THE IMPACT OF GENETICS ON ANIMAL BREEDING

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IF we would know how genetic knowledge is changing animal breeding practices or is likely soon to change them, we can probably get our best clues by asking what the animal breeders are studying now. Predictions made on this basis will not be wholly accurate, of course. The "endless frontier" nature of science precludes high accuracy in any method of predicting the future, especially the distant future. Yet always there is some time-lag in applying newly won knowledge to the arts and business of production. Predictions of the immediate future on the basis of that time-lag are likely to be a bit better than guesses.

Genuinely new knowledge and developments are more likely to be found where several investigators are delving, more or less independently, in a field than by lucky chance or sudden inspiration descending on a stray worker who is thinking of something else. To be sure, the latter does happen, even if but rarely, and its consequences are sometimes tremendously important. Saul was out looking for his father's asses when he found a kingdom! Predicting the future by studying current research is a bit like watching a river at a given point and predicting its downstream course. Usually we can see a few hundred yards with practical certainty. Often by looking at the hills on the horizon we can make a fair estimate of its general course for several miles. But we are almost certain to be wrong if we predict that it will continue indefinitely in that direction for hundreds of miles.

The first half century of genetics, dating that from the rediscovery of Mendel's laws, is described in a forthcoming book which includes many details about the impact genetics has already had on animal breeding, as well as on plant breeding and on man's ideas about biology and about himself. It would be wasteful to repeat those here in detail, but a few will provide background for what follows.

In genetics itself, the first twenty years were devoted largely to testing whether Mendel's laws were true, whether they applied to all characters or only to certain kinds such as colors and superficial details of form,
whether the gene really did remain constant or was changed a bit by its long and intimate association in the heterozygote with its slightly different allele, identifying the chromosomes as the physical carriers of the genes, and exploring the relation of gene differences to environmental differences in causing the characters we actually observe. The consequences of various mating systems and the genetics of populations, although studied a bit in the first two decades, developed mainly in the third and fourth decades out of the need to understand the results of inbreeding and selection experiments, plus a growing realization that the genes were too many and their effects and interactions were too varied to permit ever knowing the complete Mendelian formulas of any individuals. The physiology and chemistry of the processes by which the genes do their work is only beginning to be clarified even now.

Genetics first affected animal breeding by explaining the reasons for many facts which the breeders already knew and by removing much of the mystery. Mendel's laws of segregation and recombination, and the sampling nature of inheritance which they automatically cause, explained atavism, reversion, the inconsistent importance of different ancestors in individual cases, why full brothers were not exactly alike in heredity, and many other puzzling things which had seemed irregular or contradictory. Many superstitions, such as telegony and that maternal impressions would affect the young, began to melt away as it was seen that the supposed evidence for them could be explained more consistently in other ways. The psychological effect of having the mystery dispelled from animal breeding and knowing that one was struggling only to utilize natural laws, rather than against capricious, unknown and possibly hostile forces, must have been considerable although no way to measure it is apparent.

Breeders, fully convinced of the importance of heredity and that pedigrees were useful, but baffled in all attempts to predict individuals perfectly from their pedigrees, had supposed that a large flood of new heredity, . . . mutations we would now say, . . . was pouring into the population at all times. They had found no other plausible explanation for the unlikeness of full brothers and for the fact that populations continued variable in spite of the supposed blending nature of inheritance, which they thought would "swamp" individual variations. They spent much time and effort in trying to find some way of evaluating pedigrees perfectly and of controlling in their favor the causes of the supposed large amount of mutation. Mendel's laws made it obvious that no system of evaluating pedigrees ever could be perfectly accurate in its prediction of individuals, as long as either parent was heterozygous
for any genes. Pedigrees began to be seen in their proper light as rough
guides, . . . certainly worth at least a lick and a promise, . . . but
capable of being made to yield perfectly accurate predictions of
individual offspring.

As it became clearer that mutations are too rare to be of much
practical importance within the short space of time which interests the
plant and animal breeder, efforts at controlling their number or direc-
tion by supplying a particular kind of feed or care or climate diminished.
The resources thus released became available for useful purposes. To be
sure, keeping animals under special conditions will sometimes be worth
doing because it makes them show more clearly the genetic differences
between them, and thus permits selections to be more accurate. We
still shrink from following this policy to its logical limits such as, for
instance, exposing our animals deliberately to disease in order to find
which ones have natural resistance.

Breeders had long known that an animal is likely to transmit as if it
were somewhere between its own characteristics and those of its close
relatives. The controversy during the middle of the 19th century among
breeders in the German-speaking lands about the doctrine of “racial
constancy” is an extreme example of that. Galton, in his attempts to
describe the facts of inheritance quantitatively, had named this tendency
for individuals to be between their parents and the racial average,
“regression,” and he referred to it as “the pull of the race.” Many
supposed it to prove that breeders were “going against nature” in trying
to improve their animals by selection and therefore could go only a
little way in this direction. It is now understood that this tendency for
extreme parents to have offspring nearer the average of the race is little
except the automatic consequence of the non-inheritance of environ-
mentally caused variations. Also, where only one parent is considered
at a time, the other parent is likely to be nearly a random individual
of the race unless mating was far from random. Also some of the
variations in the parent may not be transmitted because they were
effects which genes cause only in certain combinations or in special
environments not repeated for the offspring.

The early enthusiasts about Mendelism could see little relation
between that and the findings of the biometricians who worked with
Galton’s methods. Some even supposed these to be in conflict. But
almost as soon as the geneticists began to work with characters affected
by three or more pairs of genes, and especially if those characters were
strongly affected by uncontrolled environmental variations, it became
clear that there was no real conflict but only some superficial differences
which came automatically because one group studied the complex result of many ingredients while the other group studied those ingredients one by one. Except for its algebraic language the biometrical approach, as subsequently modified and expanded into population genetics, is more nearly the way animal breeders usually see their problems, since the individual animal's economic usefulness or net merit is affected by more genes than can be catalogued and by many known and unknown environmental circumstances besides.

Some of the main changes in animal breeding practices between 1900 and 1950 are the following: Much more effort to measure impartially the merit of individuals...as in cow testing, trapnesting, type classification, and pig testing stations,...wider and more systematic use of progeny tests and sib tests, artificial insemination in dairy cattle for economic reasons and also as a way to intensify the selection of dairy bulls, more effort at standardizing the environment under which individual merit is measured or correcting for such environment as was not standard, and a bit more use of special mating systems like inbreeding. Distant ancestors and characters which are only breed trademarks are now emphasized less, although they still receive too much attention and thus reduce the intensity of selection for important things. The importance of non-selectivity in the data, if they are to be unbiased, is understood as concerns progeny tests and sib tests, although many do not yet see that it is equally important to judge the individual animal by the average of all its records or appraisals. Breed registry societies are spending much more of their resources in measuring individual merit and in promoting progeny tests than they did a half century ago. Production records and sometimes linebreeding count for more in the auction ring. The show ring remains a place to exalt and teach a visible ideal, rather than to appraise the probable breeding merit of any noticeable fraction of a breed. Attempts to make the awards jointly on type and production have hardly been successful, although perhaps not all of the plausible devices for doing this have yet been tried. Even the produce-of-dam and get-of-sire classes have not had much genetic effect because it seems impossible under show conditions to achieve enough non-selectivity of the offspring to give such a progeny test some useful meaning. I see no way to estimate how many of these changes would have come anyhow, even if genetics had not developed. Some, such as appreciating the importance of non-selectivity in the progeny test, would hardly have come without experience in analyzing Mendelian ratios.
The average productivity of livestock has increased markedly and rather steadily. The Bureau of Agricultural Economics estimates\(^3\) that the production per animal unit in the United States has increased more than 45 percent in the 29 years from 1919 and 1920 to 1948 and 1949. I see no valid way to measure how much of this came from improved feeding, from improved sanitation or other health measures, and how much from genetic improvement, but the latter must have been considerable.

Agricultural college herds had little *direct* effect in changing the genetic composition of the breeds. College-bred ancestors are rare in the pedigrees of random samples of the breed. The major reasons appear to be two. First is the difficulty or inappropriateness of the colleges pushing their sales of breeding stock as vigorously as seems necessary to make a herd a center from which sires go to be used in the leading seed stock herds of the breed. Second is the usual timidity or conservativeness of the men in charge of the college herds. Most of these are teachers or demonstrators, as well as research workers and breeders, and are naturally reluctant to do risky things with the public property in their charge. It is somewhat hazardous for the teacher or demonstrator to be found wrong. Certainly this detracts from his self-esteem! The research worker expects to be wrong often in his preliminary estimates although he, too, tends to be conservative in his conclusions. He rightly requires much higher odds in favor of his published conclusions than the business man can afford to require for most of his decisions.

At any rate, when the man in charge of a college herd needs a new sire he usually goes among other herds on a quest for an ideal sire, somewhat as Jason went seeking the Golden Fleece, . . . and with about as much prospect of success! If the calves in the college herd do not satisfy him, he is not seriously deterred by the fact that their sire is one which he or his predecessor selected by the same methods he proposes to try again. He appears not to ask himself what real reason there is for thinking he will be any more successful this time. Not long ago George Odlum expressed this pithily concerning a proposal that Britain import more Friesians from Holland, when he said in effect: We have imported several times before and have bred these cattle pure. If now the cattle in Holland are really better than ours, then either we did not get in the earlier importations animals equal to their best or they are better breeders than we. If the former is true, what reason is

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there to think we will do better this time? If the latter is true, we should import some Hollanders, rather than more of their cattle!

If the calves in the college herd do satisfy the man in charge, he is reluctant to use one of his own bull calves as a sire lest the inbreeding (which would usually be less intense than he thinks) might damage the herd so that he would be ashamed of it before his students and visitors. Aside from the public relations aspects of the matter, why should he not damage the herd, . . . if thereby he learns something? Most of the genes in the college herds, whether good or bad, are going to pass out of the breed anyhow, because nearly all the breeding stock sold will go to grade herds or to purebred herds just being founded. For our own education on this point there is room for more studies of what actually does happen in college herds. One might take an inventory list of the registered animals in the herd in 1900, or some other date several animal generations in the past, and trace just what did happen to their descendants. Or he might list those in the herd now and figure what small fraction of their genes probably came from animals which were in the herd even as recently as 15 or 20 years ago.

The colleges may have had an incalculably great influence on breed improvement by spreading knowledge of good breeding practices through their demonstration herds and by teaching their students, on and off campus. Certainly the college staffs played a large part in promoting production testing and in spreading the ideas of the show-ring.

The problems currently interesting to research workers in animal breeding have come largely from their having tried various plausible breeding plans in actual operation in recent years. The conferences and projects of men working in the regional swine and sheep breeding laboratories and, more recently, in the dairy cattle, beef cattle, and poultry breeding laboratories have had much to do with this. The partly parallel experience of the corn breeders also has had strong influence. In many ways corn breeding problems are more like animal breeding problems than they are like the problems of breeding naturally selfed plant species, such as oats, soy beans and wheat.

The genetic information most needed now for making rapid progress in animal breeding hinges around four questions or fields. 1. How to make selection more effective. This means making more useful selection indexes. 2. Are the non-linear interactions between heredity and environment important? 3. How important really is epistasis? 4. Is over-dominance important enough to need attention?

Also, as we quantize our breeding plans further, we need to know the vital statistics of farm animals more accurately. How intense can
our selection be? What will happen to the generation interval if we rely on the sib test more and on the progeny test correspondingly less? What rate of genetic improvement can reasonably be expected? How much could this be changed by the maximum practical use of artificial insemination? How much by transfer of fertilized ova, if that ever becomes feasible in practice? To know the answers to such questions and thus to make our plans sounder, we need to know more about the means and likely variations in such things as expectation of life, replacement rates, percentage calf and lamb crops which can reasonably be expected, generation intervals, and how much each of these can be changed by any changes in our management which are economically possible. We are beginning to be able to compare the probable results with the probable costs of a proposed change in breeding procedure, although as yet only within wide limits.

To make sound selection indexes requires four kinds of information: The heritabilities and economic values of the various traits we would consider, and their genetic and phenotypic correlations with each other.

Economic values are just another way of saying that defining the ideal is the first step in making a breeding program. The ideal is likely to change at least a little, as prices and other economic conditions do; yet the breeder cannot afford to shift his ideals that rapidly back and forth. Hence some compromise may be necessary.

Knowledge of heritabilities is increasing rapidly, although the confidence intervals for those are still uncomfortably wide in most cases. The idea of heritability is an old one, going at least as far back as Galton’s time. Davenport in 1907 even expressed it quantitatively in what he called the “coefficient of heredity”. However, in the state of genetic knowledge then they could not appreciate fully the pitfalls in assuming, as their operations did, that the correlations between relatives were caused wholly by genic likeness, and in neglecting the breeding structure of the population.

Phenotypic correlations between two traits in the same individual were widely investigated during the first three decades of genetics, but as yet we know only a little about the genetic correlations. The methods for estimating those have wide sampling errors. In cases, if there be such, where selection has been practiced for a long time and is now almost or completely ineffective, yet heritability seems high, there is a priori reason to suspect that strongly negative genetic correlations exist. This causes us to undo, when selecting for character X, what we did when we selected for character Y, and vice versa. In the limiting case where this negative genetic correlation is perfect, this becomes the
same thing as overdominance if the desirable phases of both X and Y are at least partially dominant. Probably in many more cases the genetic correlation is negative but imperfect. Then efficient selection indexes are likely to contain surprising changes in emphasis or even reversals from what we would think if we consider only the economic values. If we have the information necessary for constructing selection indexes, we can predict fairly well the average rate of improvement per year or per generation over the next few generations, although we are powerless to predict the ultimate genetic limits to such improvement.

By interactions between environment and heredity we mean merely that the phenotypic difference between genotype A and genotype B is not the same in environment X as it is in environment Y. We know that such things do exist, at least to a mild degree, between breeds. Some breeds are better adapted than others to warm climates, to lowlands, or to heavy feeding, or to early marketing, but under the reverse conditions the adaptability of certain breeds may also be reversed. Do such differences exist between individuals within breeds to such an important extent that we need to take account of this in our breeding plans? Some of the observations on identical twins in cattle suggest that they do, but that evidence can still be interpreted in other ways. If these interactions really are important, they indicate that we should have a separate breed for every kind of environment which is extensive enough to warrant such an enterprise. Or can we solve it by selecting for versatility itself as a primary characteristic which is highly important? In any event, the question of the kind of environment under which to keep the animals whose merit is to be measured becomes much more important than if the effects of variations in environment and in heredity are merely added to each other.

Epistasis surely must be important in differences between major groups, such as between species or even between distinct types within a species. That seems to follow from the rather large differences between parts or organs in such cases and the obvious importance of having these balanced with each other so that the animal as a whole is an efficiently functioning unit. But it is not so certain that epistasis is important enough in the differences between individuals within the same breed that we need to take it into account as a major factor in shaping our breeding plans. If it is that important, we need to make much use of the linebreeding form of inbreeding and selection—emphasis should be more on the family and less on the individual than if epistasis were unimportant. Highest hopes for future progress would be on the individuals which segregate out of the best crosses between
partially inbred lines which themselves average only moderately high in merit.

We know still less about the importance of overdominance. If it is common, that would explain many things which otherwise appear puzzling, such as the prevalence of heterosis and of polymorphism and some cases where selection seems ineffective although genetic variability remains. Even if only a few loci are overdominant, still those could furnish a large share of the genetic variance remaining in a population which has long been under steady selection. The most efficient breeding plans to utilize overdominance will take the form of making and maintaining relatively pure seedstocks which individually are lower in merit than the best crosses which can be made from them. These will be intercrossed to produce the commercial or market stock. The present hybrid corn plan is of this sort. It seems adaptable to chickens with few modifications. For less prolific animals the most feasible plan of this kind seems to be some form of rotational crossbreeding.

The early work with hybrid corn used the blunderbuss method of making many inbred lines and then testing in crosses whatever lines happened to result. If much of the success of hybrid corn is due to overdominance, instead of merely to eliminating undesirable recessive genes as many of us at first supposed, then it appears possible by recurrent selection or recurrent reciprocal selection to make lines superior to any yet found. In this way one could systematically build the lines so that they would fit each other, as a key fits a lock, to produce crosses with the maximum heterozygosis in loci which are overdominant and yet be homozygous for the better gene in most of the loci in which overdominance does not occur. Doing this might not even require inbreeding. Most of these ideas are new enough that we are almost certain to be partly wrong in our understanding of them. The experimenting to remedy that will mostly be done with corn and suitable laboratory organisms but it doesn’t seem too early to start some tentative explorations even with cattle and pigs.

If the breeder is contending only with partial or complete dominance, with epistasis, with environmental confusion, or even with interactions between environment and heredity, or any mixture of these, his ultimate goal remains to make a purebreeding strain as good as or better than any cross which can be made. This is what most of us have had in mind from time immemorial when we thought of breeding goals. But if overdominance really is important, this outlook will change radically. The more important overdominance is, the more we should judge the individual’s breeding worth by its offspring from some specific cross and
the less by its own qualities or by its offspring from mates in its own line or strain. The contrast is perhaps greatest in what we would do when we find two lines which cross well. If we think the excellence of the cross is due to epistasis, we will try to make better lines from among the segregates from that cross. But if we knew the excellence of the cross was due to overdominance, we would resolutely avoid using animals of that cross for breeding purposes. Instead, in seeking lines which would cross still better with line X, we would try to find them by crossing lines which all do better than average with X but do not cross especially well with each other. Then by interbreeding these somewhat mediocre crosses we would try to make new lines which would cross with X still better than any lines we yet have.

In recent years the corn breeding literature has contained much about “general” and “specific” combining ability. These are operational definitions and pertain to the population on which they are measured. Differences in general combining ability mean that one line averages better than another when both are crossed on other lines in that group. Differences in specific combining ability exist when a line does better or worse in a cross with one of these lines than one would expect from the way it behaves in crosses with the other lines.

Genetic improvement in general combining ability is to be sought by selection, perhaps with more use of progeny tests and sib tests and more careful standardizing or correcting of environment and more use of selection indexes than is traditional. Under those circumstances inbreeding is used mainly to build a line around an individual or to hold a line together until the real breeding value of that individual or line is known accurately enough to decide whether to discard it or to use it widely or moderately.

So far as differences in specific combining ability are due to partial or complete dominance or to epistasis, genetic improvement is sought by the same methods, but with more use of inbreeding to identify the breeding values of individuals and lines and, in the case of epistasis, to keep the good combinations together. Special tester strains begin to have some use, as homozygous recessives are useful to test for heterozygosis when dominance is complete and especially weak strains are useful for finding which lines have the larger factors of safety when epistasis is of the threshold or ceiling kind. But when specific ability is due to overdominance, choice of the tester strain, . . . and building still better ones, . . . becomes of paramount importance. The cross becomes
the center of attention, not only for commercial production but also for judging the parents.

If some one can devise a way to measure the effects of overdominance separately from other causes of specific combining ability, a long step forward in breeding plans will be possible. Unfortunately the tests available so far are not adapted to organisms which cannot be selfed. They are not very sensitive even for those. It remains possible that overdominance is unimportantly rare after all and that we are much too excited about it. Perhaps not!