excellent conformation are not rare. This may often be the result of faulty husbandry rather than of faulty heredity, yet there is always the suspicion that possibly selection from the production standpoint may have affected the endocrine balance to the detriment of reproductive power. There must be an ideal for reproduction as well as for production, and the two must be so balanced that the producer can maintain the ratio of numbers to quality that will yield the maximum return.