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EVALUATION OF A BREEDING PLAN FOR SWINE BY MONTE CARLO SIMULATION

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THE rate of genetic improvement in a population is largely determined by the breeding plan that is used. Considering the cost and long generation intervals involved in large domestic animals, it would be very difficult to overemphasize the importance of selecting a breeding plan that would maximize the use of existing genetic variability in such populations.

The object of this study was to evaluate the amount of improvement for performance traits in crossline swine which would result from a specific selection procedure. The procedure was to select in one line for two traits, select in another line for two other traits and then cross the two lines.

To estimate these changes, simulated swine herds were generated. A computer was used to generate herds that have heritabilities and genetic correlations like those in swine breeds.

Pure mathematics [Griffing (1960), Kimura (1954, 1958, 1962), Kojima (1961), Robertson (1960)] and Monte Carlo simulation [Baker and Comstock (1961), Barker (1958a, 1958b), Barker and Butcher (1966), Bereskin, Shelby and Hazel (1969), Bohidar (1960), Fraser (1957a, b, 1960a, b, c) Fraser, Burnell and Miller (1966), Gill (1963, 1965a, b, c), Martin and Cockerham (1960), Parker (1966), Qureshi (1963, 1964), Young (1966)] have been used in other studies to evaluate expected genetic changes due to selection. In this case, it did not appear feasible to use a pure mathematics approach to obtain estimates of the expected progress in crossline pigs by selecting within the lines because of the complexity of the model and breeding plan.

In addition to evaluating the expected changes due to the specific breeding plan, the study provided information which may be relevant to the general question of whether performance in crossbred animals can be improved by selection for performance traits within the breeds.

The paper by Bereskin *et al.* (1969) gives an excellent presentation of the expected response to selection for litter size and growth rate using an index in herds of different sizes. However, it does not give an estimate of how these responses would change a crossbred population.

Materials and Methods

Breeding Plan. The goal of the breeding plan used was to improve the production in crossline pigs for four production traits by selection within the lines. The traits selected for and mode of their selection were different in the two lines. Therefore, each line will be discussed separately in two later sections.

For application to the commercial swine industry it would have been better to use two breeds rather than two lines. However, the authors were unable to determine any estimates of how breeds in the United States differ in their gene frequency. Since estimates of differences in gene frequency could not be made, all generated groups started from the same population and thus should be called lines.

Line Development. Each line was selected for five generations. However, before the first and after the fifth generations of selection, a cross was made to allow for the determination of the amount of progress selection within the lines made toward improving the performance of the crossline pigs. The crossline offspring were produced by mating four line I boars to 20 line II gilts, and each mating produced five offspring, all of which were evaluated for all four traits. Litter size was measured as the average phenotype for litter size of the 20 line II gilts used to produce the crossline pigs.

Mechanics of Simulating Animal Performance. The phenotype for each animal was generated by adding a random environmental effect to the effect of the genotype for the animal.

The simulation was done on a CDC 3600 computer. Uniformly distributed pseudo ran-

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dom numbers for the interval 0 to 1, which have a period of 2^{45} in the CDC 3600 were generated by the procedure described by Rotenberg (1960). These random numbers were used to generate the genotypes of all animals produced. To establish the desired initial gene frequencies the random numbers were compared to a constant, 0.6 in most cases. If the random number was less than or equal to the constant, the gene at a particular locus was considered to be the favorable allele. If greater than the constant, it was considered to be the unfavorable allele. These random numbers were also used to produce offspring from a particular mating. In this case a random number was compared to the constant 0.5 and if less than or equal to 0.5, the first allele would be taken from a parent. If greater than 0.5 the other allele would be taken from the parent. Thus, this random walk along the parent's genotypes produced offspring which had a random sample of half of each parents genes, one from each locus from each parent. Random normal deviates were used to produce the environmental effects for each pig. The random normal deviates used were those published by Rand Corporation (1955) which were stored on magnetic tape.

In developing the records, litter size was considered as a phenotype of the dam. As with other traits, the phenotype was developed by combining the effect of a sow's genotype with a random environmental effect. One of the traits used for selecting pigs in line II was litter size. To get a better estimate of the genetic ability of a sow for litter size, two phenotypes were developed (using two random draws of environmental effects) for each sow put into the breeding herd. The average of the two phenotypes for each sow is called the index for litter size. Litter size is not known until a sow is 18 months old. In order to keep the generation interval at one year for all animals, sows were not seletced on the basis of their phenotype for litter size. Selection was on the basis of saving pigs from sows that had the highest indexes for litter size. The index for a sow is known before her pigs must be selected for breeding if the pigs are selected only from the sow's first litters. In this experiment pigs were saved only from first litters.

The procedure followed in the program of developing performance of animals, was that the only offspring produced were those to be evaluated for possible selection. Thus, even though a sow in line I had a phenotype for litter size of 10 pigs, only five pigs, three gilts and two boars were generated from each mating since only this number of pigs were tested from a litter. The five pigs were a random sample of pigs from the litter. This procedure was followed as a way to simulate the conditions on which many testing programs are based, i.e., testing a set number of pigs from each litter. In actual swine herds, some litters would not have three gilts and two boars to be evaluated. Random sex distribution was not included as a variable in this study. The authors did not feel the inclusion of random sex distribution for each litter would change the selection differentials enough to justify including this factor in the model.

The procedure of selecting on index of litter size in line II had an effect on the number of litters from which pigs were generated to be evaluated for backfat probe. Each generation 20 sows were selected to go into the breeding herd. In the base generation no information was available on the litter size of the dams, so selection was on backfat probe alone. In all following generations selection was on the basis of the backfat of pigs from the 12 sows which had the highest index of litter size. Pigs to be probed for litter size were generated for only the matings involving the 12 sows which had the highest index for litter size. In actual swine herds the 20 sows would have to farrow in order to determine their index for litter size. In this study, no pigs can be saved from the eight sows with the lowest index for litter size so no pigs were generated for them.

The details of the selecting and mating of boars and gilts are given in later sections.

Initial Population Parameters. The genetic ability for each of the four traits was determined by genes at 20 independently segregating loci, all of which had equal effects. There was no epistasis or linkage. Daily gain, feed efficiency and litter size were under a complete dominance model of gene action, while backfat probe was under an additive model. The frequency of the desired gene was arbitrarily set at 0.6 for daily gain, feed efficiency and litter size, while it was 0.4 for backfat probe.

The authors are aware that these specific conditions do not exist in actual swine populations. However, it appears that there is no way to determine the specific conditions in our swine breeds. Thus, if the procedure of simulated populations is to be used in swine breeding studies, the experimenter will have to use parameters that will generate a population that has the general characteristics of swine breeds without knowing the exact number of loci, type of gene action or gene frequency in the breeds. The important characteristics which should be met are: traits are controlled by many pairs of genes, at most loci the dominant gene is the preferred gene, at other loci there is no dominance, genes at some loci have pleiotropic effects while genes at other loci do not, there are individual environmental effects influencing the performance of each trait and the mode of inheritance is Mendelian. The descriptive statistics which can be calculated from a generated herd using these parameters are phenotypic variance, heritability, genetic correlations and increase in homozygosity due to restricted population size. The authors feel that the model used gives generated herds which have descriptive statistics like those in present swine breeds. Thus, changes in performance in the generated herds should give reliable estimates of change to be expected in actual swine herds for at least 5 generations of selection and crossing.

An extensive review of the literature was made, and the following population parameters were, in most cases, the weighted averages of all estimates found, where the weight used was the number of animals on trial in each experiment. There was 0.6 genetic correlation between feed efficiency (gain/feed) and daily gain, and a 0.4 genetic correlation between daily gain and backfat probe. The genetic correlations were attained in this study by genes which had pleiotropic effects, i.e., 0.6 of the genes which determined an animal's genotype for daily gain were also genes in his genotype for feed efficiency, and the other 0.4 of his genes for daily gain were also genes in his genotype for backfat probe. All other genetic correlations were zero.

The initial heritability of both daily gain and feed efficiency was 0.3, while it was 0.1 for litter size and 0.5 for backfat probe. The population phenotypic variances in the original population for each of these traits were 0.00598 kg^2, 0.00072, 5.30 and 0.2632 cm^2 for daily gain, feed efficiency, litter size and backfat probe, respectively. The initial means were set at 0.73 kg, 0.31, 8.0 pigs and 4.06 cm for the respective traits.

Increased production due to hybrid vigor of the crossbred dams is not included in the model used. Commercial swine operations will often involve the use of three breeds where crossbred dams are used. However, the authors felt that the expected response due to crossing two breeds should be evaluated before attacking the expected change with three breeds.

Line I. Selection was for feed efficiency (gain/feed) and daily gain. In the initial generation an individual feeding trial was simulated for each of 20 randomly generated boars, and the two most efficient were selected. Thirty gilts were randomly generated and the 10 gilts with the greatest daily gains were selected. In each succeeding pig crop, three gilts and two boars were chosen at random from each litter for simulated performance tests. From these 20 boars and 30 gilts, two boars and 10 gilts were selected to produce the next generation. The expected selection differentials in terms of standard deviations were 1.6 for the boars and 1.1 for the gilts (from Fisher and Yates, Table XX, 1949).

Line II. The selection in the second line was more complicated than that in the first. In this line selection was for litter size and backfat probe. In the base generation 48 gilts and 24 boars were generated. The 20 leanest gilts were selected and bred to the four leanest boars. Line II was maintained at twice the number of line I since it was to be the dam line. With larger numbers, inbreeding depression on litter size should be less than in the line with fewer individuals. As stated in the Mechanics of Simulating Animal Performance section, pigs were generated from only the mating where the sow had an index for litter size which was in the top 12 of that generation. In each of these litters, three males and four females were generated. Thus, there were 36 boars and 48 gilts produced each generation. Only the 24 boars from the eight largest litters were considered available for selection on the basis of probe. From these the four leanest boars, with the restriction of not more than one boar per litter, and the 24 leanest gilts were selected to produce the next generation.

Selection Differential. The selection differential for each trait is measured as the average of the selected group minus the average of all the animals of the same sex available for breeding that generation. In line I, both selection differentials are primary selection differentials since selection is for feed efficiency in one sex and for daily gain in the other sex. In line II, selection is for litter size and then for backfat in each sex. Since the two traits are not correlated genetically or phenotypically in this simulation experiment, these selection differentials can be called primary selection differentials (Magee, 1965).

Results and Discussion

The results are based on the outcome of 20 replications of the selection procedure. Each replicate began with a different set of random normal deviates and at a random starting point in the random number generator.

Changes in Trait Means and Desired Gene Frequenices

Crossline Results. Table 1 shows the changes in the phenotypic means and the changes in the frequencies of the desired genes for each trait except litter size in the crossline pigs after five generations of selection within the pure lines. In the case of mean litter size the crossline pigs could not express their genetic potential unless they were crossed among themselves since litter size was assumed to be a maternal trait and the dams of the crossline pigs were purebred line II dams. Also presented in table 1 are the standard erorrs for each trait. The standard errors were computed from the generation by replicate interaction mean square in a two-way analysis of variance. In no case was a replicate result significantly ($P<.05$) different.

When comparing the means, the most improvement was made in backfat probe, 8.3%, which is statistically highly significant ($P<.001$). The second most improved trait was feed efficiency, 3.6% improvement and again statistically highly significant ($P<.001$). The improvement in daily gain was 2.7%, also highly significant ($P<.001$) and mean litter size improved 1% which is not statistically significant.

When the changes in the frequencies of the desired genes were analyzed, the results were very similar, except for a reversal in the rank of daily gain and litter size. The frequency of the desired gene for litter size increased 9.8% which is highly significant ($P<.001$), while the frequency of the desired gene for daily gain increased only 3.8%, but is still highly significant ($P<.001$). Mean litter size did not increase appreciably, even though there was a substantial increase in the frequency of the desired gene for litter size. This is because the dams of the crossline pigs were from line II which were inbred about 23%. The effects of the inbreeding on mean litter size were about the same magnitude as the effects of the increased frequency of the desired gene and thus the mean litter size showed little improvement. Heterosis could not be a factor here because litter size was assumed to be a maternal trait. Although boars do effect litter size, especially in comparison of straightbred and crossbred litters (Robison, Louca and Legates, 1964), it is nearly impossible to quantify the effects in a simulation model because of the complexity of the trait. Certainly in a real swine population more improvement in litter size would be realized. The reader should realize that mean litter size for the fifth generation cross is the mean litter size when the crossline pigs were produced by purebred dams, and is not a measure of how large the litters of the crossline pigs themselves would be if they had been mated. The size of litter produced by the crossline gilts was not considered because the breeding plan

TABLE 1. PERFORMANCE OF CROSSLINE PIGS PRODUCED BY CROSSING THE LINES BEFORE THE FIRST AND AFTER THE FIFTH GENERATION OF SELECTION

Trait	Generation	Mean	Std. error[a]	Freq.	Std. error[a]	Heterosis %
Daily gain (kg)	Base	0.73	0.0039	0.607	0.0050	0
	Fifth	0.75		0.630		6
Feed eff.	Base	0.317	0.0011	0.633	0.0059	0
	Fifth	0.329		0.698		4
Litter size	Base	8.06	0.371	0.605	0.0074	..[b]
	Fifth	8.14		0.664		%[b]
Backfat (cm)	Base	3.99	0.021	0.423	0.0066	0
	Fifth	3.66		0.524		0

[a] Based on the Rep. x Generation interaction mean square in a two way analysis of variance.

[b] Heterosis cannot exist in litter size since in the model used it was considered to be a completely maternal trait and the dams of the crossline pigs were purebred dams.

did not call for ever mating the crossline pigs. Certainly the crossline gilts would produce larger litters than these purebred sows. The frequency of the desired gene for feed efficiency increased 10% which is highly significant ($P<.001$) as was the 25% improvement in backfat probe. In addition to the improvements in the means due to the increased gene frequencies, the means for daily gain and feed efficiency expressed 6% and 4% heterosis, respectively.

Line I Results. Line I was selected for improved feed efficiency and daily gain. Figures 1.1, 1.3, 2.1 and 2.3 show the improvements in the gene frequencies and the means for the respective traits. The improvements in the means of these traits are very similar, 5% and 6% respetcively, and are statistically highly significant ($P<.001$). The changes in the frequencies of the desired genes for the two traits were very similar, approximately 26% and again highly significant ($P<.001$).

Both traits which were not selected for in the first line, litter size and backfat probe, deteriorated over the five generations of selection. The mean litter size (figure 2.2) decreased by nearly one pig per litter due to inbreeding depression which is a highly signficant decline ($P<.001$), while the desired gene frequency fluctuated about the initial 0.6 and showed no significant change. Since backfat probe was positively correlated with daily gain, the pigs became 0.1 cm fatter (figure 2.4) by generation five as a correlated response to selection for daily gain. The change is significant ($P<.05$). This resulted from the decrease of 8% in the frequency of the desired genes for less backfat (figure 1.4).

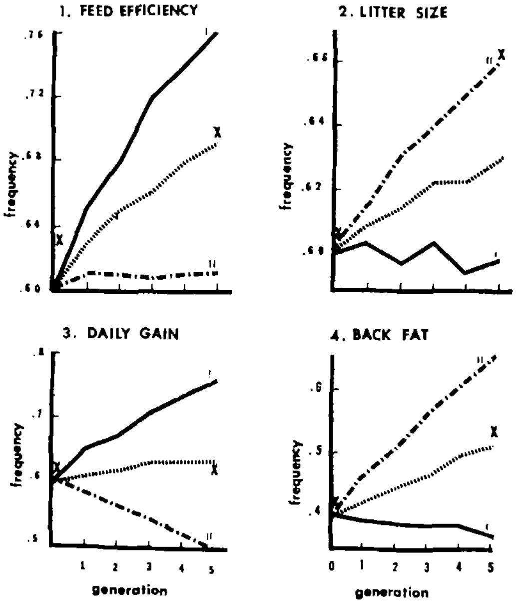

Figure 1. Changes in the gene frequency for line I, line II and the average of the two lines (dashed line). X is the gene frequency in the base and fifth generation cross between the two lines.

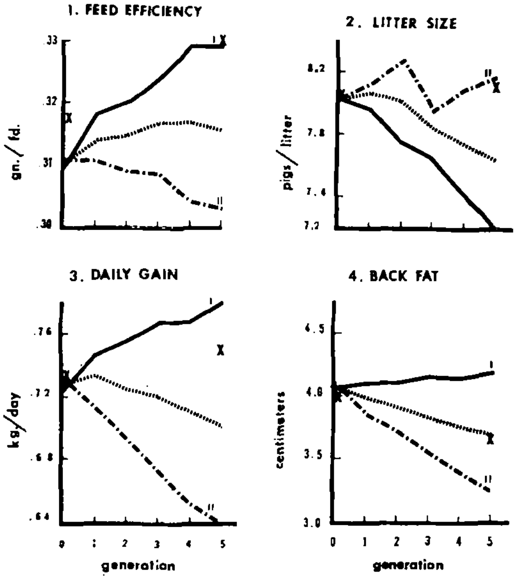

Figure 2. Changes in the mean for line I, line II and the average of the two lines (dashed line). X is the mean in the base and fifth generation cross between the two lines.

The rate of change in this line is more rapid than in Group 2 of the study of Bereskin *et al.* (1969). However, their Group 2 included selection for litter size as well as growth rate.

Line II Results. Line II was selected for increased litter size and thinner backfat probe. Figure 2.4 shows there was 0.76 cm (19%) decrease in mean backfat probe, and a 0.15 or 38% increase in the frequency of the desired gene for backfat probe. Both changes are highly significant ($P<.001$). However, the mean litter size (figure 2.2) stayed relatively constant, although the frequency of the desired gene increased 0.06. The reason for this situation was discussed earlier under the crossline results. The situation is the same in this case since line II dams were the dams of both the crossline and line II offspring, and litter size was treated as a strictly maternal trait.

As was the case in line I, both of the unselected traits declined over the five generations of selection. The mean daily gain (figure 2.3) decreased 0.1 kg/day (13%) and the frequency of the desired gene for daily gain decreased 0.1 (16%) as a correlated response to selection for thinner backfat. Both changes are highly significant ($P<.001$). Although the frequency of the desired gene for feed efficiency (figure 1.1) remained relatively constant, the mean feed efficiency (figure 2.1) declined 3% which is significant ($P<.05$) and was due to inbreeding depression.

Inbreeding

The amount of inbreeding which accrued as a result of the breeding plan is presented in table 2 for each line.

Inbreeding was measured basically as the percentage decrease in heterozygosity. The number of heterozygous loci was counted each generation, and any decrease in addition to that expected as a function of increased gene frequency was taken as that due to inbreeding. The equation used to compute the realized inbreeding was $F=(P'-P_A)/P'$, where P' is the initial number of heterozygous loci and P_A is the present number after being adjusted for any change in gene frequency. Kemp (1967) showed that the number of heterozygous loci expected when gene frequency is changing can be computed as $P_A=[2q'(1-q')/2q(1-q)]P$, where q' is the frequency of the desired gene in the initial generation, q is the same for the present generation and P is the unadjusted number of heterozygous loci.

The amount of inbreeding in both lines is very similar and fairly high by most standards. The accumulation of inbreeding at such a rapid rate is undesirable since it depresses the performance of the purebred animals and causes the fixation of undesirable alleles due to chance, thus reducing the effectiveness of selection.

TABLE 2. PERCENT OBSERVED AND EXPECTED INBREEDING BY GENERATIONS WITHIN LINES

	Line I		Line II	
Generation	% F Observed	% F Estimated[a]	% F Observed	% F Estimated[a]
Base	0	0	0	0
1	1	0	1	0
2	8	8	8	4
3	13	14	12	8
4	19	20	18	12
5	23	25	23	15

[a] Based on $F=F'+\frac{(N_m+N_f)}{8N_mN_f}(1+F''-2F')$ where ′ indicates F in preceeding generation and $^{a\prime\prime}$ indicates F two generations previous.

The realized inbreeding is very similar in both lines. This would at first seem surprising since the effective number of parents (Wright, 1931) is nearly twice as large in line II (12) as in line I (6.7). However, Robertson (1961) theorized that the inbreeding effect is larger than the amount calculated from population size when both selection intensity and heritability are high. This received tentative confirmation from Gill (1965a) when the inbreeding expected for the 20th generation had already been realized by the 15th.

The expected inbreeding due to finite population size was calculated according to the equation $F=F'+\frac{N_m+N_f}{8N_mN_f}(1+F''-2F')$ (Lush, 1948). N_m and N_f are the numbers of male and female parents each generation, respectively. The primes on the inbreeding coefficient (F) indicate previous generations. Each additional prime indicates one generation further back. The expected and realized inbreeding in line I compare very well, but the realized is considerably higher than the expected in line II for the reasons stated previously. The probable reason that line I was not affected the same as line II, making the realized inbreeding higher than the expected, is that the inbreeding due to finite population size was a considerably stronger effect in line I than in line II, making the effect of selection relatively less powerful. Also, in line I the parents were seletced for different but correlated traits, rather than for the same traits as were the parents for line II. This would tend to make line II parents more alike in genotype than line I parents.

The increase of inbreeding is more rapid in line I, but less rapid in line II, than similar sized lines in the study of Bereskin *et al.* (1969). Differences in selection criteria and chance appear to be the most logical explanations of these differences.

Genotypic Variance

The changes in the genotypic variance (computed as the variance among genotypes within generation) for each line are shown in table 3 standard deviations are presented in order to conserve space). In all cases the unselected traits showed less decrease in genotypic variance than did the selected traits.

In line I there was a 31% decrease in genotypic variation for daily gain and a 35% de-

TABLE 3. GENETIC STANDARD DEVIATIONS IN LINE I AND LINE II

Generation	Daily gain		Feed efficiency		Litter size		Backfat probe	
	Line I	Line II	Line I	Line II	Line I	Line II	Line I	Line II
Base	0.055	0.056	0.020	0.020	0.98	0.99	0.24	0.26
1	0.047	0.056	0.016	0.019	0.90	0.89	0.22	0.23
2	0.046	0.059	0.016	0.021	0.91	0.90	0.23	0.23
3	0.044	0.057	0.016	0.019	0.95	0.90	0.22	0.20
4	0.041	0.059	0.014	0.020	0.90	0.83	0.22	0.21
5	0.038	0.058	0.013	0.018	0.90	0.86	0.22	0.19

crease for feed efficiency by the fifth generation of selection. On the other hand, for the unselected traits in line I there was only an 8% decrease in the genotypic variance for litter size and the genetic variance for backfat probe. The decreases in the selected traits in line II, litter size and backfat probe, were only 13% and 26%, respectively. The authors can find no explanation of why the genetic variance for backfat probe did not increase in generation one and two when the gene frequency increased toward 0.5. The genotypic variance for feed efficiency in line II declined 10%, but the genotypic variance for daily gain increased 4% due to the gene frequency approaching 0.5 in the fifth generation of selection.

These decreases in the genotypic variances have detrimental effects on the progress which can be made by selection since they cause both the selection differential and the heritability to decline. Thus, it would seem advisable to increase the population size in order to reduce the amount of genetic variation lost due to inbreeding which accrues as a result of finite population size.

Genotypic Correlations

The changes in the genotypic correlations are shown in table 4.

The variances and covariances used in these calculations were among the numeric values determined for each animal by his genotype.

Generally the genotypic correlations were maintained and showed little change from the base to the final generation. The only exception occurred in line I, where the observed genotypic correlation between daily gain and feed efficiency declined from 0.59 in the base generation to 0.48 in the final generation. This decline can be accounted for by the fact that selection for genes which had a favorable effect on both the traits produced a greater increase in the frequency of these genes than selection for the genes which influence only one of the traits. For loci where the type of gene action is complete dominance and initial gene frequency is above 0.3, the additive genetic variance decreases as gene frequency increases. This means that in the final generation the genes with the pleiotropic effects contribute a smaller part of additive genetic variance of each trait than they did in the base generation. Thus this change reduced the genotypic correlation between the two traits in the final generation relative to the base generation.

TABLE 4. GENOTYPIC CORRELATIONS BETWEEN CORRELATED TRAITS WITHIN LINES AND GENERATIONS

Generation	Line I		Line II	
	Daily gain and feed efficiency	Daily gain and backfat probe	Daily gain and feed efficiency	Daily gain and backfat probe
Base	0.59	0.32	0.62	0.34
1	0.56	0.24	0.56	0.30
2	0.58	0.29	0.61	0.34
3	0.55	0.33	0.61	0.31
4	0.54	0.31	0.58	0.38
5	0.48	0.33	0.58	0.35

Discussion

This study should be of interest to commercial breeding establishments who are considering the feasibility of developing a swine breeding program to utilize selection within herds to produce better crossbred pigs. The results indicate that backfat, growth rate and feed efficiency can be improved in crossbreds by selecting within the breeds. These results appear to be different than those indicated by Robison, Louca and Legates (1964).

This study also indicates that homozygosity increases rapidly where intense selection is practiced in lines with only two or four sires. Thus, lines with more sires should be considered for long term selection programs.

Summary

A proposed breeding plan for swine was tested using the Monte Carlo procedure. The

goal of the breeding plan was to improve crossline offspring for four major production traits as a result of selection within lines. The four traits selected for were daily gain, feed efficiency, litter size and backfat probe. Boars of the first line were selected for feed efficiency, while the gilts were selected for daily gain. In the second line, both the boars and gilts were selected for litter size and backfat probe. Selection within both the lines was continued for five generations.

The breeding plan proved to be effective in improving the performance of the crossline pigs for three of the traits. The crossline pigs had 8.3% less backfat after the fifth generation of selection than in the base population. Feed efficiency improved 3.6%. Daily gain improved 2.7% and litter size improved 1%. All the changes, except for litter size, were highly significant. In the case of litter size there was a 9.8% increase in the frequency of the desired gene, but it was not expressed since the crossbred pigs did not produce any offspring. Had they produced offspring there would have been a significant improvement in litter size also.

The changes in the two lines were evaluated with respect to the generation means, gene frequencies, inbreeding, genotypic variance and genotypic correlations. Generally the trait means and the frequencies of the desired genes increased for the seletced traits and declined slightly for the unselected traits. The realized inbreeding reached 23% in each line by the fifth generation of selection. There was a considerable decrease (about 30% in most cases) in the genotypic variance for the selected traits, while there was a 10% or less decline in that for the unselected traits. The genotypic correlations were generally maintained near their initial values.

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