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THE USE OF INBREEDING IN ANIMAL IMPROVEMENT

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THE theory behind the effect of inbreeding is very incomplete, and as far as it goes, fairly complicated, so I can hope to give only a rough outline of it, and then to discuss how the ideas work out in practice.

Charles Darwin studied various plants to try and find the reason for the advantage of their cross-fertilizing habits. It would seem that self-fertilizing would be the most efficient method of pollination, but many plants have built up mechanisms to make cross-fertilizing easier than selfing, or to make selfing impossible by having the two sexes in different plants. Darwin's experiments showed that growth rates were generally higher in the offspring of crosses than in those of selfings, and this meant that natural selection could have established the various mechanisms favouring crossing. The effect of the inbreeding on the selfed lines was deleterious, but with important reservations; there was not necessarily any permanent injury to the stock, for some descendants showed no signs of deterioration, and cross-fertilizing poor-looking inbreds produced quite normal plants again.

The theories of genetics lead to some understanding of the effects of inbreeding. The only effect on the genetic make-up is to increase its uniformity. Cross-breeding species are heterozygous for many pairs of genes, and inbreeding will increase the total variability by producing homozygous types, so that there will come to be more variation between inbred lines, and less variation within them. When a recessive gene becomes homozygous its effect may show up for the first time, and it seems that many of these recessive genes are unfavourable. The reason for unfavourable genes tending to be recessive is that whereas dominant genes produce effects which can be seen, and selected against if not wanted, recessives unless very common will hardly ever show up, though they will remain in the stock. A better explanation is that a new gene entering a population, by mutation say, will be out of balance with the rest of the genes, hence disadvantageous, particularly if homozygous. If it should become established there will be scope for selection of modifying factors, other genes or gene combinations which will repress or nullify its effect in the heterozygous state, and this means that it will become a recessive gene.

So the effect of inbreeding will be to expose some of the defects of the genetic makeup, particularly lethal factors, but the genetic material is not damaged and the original excellence should be recoverable by outcrossing. The bad effects are avoided by crossbreeding mechanisms, and by human instincts, though whether the human instincts regarding incest were built up by experience of the effects of inbreeding or by the need to preserve a stable family structure is hard to say. Inbreeding offers a means of locating and hence eliminating genetic defects and of getting a more uniform and reliable breeding stock. The procedures used will depend to some extent on the genetic situation in the material, but the first step is to choose a foundation stock and then build up a number of nearly homozygous lines from it by inbreeding. Some lines will die out and some will be obviously very poor, but those which look reasonably satisfactory would then be tested for "combining ability," to see if any of the crosses between lines are particularly good. These crosses will not breed true but they should average better than the original parents, and uniform and

true-breeding lines can be built up from them by further inbreeding. Alternatively the original inbred lines can be maintained and crossed to give high producers which are not good breeding stock, in the way we cross Southdowns with Romneys or Leicesters for fat lambs. This maintenance of highly inbred lines as parent material only is the basis of the American hybrid maize industry and is coming into use in poultry too. The improvements obtained will be partly due to the selection of good individuals to start with, using intelligent guess-work, and partly to purification by eliminating some of the recessive defects, but these are not nearly enough to explain for instance the colossal increases in yield of maize which have been obtained. The advantage seems to be in the precision and reliability of breeding performance in the inbred lines and hence the accuracy possible in selection for characters which have a low heritability in random breeding populations, or characters which have not even been noticed before. The inbred lines may be poor but they are uniform, and by the right crossing they will produce uniform offspring of good or of outstanding quality.

Now to discuss actual breeding systems, and some of the problems which arise in practice. Any mating scheme in which the relationship between mates is closer than the average relationship in the whole population is strictly inbreeding, but usually the term refers to the mating of fairly closely related individuals. In practice what is usually wanted is the fastest possible inbreeding, mating brother to sister or parent to offspring continually. R. A. Fisher, in his book "The Theory of Inbreeding" has shown that these two systems make the same amount of progress, per generation, and that any mixture of the two is slower. Actually with brother-sister mating, where only one offspring is expected per year as with cows and sheep, on the average there will be a delay of two years after the first is born to get one of the opposite sex, so parent-offspring mating would be quicker in time. Whatever method is used each generation takes several years. There is a lot of work in it; many lines should be raised because some will fail, and they must be tested. For crossing it is their combining ability which is important. This has a genetic basis and is not predictable from the performance of the line by itself, but has to be found by trying the line out in crossing. The inbred lines are often poor, expensive to raise and low in fertility, so the method is slow and expensive. The uniformity produced in both inbreds and hybrids may be dangerous. The original genetic variation of individuals is changed into variation between lines and some of it will be lost, though this is not serious if the original crossbreeding population is preserved so that new lines can be started up at any time. Uniformity in hybrids may be a disadvantage in adverse conditions where adaptability is needed. Although the progress made by selecting between inbred families may far exceed the progress obtainable by other kinds of selection, the selection can be practised only once in each cycle of inbreeding, so that the average progress made per generation or per year may be less than in other schemes operating in each generation. However in maize the other schemes had proved almost useless in improving yields so that inbreeding was not just the best way, but the only way to get anywhere.

For historic examples of the effectiveness of inbreeding in improving breeds of animals we only need to look at British live-stock history; Bakewell's Leicester sheep and Longhorn cattle, the Colling Brothers' Shorthorns, all were highly inbred; Watson's Aberdeen Angus was produced by 50 years of close inbreeding; the improvement of Berkshire pigs in the States, of Merino sheep in Australia, and of course the development of Corriedales are other examples. One promising attempt which came to nothing was Bates' Duchesse herd of Shorthorns which became less and less fertile, and died out.

Among recent studies of the disadvantages coming with inbreeding I should like to mention two, both reported in "Genetics" last year. The first was on a closed poultry flock, Rhode Island Reds, which had been selected for high production for 25 years. In the five years of the actual experiment, matings were made to keep the level of inbreeding as low as possible, and actually the inbreeding and the level of production were fairly uniform over that time. The laying birds throughout were classified according to their own amount of inbreeding, that is according to how closely their parents were related, and they found that the more inbred hens layed a few less eggs, particularly in the winter, and were less fit generally. The size of the eggs was not affected. The inbreeding ranged up to about the level got by mating offspring of unrelated parents.

A study of growth in Jersey cattle gave some important results. The average amount of inbreeding in the herd was fairly high, a few animals approaching the level obtained by self-fertilizing. The heifers were measured as they grew, body weight, height to the withers and chest girth, and all these were lower in the more inbred animals. The greatest effect was on weight, and the biggest difference was at six months of age. By a year the inbreds were growing faster, and they had nearly caught up by four and a half years. Results from Holsteins have been slightly different in that on the average the reduction in size due to inbreeding seems to be greatest at birth, not at six months. This may be only a consequence of the fact that there is a greater increase in calf mortality on inbreeding Jerseys than is found with Holsteins.

In conclusion, rather than try to sum up all the advantages and disadvantages of inbreeding as a means of getting better animals, I would say just this: It is costly, tedious, very necessary and very rewarding, if you're lucky.

Discussion on Mr. Wright's Paper

MR. STEWART: The term "inbreeding" is usually applied very loosely in animal breeding. The need for clear definitions of the relationship between animals mated together is of first importance. Instead of defining a mating as involving a half-uncle and half-niece or something equally difficult to visualise, more attention should be paid to the use of Wright's Coefficients of Inbreeding and Relationship. While both coefficients have limitations, they are no greater in these respects than the verbal definitions usually employed and they do have the great merit of expressing the probable result of a certain mating in figures which, with certain reservations, may be compared.

With regard to the virtues of inbreeding, the close breeding practised by the "master" breeders has been mentioned. The extent to which these early pedigrees may be accepted is largely a matter of personal preference. In view of experiments in inbreeding cattle, reviewed by Robertson, who points out that deleterious effects are increasingly encountered after the 20% level of inbreeding has been passed, together with an examination of the way Coates compiled his first herd book some thirty years after the Colling brothers commenced breeding Improved Shorthorns, I am rather sceptical of their authenticity.

Mr. WRIGHT: The trouble with coefficients of inbreeding and relationship has been that they are laborious to work out if the pedigrees are at all involved. Some simplifications have been made recently in the methods, and Miss Castle of the Dairy Board has started studies using them.

Mr. LAMBOURNE: Would outbreeding to animals of high individual merit and inbreeding high producing strains not produce the same result?

MR. STEWART: When inbreeding is accompanied by very intense selection the breeder would have to be prepared to discard hundreds of lines before finding one up to standard.

MR. RANSTEAD: The early breeders inbred to a few outstanding animals and multiplied up on them, for example the Collings bought one good cow. I had two good animals and used them as much as I could.

MR. STEWART: I agree with Mr. Ranstead that the early breeders inbred to their outstanding animals and brought about marked improvements. But I feel that the improvement effected resulted from the individual excellence of the animals selected as parents rather than the relationship which existed between the parents.

MR. FLUX: What do you think of the policy of maintaining the level of inbreeding at about 10 to 20% for a time and selecting at that level the animals with which to proceed inbreeding more intensively?

MR. HANCOCK: Inbreeding work in the States with animals has been stimulated by the results with maize. Wallace has developed hybrid chicks, the project quite successful but very expensive, needing assistance on the scale of a Senate grant. Winters with his Minnesota pig No. 1) claims some heterosis in outcrosses. I doubt the value of crossbreeding between inbred lines of up to 15% inbreeding, as defects would probably not have been exposed for selection; Johnstone bred a line of pigs up to 45% inbreeding without any apparent deleterious effects, but a few further generations at Ruakura showed up several lethals in this line.