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# Application of Genetics to Animal Breeding - Paper Presented at the Fifty-Fifth Annual Meeting

Jay L. Lush
*Iowa State College*

# APPLICATION OF GENETICS TO ANIMAL BREEDING

JAY L. LUSH

Animal breeding is is an old art, which long ago developed far beyond the scientific knowledge of the subject. By actual experience men built up certain rules as to what practices were or were not good procedure for a given set of conditions. Man naturally devised philosophical explanations which more or less satisfied his intellect as he went along. But it would be a far stretch of the imagination to call those explanations scientific.

The age of animal breeding as an art is neither known or important. Certainly it goes far back into prehistoric times. A smattering of literature bearing on it from Roman times has been preserved and perhaps much more was lost. For brevity we generally say that modern animal breeding began in England late in the eighteenth century when it became standard doctrine that purebreeding was the best system for producing breeding stock, while cross-breeding was the better system for producing market animals. The oldest of our pure breeds began then to have pedigree walls erected around them. New breeds and breed societies to promote them were organized in ever increasing numbers until around 1880 or 1890, since when the rate of forming new breeds has declined although it has not come to a complete stop. The efforts of the breed societies were first directed toward preserving breed purity and expanding breed numbers but all of them also encouraged selection within the breed in the hope of making further improvement. In some cases, as with many dairy cattle associations which have supervised thousands of production tests, encouraging intra-breed selection has occupied a large share of their efforts.

## THE COMING OF MENDELISM

Thus when Mendelism was rediscovered in 1900 there was already a well established art of animal breeding with many refinements and firmly cherished beliefs but still practically no scientific explanation beyond what was known about the anatomy and physiology of reproduction. The nearest approach to a scientific explanation of the practices of animal breeding prior to 1900 was in Darwin's speculations and explanations of species changes in nature, and in Galton's work which attempted to describe in quantitative terms how nearly various kinds of relatives resembled each other.

The new knowledge about Mendelism actually altered animal breeding practices very little. Chiefly it explained to the animal breeder why things occurred which he already knew did occur, such as reversion, non-identity of heredity and pedigree, one parent sometimes appearing to predominate, etc. Only now and then, in special cases, did knowledge of Mendelism permit direct application. The number of genes is so large, their interactions are so many and the animal breeder must simultaneously consider so many different things in evaluating his animal that he can rarely make use even of the simple Mendelism of a character like black and red or polledness and horns in cattle. The Mendelian nature of inheritance is to animal breeding what the atomic theory is to industrial chemistry. The animal breeder, like the manufacturing chemist, must use mass methods and can no more make his decisions or selections gene by gene than the chemist can make his compounds by picking out the desired atoms one by one with a pair of tweezers.

Perhaps the first important effect which genetics really had on applied animal breeding was in laying clear the distinction between genotype and phenotype. Again the first effect of this was merely to eliminate some superstitions and to show that certain practices were useless or at least did not work in the way they had been thought to work, although they might still be useful in some other way.

For example, although the non-inheritance of acquired characters is now fairly well accepted, it still remains true that in much animal breeding practice it is desirable to keep the animals under at least moderately good conditions so as to make larger differences in their performance. We still do much the same things which were done before Weismann and before Johannsen but now we explain that these practices help only because they make selections more accurate, whereas formerly breeders thought the favorable environment had a direct effect by producing what we would call in modern genetic terms "desirable mutations." The history of animal breeding practice is full of such examples where a practice was widely adopted and justified on one ground and when later those grounds were found faulty, other reasons for justifying the practice were found and therefore the practice continues nearly as it did before our *explanation* of it shifted.

Scientific advances in genetics have led to more extensive use of the progeny test to estimate an animal's breeding value. This is not an entirely new idea either, as animal breeders have used it more or less irregularly at least as far back as Roman times. Now it is beginning to be applied more systematically but this is yet limited mostly to dairy bulls and to roosters. For these animals we have a numerical measure of the practical usefulness of their offspring to the breeder which is more nearly complete than similar measures of merit in other classes of animals. Also the main product (milk or eggs) comes only from the female sex. Because we have no direct measure of productivity in the rooster or dairy bull himself we need a progeny test of him more desperately than we do for the beef bull or the boar where one can to some extent see whether the male himself has the characteristics we want.

The genetics of populations and of breeding systems of course developed a step at a time but it took long strides about 1919 to 1921 when East and Jones published their book "Inbreeding and Outbreeding" and Wright made the first extensive analysis of the consequences to be expected from a wide array of mating systems. Since Fisher's book on natural selection in 1930 and Wright's broader analysis of population genetics the next year, this aspect of genetics has begun to be closely enough attuned to actual breeding populations and situations to begin to affect breeding practices. Already the analysis of breeding systems has led to some modifications and extensions of such old and popular breeding systems as linebreeding but those have not gone nearly as far as the violent alternation of inbreeding and outbreeding which characterizes the production of hybrid corn.

Pure breeding for producing seed stock and cross breeding for the market have been fashionable for more than a hundred years and may be considered an extremely mild form of the same principles which the hybrid corn producers use. Whether the economic and biological nature of animal material will permit us to use far more intensive inbreeding and more violent subsequent outbreeding than has been done hitherto is not yet clear. Active experiments concerning that are already under way. They center chiefly in various poultry institutions and in the federal swine and sheep breeding laboratories. Obviously the techniques will need to be materially different from those used in either corn or sugar beet breeding because of the impossibility of selfing, the extra cost of maintaining reserve material, the limited number of lines which one man can develop, etc. At present it seems that the most intensive inbreeding plan which can be followed without giving up practically all freedom to select is keeping a one-sire herd entirely closed to outside blood with replacements coming entirely from within itself. About three or four generations of that will be necessary to do as much inbreeding as is done in one generation of self-fertilization.

The milder systems of inbreeding seem biologically possible but they involve more time which costs money and that is supremely important in the applied field.

The animal breeder must consider many different characteristics at once but in the past he has often based his selections far more on some and far less on others than he intended to do. The development of selection indexes promises to systematize selection so as to make the actual selections correspond to their intended basis. A man in charge of a large herd of swine once told me he had been selecting intensively for high prolificacy but had achieved no results. Upon analyzing his records I found that the average number of pigs produced in the first litter of those gilts which were kept for at least one more litter was only .02 pigs higher than in the first litters of those which left the herd after producing only one litter. This man had paid attention to litter size, had recorded it, and had studied it, but his actual decisions about discarding or keeping a gilt were based almost wholly on other characteristics or circumstances. Selection for prolificacy had never really been tried.

As an example of problems in this field, we recently investigated the advantages of selecting weakly for many characteristics at once as compared with selecting strongly for one characteristic until it is improved, then for the next, then the next, and so on. Where the $n$ characteristics are uncorrelated progress turns out to be $\sqrt{n}$ times as fast under simultaneous selection for many things at once as under the tandem method of trying to improve the characteristics one at a time. Where characteristics are positively correlated, the superiority of the simultaneous selection is not this large but where they are negatively correlated it is even greater.

The essential ingredients in constructing a selection index are a decision, based primarily on economic reasons, as to how important each different characteristic is, and enough biological knowledge to modify those proportions according to the degree of heritability of each characteristic. The rest is ingenuity in measuring or scoring each characteristic with reasonable accuracy and simplicity.

In applied animal breeding we must always face the problem of whether the information we can get per unit of expense in collecting or studying records will hasten progress enough to be worth its costs. This viewpoint is somewhat different from what most of us were told should be the ideal in the cloistered laboratory devoted to the pursuit of truth undisturbed by mundane thoughts of costs! Yet I am sure the difference is only one of degree since even the most highly endowed laboratory has budgets of some kind, and one must always wonder whether to invest his time and equipment in one way or in an alternative way, since he cannot do both. The necessity of comparing the expected gain with the labor and other expense needed to achieve it in the applied field leads us to many more inquiries concerning the design of experiments, plans for testing and measuring or appraising characteristics, etc., than is usual in laboratories aimed primarily at seeking fundamental principles. This has not progressed as far in animal breeding as in plant breeding largely (I suppose) because of the smaller numbers and greater value of our animal units.

It appears difficult or impossible to devise an accurate general formula for evaluating all of the relatives where these are of various degrees of closeness, and there are various numbers in different sibsips and the information is not equally complete for each animal. But in animals like poultry and swine, where the number of the full brothers and sisters of the animal in question is often large, the cream of what can be done even by the most extensive pedigree selection can often be had merely by using the information about the sibs. As an example of what may be done in this direction and of the kind of problems encountered in the applied field, I will describe the procedure we now use at the swine breeding laboratory for considering an animal's brothers and sisters to just the desired amount when deciding whether to keep or cull that animal. Statistically the problem is one of combining information about the pig itself with information about all of its $n-1$ sibs, in order to reach the best estimate of the genotype of the pig concerned.

It turns out that a unit deviation in the average of the litter (including the pig in question) should receive $\frac{x-y}{1-x} \quad \frac{n}{1+(n-1)y}$ times as much attention as the same amount of deviation in the pig's own characteristics, where:

x=genotypic correlation between full sibs (generally not far from .5)

y=observed (phenotypic) correlation between full sibs.

n=number of pigs in that sibship.

In practice we observe y (subject to a sampling error, of course), compute x within that particular population by Wright's coefficient of relationship, and make out a table of factors for the values of *n* likely to be encountered. Then the deviation of the litter average from the herd average is multiplied by the appropriate factor to obtain "sib credits" which are added to or subtracted from the pig's own index.

The accuracy of such sib credits is of course limited biologically by the part which chance plays in Mendelian segregation in determining what the genotype of that one individual will be. It is theoretically possible for one pig in a litter to have a high breeding value when all its sibs are poor or vice versa, but of course that doesn't happen often. So much emphasis *could* be laid on the litter average that selections would thereby be made less accurate than if sibs were disregarded altogether. Yet properly used the information about sibs should increase accuracy. If the present procedure which has now been in use for about two years works well enough experimentally, we hope to simplify it enough that it can be used generally in animal breeding practice without losing much in accuracy.

Techniques for artificial insemination are receiving much attention now. Of course the process of artificial insemination makes no change at all in the genes or in the ratio of the gametes which an individual will produce. It impinges on the breeder's problems only in an economic way or biologically in that it will permit more intense selection than can be practiced without it. It does not help the breeder in his problem of deciding which of the available sires has the most desirable genotype. But artificial insemination will permit him to use more extensively the sire he thinks is best and to cull many which are thought less desirable but would have to be used if artificial insemination were not available. In some states there is already a considerable backlog of experience in organizing cooperative artificial breeding societies, particularly for dairy cattle. Economic problems are prominent here. These concern such things as having enough members and enough cows that the overhead cost of the salary and expenses of the man who does the work will not place too great a charge against each calf produced. General experience is that something of the order of 1500 cows is about the minimum which such an association needs in order to avoid excessive cost. These cows cannot be widely scattered geographically or transportation costs and the outlay of time become too high. Doubtless we in Iowa can profit by the experience of our neighboring states if artificial insemination does eventually take an important place.

As yet there is almost no attempt to breed farm animals for resistance to disease. Our mental outlook and plans for disease control in animals are almost completely under the sway of Pasteur's discoveries. Interest centers in the pathogenic organism and in attempts to eradicate or quarantine it. Variations in host resistance or immunity have been largely ignored, at least in practice, although they were widely discussed prior to the last half century and you are doubtless familiar with Pasteur's own experience concerning resistance to anthrax in Algerian sheep. The control of animal diseases has been sought through medicines or vaccines or killing the infected animals in the hope of eliminating the germ. This has met with considerable success for tuberculosis although it does not lead to complete eradication. How much success was achieved by this method for brucellosis in cattle is a highly controversial subject, but control is more expensive and less complete than for tuberculosis. More and more one hears the thought expressed that for diseases which spread rapidly, and which frequently assume epidemic proportions, and for which no very good vaccine has yet been developed, the ultimate solution may have to be the development of disease resistant strains of animals, as has been done much more widely in plants.

The preliminary work in exploring this in farm animals has been confined mostly to poultry. Experiments with disease resistance in mice, rats and other laboratory animals in genetic laboratories make it seem likely that the method is biologically possible for the farm animals although its economic possibility probably must be determined for each case separately. In the larger and more slowly breeding animals economic reasons seem to make medicinal treatments or vaccination (wherever those are effective) better methods of control than the slower and usually more costly method of breeding for disease resistance. Perhaps, however if we could see far enough into the future, breeding for disease resistance might be cheaper in the long run. This is a field which will bear watching, but such breed and racial differences as already exist in disease resistance in farm animals were brought about by the older empirical methods and natural selection.

IOWA STATE COLLEGE,
AMES, IOWA.