L. M. WINTERS
University of Minnesota

Chapter 23

Rotational Crossbreeding and Heterosis

It is well for all of us, including our most eminent scientists and philosophers, to reduce our thinking to relatively simple terms. Genetics is, after all, basically rather simple. A fertilized zygote results from the union of two germ cells, each of which carries a haploid number of chromosomes, and a haploid number of genes which are resident in the chromosomes. By the very nature of the procedure, genes are paired which are alike or not alike. As the pairing of similar genes is increased, the population approaches increased purification. As the pairing of dissimilar genes increases, the resulting population becomes more heterozygous. Increased heterozygosity has been generally associated with increased vigor which is generally spoken of as hybrid vigor.

PLANNING THE MINNESOTA EXPERIMENTS

I believe the best way to discuss rotational crossbreeding is to relate briefly how the system was developed. When I was asked in 1928 to head the research in animal breeding at the University of Minnesota, I brought with me several proposed projects. One of these was a study of crossbreeding swine. A review of the literature of crossbreeding experiments conducted previous to 1928 shows that for the most part they were small-scale experiments. When the data were all put together, however, the evidence was in favor of crossbreeding. Yet, the general sentiment at that time among the stockmen was overwhelmingly opposed to the practice of crossbreeding. The statement frequently heard was that crossbreeding was quite satisfactory for the production of one crop, but all of the crossbreds must be marketed because it was absolutely disastrous to use any of the crossbreds as breeding animals. By 1928, it was quite evident that corn breeders were revolutionizing the system of breeding corn, and that hybridization was to become the rule rath-

er than the exception in the production of commercial corn. Wright (1922) had several years previously published what has since turned out to be a classic: *The Report of the U.S.D.A. Studies of Inbreeding and Crossbreeding with Guinea Pigs.* Why then should the situation be different in livestock than in corn and in guinea pigs? Was it true that livestock failed to respond to crossbreeding, and if so, why? A likely explanation appeared to be that our breeds of livestock were not truly comparable to inbred lines of guinea pigs and corn because they did not possess sufficient genetic purification.

I am sorry now that I did not record in advance of this experiment the results that I expected to derive. Had I recorded them, they would have been something like this: The crossing of the breeds of livestock will result in a slight increase in vigor. The increase will be so slight that it is scarcely worth while for the commercial producer, in contrast to the more simple procedure of grading or the maintenance of a registered herd. Most of my severe critics regarding crossbreeding will be quite surprised to read this statement. As nearly as I can tell at this time, there were two major reasons for my belief. The first was the accumulation of the continued absorption of a large amount of teaching toward that end. The second was the general belief on the part of geneticists that our breeds of farm animals had not been sufficiently purified nor separated genetically to yield hybrid vigor when crossed.

If I had recorded all of my thoughts, they would have included this reservation: If the crossing of the breeds *does* result in increased performance sufficient to make crossing worth while, then the standard advice that had been given through the years regarding the use of crossbred females for breeding must be erroneous. This reservation was based on the results that Wright had previously obtained in his use of crossbred guinea pigs as dams, and from the information already available regarding the production of hybrid corn. At this time there was no thought regarding continuous crossbreeding by either rotation or crisscross breeding. The objectives were merely to find out if there was any advantage in crossing the breeds for the market production of swine. If there was an advantage in crossing the breeds for market production of swine, was there then any advantage in retaining these crossbreds to become future parents?

In planning the experiment, provision was made whereby as nearly as possible the same genetic material was put in the crosses as was produced in the purebreds. In planning the use of crossbreds as parents, the original plan called for the use of both crossbred females and crossbred males. My senior officers informed me that they were willing to go along with me quite a way in this crossbreeding study, but that when it came to the use of crossbred males, that was going just a bit too far and I would have to compromise. I compromised on this point all too willingly. How I have wished, during the last few years, that I had insisted on carrying out my original plan of using both crossbred females and crossbred males in the experiment. But little

did any of us realize at that time that within twenty-two years we would be in the midst of a flourishing hybrid boar business. None of us know much about their true merits and demerits. Nevertheless, the crossbred boars were not included in the experiment.

Experimental Results

The experiment did proceed as planned for the production of first cross offspring from the mating of purebred females of one breed to purebred males of another breed. Crossbred females were then retained as breeding animals to be mated in one case to a boar of one of the two parental breeds and in the other case to a boar of a third breed. The results of this experiment showed that there was a very definite advantage in the production of firstcross pigs. There was a slightly greater advantage in the production of backcross pigs (that is, where crossbred females were mated back to a boar belonging to one of the parental breeds). There was a still greater advantage where the crossbred females were mated to a boar of another breed.

As I mentioned before, you bring together either genes that are alike or genes that are not alike. There appears to be very little likelihood of bringing about any more heterozygosity as a result of a three-breed or a four-breed cross than there is in a two-breed cross. The advantages derived from the backcross and from the cross to a third breed appear therefore to have been derived from the fact that the female parents were crossbreds or in a more hybrid state than their purebred half sisters. Why should this be the case? The female produces the eggs, carries the fertilized eggs, and develops them to the point where, after a period of about 114 days, they are ready for birth and then nurses the little pigs for another 56 days. In general, the advantage derived from the crossbred female in contrast to the purebred female is about equal to that derived from having the progeny crossbred in contrast with having progeny that are purebred.

The above are the general deductions that I made at the close of our crossbreeding experiment. Now I am not so certain that this interpretation is absolutely correct. The reason for my questioning is that recently I had a long visit with one of the largest hybrid seed corn producers in this nation. He is a man who has had many years of experience in the field. He told me that he had not yet seen a single cross of hybrid corn that was as useful for commercial corn production as the double hybrid. He elaborated further to the effect that the single cross hybrid often would yield as heavily as the double hybrid, but that under adverse environmental conditions the double hybrid fared better. This he attributed to the fact that the double hybrid developed from four inbred lines possessed greater genetic diversity toward adversity. This appears to be somewhat in contrast to the experimental results and interpretations of those results in some of the present-day fundamental studies of Drosophila genetics. Undoubtedly, with time and more

experimental results, we will be in a better position to bridge this gap. My experiences have convinced me, however, that it is a mistake not to take seriously the observations made by competent practical men in the field of operations. I am inclined to believe that very often these men see more, although they measure less accurately, than we in the field of research, with our eyes glued carefully to the job of measuring certain details.

In this experiment we used four standard measurements for appraisal of the pigs' worth. These were: number of pigs born alive, number of pigs weaned, rate of gain, and feed per unit of gain. Since then we have added a fifth measure—appraisal of body form on the basis of judgment. When we took the first four factors and compared the performance of the crosses with the comparable purebreds, we obtained an advantage of the crosses over the purebreds of 6.3 per cent for the first cross, 7.5 per cent for the backcross, and 11.7 per cent for the three-breed cross. This was obtained by throwing the four factors together as equal in importance.

By another method of comparison, wherein more factors were thrown into the pool, we obtained an advantage for the first cross of 7 per cent, the backcross 6 per cent, and the three-breed cross of 17 per cent. If, however, we were to take litter weight at weaning, which in one sense is comparable to yield in corn, we would have an advantage of the first cross of approximately 25 per cent, the backcross 39 per cent, and the three-breed cross 61 per cent. If we were to take total litter weight at the close of the experiment, the advantages of the crosses would be still greater. In my opinion, total litter weight as a sole measure of merit exaggerates the difference. On the other hand, I do not consider the method we have used entirely satisfactory. I do not know of an entirely satisfactory measure of performance in livestock. We in the livestock field need to do a great deal in the matter of perfecting our methods of measurements. The important question to the practical man is whether one procedure is better than another, rather than whether this procedure gives me exactly 20 per cent or 18 per cent increase.

ROTATIONAL CROSSBREEDING

On the basis of these results, we developed and put forward our plan of rotational crossbreeding. Even at the time that I started to analyze the data, I did not believe that our three-breed cross had given us any worth-while advantage over the single cross. I mention this merely to show how strongly entrenched the old teaching had become regarding the limitations of crossbreeding in livestock production. The results of the experiment were, however, very definite. I calculated and recalculated, and the results were always essentially the same—the three-breed cross possessed distinct advantages over the first cross and over the backcross.

Simple calculation shows that, on the average, the first cross will possess 50 per cent of the chromosomes, or more properly speaking, linkage groups

of breed 1, and 50 per cent of breed 2. The second year, wherein three breeds are used, the resulting pigs will, on the average, possess: 25 per cent of the chromosomes from breed 1, 25 per cent from breed 2, and 50 per cent from breed 3. The third year, the pigs will possess 62.5 per cent of the chromosomes from breed 1, 12.5 per cent of breed 2, and 25 per cent of breed 3. The fourth year, the pigs will carry, on the average 31.25 per cent of the linkage groups from breed 1, 56.25 per cent from breed 2, and 12.5 per cent from breed 3. The fifth year, the pigs will possess, on the average: 15.63 per cent from breed 1, 28.12 per cent from breed 2, and 56.25 per cent from breed 3. From that time on, they will remain in a continuous cross, in about that general state of equilibrium, but the percentage of relationship to the different breeds will change.

On the basis of these calculations, we advocated rotational crossbreeding. Some of our critics could not understand how we felt justified in recommending rotational crossbreeding when our experiments had been carried only to the three-breed cross. Calculations showed so clearly that if the three-breed cross was good, then the continuous cross, by rotation, could not help being successful, insofar as the system of breeding was concerned. On the basis of the theory I have always contended that there was very little advantage in a four-breed cross. Now, however, I am not so sure that that is correct, if we are to take seriously what my commercial hybrid corn producer told me regarding the merits of the double cross of corn in contrast to the single cross. There may be merits in the four- or even the five-way cross that are not generally revealed in short-time experiments.

We have recommended rotational crossbreeding for commercial swine production, and it seemed, on the basis of theory again, that the rotational scheme of crossing had a particular aptitude for swine production, and was perhaps questionable with other classes of four-footed farm animals. The reason for this is that in swine it is possible for the commercial producer to turn a generation every year if he so desires. I have, however, a number of friends who are breeding commercial flocks of sheep after this general pattern with remarkably good results. If you look at their flocks with the strictly commercial viewpoint, they do not have the variance that most critics of the plan have contended would result. Further than that, the experiments conducted by the United States Department of Agriculture with beef cattle and dairy cattle have shown that the same basic principles apply to these classes of livestock as in swine. Dairymen have perhaps been more reluctant to depart from the purebred philosophy of breeding than any other group of livestock breeders. Yet by a strange coincidence, the experiments of the United States Department of Agriculture are showing a greater increased yield as the result of crossing dairy cattle than the crossing of any of our other species of farm animals. Their data show an increase of 25 per cent in milk and 32 per cent in butterfat yield.

ROLE OF INBRED LINES

The next logical question then is: Where and how do inbred lines enter this general picture? I cannot see that it changes the picture appreciably unless perhaps it gives an added reason as to why four or five inbred lines may (theoretically speaking) prove of advantage over the three-line rotational cross. We have now carried the continuous rotational cross of three inbred lines in two series of crossings to the seventh continuous generation of crossing. We have several others in the sixth, and several in the fifth generation. The comparative results of the different line crosses have been remarkably similar and uniform from generation to generation.

I have already given the average increased performance of the different breed crosses as being 6.3 for the first cross, 7.5 for the backcross, and 11.7 for the three-breed cross. What then are the increases obtained from crosses of inbred lines? By the same method of comparison used in breed crosses, except in this case including an estimate on type, we obtained an average of approximately 12 per cent increased performance for the crossing of inbred lines belonging to the Poland China breed, and an increased performance of 18 per cent when we crossed the Minnesota No. 2 with our inbred Poland China lines, and 20 per cent when we crossed Minnesota No. 1 with Minnesota No. 2 or crossed Minnesota No. 1 with our inbred Poland China lines. This is an increased performance over the performance of the inbred lines.

I am constantly asked what the comparative performance of our crosses of inbred lines with the performance of outbred stock is. By the best methods with which we have been able to make comparisons to date, the increased performance of our crossbred lines in comparison to the performance of the old-line breeds is an increase of about 20 to 25 per cent. One of these comparisons was made with outbred stock from our own University of Minnesota purebred herds. The other comparison is with the performance of purebred herds as given by Lush and Molln (1942). I do not regard either of these comparisons as entirely adequate, and again I will frankly state that I do not know how to make a comparison that will be entirely adequate. I would be much obliged if someone would present me with a plan by which a satisfactory comparison can be made.

I cannot conceive of any sampling method (sampling of the breeds) that will constitute an adequate sample of the breeds for comparative purposes, unless we go far beyond any funds that I can conceive of being made available for this purpose. Field trials such as have been conducted for comparisons with corn have been advocated. Some of the corn breeders inform me that they are not at all satisfied that these field trials are adequate. One reason is that yield is not a sufficient measure. Many farmers have told me that our own estimates of the advantages of crossing both the standard breeds and the use of our inbred lines is in error, due to an underestimate rather than an overestimate of the benefits.

Contrary to expectations, our three-line crosses have not given us as much increased performance over the two-line crosses as I expected on the basis of the results with breed crosses and theoretical expectations. I do not know the cause, but I am inclined to believe that it is due to inadequate sampling, and that as our samples become larger the advantages of the three-breed continuous cross will become more pronounced.

FARM APPLICATIONS

How does this work out on farms? The records on one of the large farms with which I am working show that their percentage of survival from the purified lines (230 litters) is 75 per cent, whereas their survival from the crosses of lines (248 litters) is 92 per cent under the same conditions. The survival of crossbred pigs out of crossbred sows is 91 per cent, but the crossbred gilts weaned an average of 9.1 pigs, to 8.3 for the first cross pigs and 7.2 for the purified lines.

This discussion would not be complete without reference to hybrid boars and how they are entering the picture. I have not seen sufficient data to allow me to appraise properly the advantages and disadvantages of the so-called *hybrid* boar, but he does seem to be proving popular with a number of farmers. If, then, the hybrid boar is here to stay, what is his place in rotational breeding? In my opinion, it will not change the basic situation materially, except that at least six inbred lines will be needed to produce the boars for the rotational crossing of the production of commercial stock. In this case, we will then use hybrid boar of lines 1 and 2, the following year hybrid boar of lines 3 and 4, the next year hybrid boar of lines 5 and 6, and then we will go back to 1-2, to 3-4, and to 5-6 in rotation.

In thinking about rotational crossing, we need to keep in mind that it is merely a procedure whereby we are able to maintain our breeding females (and perhaps our breeding males), as well as the offspring, in a relatively permanent hybrid state. It in no way affects the basic concepts of hybridization. It is just a means of utilizing hybridization, and if at some future date our methods of production change, as for instance the general development of so-called *pig hatcheries*, then we may well find some other method of crossbreeding better suited to the swine industry.