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ABSTRACT

EVALUATION OF RESPONSE TO SELECTION AND MATING SYSTEMS WITH DIFFERENT LEVELS OF HERITABILITY, SELECTION INTENSITY AND PROGENY TESTING THROUGH THE USE OF SIMULATION

Daryl Ralph Strohbehn

The data used in this study were collected from the simulation of approximately 295,000 animals. A biological model was used to simulate the performance of animals based on genic effects from the parents, Mendelian sampling and environmental effects. The selections and mating of all animals were accomplished by using different FORTRAN IV computer programs.

Random mating (RM) and phenotypic positive assortative mating (PAM) were the two mating systems compared, along with two bull testing procedures, within the purebred herd and with a commercial test herd. Other independent variables included in the study were three levels of yearling weight heritability (YWH), 20, 40 and 60%, three different bull combinations, 0 progeny tested and 6 non-progeny tested, 2 progeny tested and 4 non-progeny tested, and 3 progeny tested and 3 non-progeny tested, three levels of percent heifer calves saved (PHCS) 20, 50 and 80%, and three selection criteria, estimated breeding value of yearling weight (EBV), yearling weight (YW), and average daily gain (ADG). When selection was practiced on YW or ADG, the bull and heifer calves were selected on their phenotypic expression, while the older, producing bulls and cows were selected totally on progeny averages.

Traits investigated in the study were phenotypic and genic means and variances for weaning weight (WW), ADG and YW for calves, sires and dams. Also summarized were EBV averages for calves, sires and dams, plus progeny means for parents and average number of offspring per parent. Genetic and phenotypic correlations between mated parents for ADG and YW, plus the correlation between EBV's of mated parents were analyzed.

A two part analysis of variance was done, with one procedure analyzing the two mating systems and the four factorialized sources of variance, while the second procedure analyzed the two sire testing procedures and the four factorialized sources of variance.

PAM and RM were not significantly different in the amount of improvement they caused in YW over ten calf crops. PAM caused an insignificant increase in phenotypic and genic variance for YW. The phenotypic correlation for YW between mated individuals for PAM was .88, while -.06 for RM. Even though the difference in YW genetic correlation between mates for the two mating systems was significant ($P < .01$), it was much smaller, .16 for PAM versus -.06 for RM.

PAM made superior genetic and phenotypic gains in ADG over RM. PAM populations at calf crop 10 averaged .04 lbs. per day higher than RM populations in ADG. Furthermore, PAM caused significantly greater genic and phenotypic variance at calf crops 4 and 10. The average phenotypic and genetic correlations between mates for the three calf crops for ADG selection in PAM were .90 and .30, respectively, while in RM populations the same respective figures were .02 and .01.

Sire testing within a commercial test herd, as done in this investigation, was inferior to purebred herd sire testing for genetic improvement of all performance traits monitored. The populations utilizing the commercial test of sires were 98.4 and 97.3% as heavy as the other sire testing procedure at yearling time in calf crop 4 and 10, respectively. In calf crop 10, the populations utilizing commercial testing of sires were 97.5 and 97.0% as heavy for WW and ADG, respectively, when compared to purebred herd testing for sires.

The means for the three YWH levels, for all performance traits monitored, appeared to be significantly different from one another. WW, ADG and YW responded in a linear fashion to increases in YWH, while genic maternal ability was not affected by YWH changes.

The different bull combinations utilized in this study caused no significant change in the amount of genetic improvement made in YW over time. However, data were presented to show that the combination of 2 progeny tested and 4 non-progeny tested bulls gave the highest averages for the three calf crops and three traits analyzed, with the exception of ADG in calf crop 7 of the mating system analysis.

Increased heifer saving rates had a positive effect on YW improvement. Fifty and 80% levels were significantly ($P < .01$) greater in YW improvement than the 20% retention rate. Direct genic value for WW was the highest for the herds incorporating 50 and 80% saving rates. The genic maternal ability increased as PHCS increased up to 50%, however, a leveling off occurred in the mating system analysis and a nonsignificant depression in the sire testing analysis occurred when PHCS changed from 50 to 80%.

The two higher PHCS levels did not differ significantly from one another in ADG improvement, however, both were significantly superior to 20% PHCS in genic and phenotypic averages. The 20% level of PHCS had 19% more phenotypic variance and 34% more genic variance at calf crop 10 of the mating system analysis than 50 and 80% PHCS.

The unadjusted WW was higher for the 20% PHCS level through calf crop 7. However, by calf crop 10, 50 and 80% PHCS levels were superior due to their advantage in genic maternal ability and direct genic value for WW. The unadjusted YW averages were significantly higher for 50 and 80% PHCS levels than for 20% by calf crop 7 because of superiority in genetic gain for ADG.

Generation interval was affected to a major degree by level of PHCS. At calf crop 10 of the mating system analysis, the calculated cow turnover rates were 7.6, 5.1 and 4.1 years, respectively, for 20, 50 and 80% PHCS.

Selection by YW or EBV caused the most improvement in YW. Through calf crop 7, EBV selection consistently gave greater improvement in YW, but by calf crop 10, YW selection produced heavier calf YW. However, EBV and YW selection did not differ significantly from one another.

A possible, serious bias in older female EBV was found. The EBV of a selected female is biased upward in herds that are rapidly improving in performance. This occurs because the females' individual deviation from herd mean was not readjusted, plus the fact that the records for calves produced in the early part of a cows' productive life are included in the EBV calculation as deviations from herd means

that are below the herd genetic mean at the time of older cow selection.

YW selection caused the greatest amount of correlated improvement in direct genic value for WW and genic maternal ability.

ADG selection had significantly ($P < .01$) greater improvement in ADG when compared to EBV and YW selection, which were not significantly different from one another.

Many interactions between the independent variables occurred, however, five of the seven discussed in the thesis involved YWH. One of these was the interaction of mating system and YWH for ADG. ADG was equal in RM and PAM when YWH was 20 and 40%, however, with 60% YWH, ADG averaged .07 lbs. per day higher in PAM than with RM.

Sire testing interacted with YWH in calf crop 10 for ADG and YW. A greater increase in both ADG and YW occurred as YWH increased for the case of within purebred herd sire testing than for sire testing in a commercial test herd. Sire testing also interacted with PHCS for YW and unadjusted YW in calf crop 10. It resulted because sire testing within the purebred herd responded to increases in PHCS more than sire testing within a commercial test herd.

YWH interacted significantly with selection criteria in WW, ADG, and unadjusted WW in both analyses and in all three calf crops analyzed. Also it occurred for genic maternal ability in calf crops 7 and 10 of the mating system analysis. ADG selected populations did not respond as much to YWH increases as YW and EBV selected populations

for the above traits. However, in the mating system analysis, ADG selection gave more improvement in ADG than either EBV or YW selection as YWH increased.

The interaction of YWH and PHCS was significant for YW and ADG in all three calf crops of the mating system analysis. Improvement increased linearly across PHCS levels with 20 and 40% YWH, however, with the 60% level of YWH, a leveling off occurred in ADG and YW when PHCS changed from 50 to 80%. Significance of the interaction, with the same action as described in the previous sentence, occurred in genic value for WW in calf crops 7 and 10, but only in calf crop 7 for WW phenotype.

The final independent variable YWH interacted with was bull combination. At low YWH in the mating system analysis more improvement in ADG was made when more progeny tested bulls were incorporated into the breeding system. However, at the highest YWH level the use of fewer progeny tested bulls enhanced the rate of improvement.

The last interaction discussed in the thesis was between selection criteria and PHCS. It was significant for ADG in the mating system data. EBV and YW selected populations had an average improvement in ADG of .08 lbs. per day when PHCS increased from 20 to 80%, while ADG selected populations improved .20 lbs. per day as PHCS went from 20 to 80%.

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INTRODUCTION

The quest of mankind for years has been to breed our domesticated animals for efficiency of meat and milk production. Because goals change with time, beef production has been altered immensely which retroactively causes changes in breeding schemes and the amount of emphasis placed on traits which vary in heritability and accuracy and ease of measurement.

In today's beef industry it is generally an accepted fact that purebred breeders must raise breeding animals that will satisfy the production segments of the industry. The animal must be an efficient converter of feedstuffs into pounds of live weight at all stages of development. Breeders further realize that to become divorced from consumers' demands of lean, high quality beef is archaic and one which could destroy the future of the beef industry. Due to these facts, much effort is being put forth by breeders to learn more about new, scientific approaches to selection and mating problems. However, many of the more scientific approaches to selection and mating have not been utilized in improvement programs long enough to give answers, thus scientists in many cases are making educated guesses at what problems and ramifications might result from these approaches.

In order to restore confidence to our extension activities in the field of animal breeding, data must be made available which will either back up or disspell certain theories and methodology being incorporated in breeding schemes. But to overcome the obstacle of data collection is not easy, indeed it is expensive and very time consuming. In fact, it can be so time consuming, that many breeders may utilize a theoretically sound scheme which ends up after years of data collection to have less merit than other simpler or more complex approaches.

A partial solution to the problem of data collection is the use of a production model which employs the use of a high-speed computer, a well-developed algorithm and combinations of many factors controllable by a breeder. With the use of this type of system one can seek answers on what possible combination will allow optimum genetic improvement in performance traits. Indeed to acquire informative data requires the use of proper methodology and establishment of correct parameters. Without the first, the proper parameters will be to no avail, and likewise, without proper parameters, the correct methodology will give no help in finding solutions to dilemmas breeders face.

The main objectives of this investigation will be to establish trends with simulated populations which may need to be further researched at greater length. The objectives as seen for this investigation are:

1. Compare how random mating and phenotypic positive assortative mating systems affect beef populations.

Phenotypic and genetic trends will be monitored along with changes which may occur in phenotypic and genic variance at three heritability levels.

2. Investigate what differences occur in improvement of performance traits when two sire testing procedures are used.
3. Compare different bull turnover rates in the amount of improvement they cause.
4. Study the potential involved in saving different fractions of the heifer calves produced. Both age of dam adjusted and unadjusted weight trends will be evaluated to find in what range of heifer replacement rates lies maximum improvement and minimum weight loss due to age of dam adjustment.
5. Compare the results obtained when selection criteria is varied. An investigation into the advantages and disadvantages of selection by estimated breeding value for yearling weight will be done, along with comparing it to selection by yearling weight and average daily gain. The effects these have on phenotypic and genic means and variances will be analyzed.
6. Three levels of heritability will be used. This should help to extrapolate the results of other traits.

7. The last objective of the investigation is to study what interactions occur in the above independent variables and whether they cause any serious detrimental effects on improvement of performance traits.

REVIEW OF LITERATURE

Without a doubt there are many aspects involved with genetic improvement and to survey them in totality would be exhausting and quite unnecessary in regards to the task of this work. Indeed a review of many topics is needed for this investigation, but light coverage is given to some areas because documentation of research is slight and often sketchy in those areas. Therefore, emphasis will be placed on the important aspects to this research with a degree of completeness to the following three topics: Methods of Selection, Mating Systems, and Estimates of Genetic Parameters.

Methods of Selection and Their Impact on Improvement

Selection has been given many definitions, but one which most animal breeders can live with was given by Lush (1948, p. 171). He defined it as differential reproductive rates. His more precise definition is "... number of offspring which reach breeding age for each individual which reached breeding age in the preceding generation." Falconer (1960, p. 26) similarly describes selection as "the proportionate contributions of offspring to the next generation which is also called the fitness of the individual, or sometimes the adaptive value, or selective value." Many complications arise in quantitatively describing selection. Differences in viability and fertility can

cause a disproportionate effect on selection and bring about discrete changes in intensity of selection which usually amount to a slow down in genetic improvement. However, the important thing to observe is that, even though natural selection has an active role, man can cause differential reproductive rates and bring about genetic changes. Of course, this genetic change is produced by changing gene frequency which for performance traits appears to be a small alteration at each of a large number of loci. Gene frequency changes have been theorized and published for cases of different reproductive rates, dominant gene action, overdominance, etc., but because of its basic unimportance in this work these will not be reviewed.

Truncation selection is the most extreme type possible once a culling level is established. When a normal distribution is truncated the mean of the truncated population is $z/b \cdot \sigma$ from the mean of the whole population. The b is the fraction of the population selected and z is the height of the ordinate at $k\sigma$. The magnitude of average selected parent superiority (or selection differential magnitude) is dependent upon the proportion saved and the phenotypic standard deviation. With smaller population variances less genetic reach can be practiced resulting in decreased rates of improvement. Because of truncation selection's severity most breeders use modified versions which allow them to bring up animals not meeting certain requirements, but excelling in other traits. If truncation selection is adapted by a breeder it usually is used when an index is formed utilizing data on economically important traits.

The z/b figures given by Lush (1945) are exact only for truly normal curves. Since departures from normality are common these figures will not be exact in many cases. When skewed toward low merit small amounts of truncation will have more effect and heavy truncation will have less effect than if the distribution were truly normal. If the curve is skewed in the high merit direction the opposite will fit. Lush (1948) further explains that if the distribution curve is flatter, very small and very large amounts of truncation will have greater effects than in normal distributions, while moderate truncation will give little difference. However, if more individuals are concentrated about the average and few are in the extremes, extremely light and heavy culling will cause minimal change while intermediate levels will bring about greater changes than they would when the population is normally distributed.

Random environmental variations along with dominance and epistasis affect the rate at which selection changes gene frequency. The former acts to spread genic classes out over several phenotypic classes, thus creating situations which bring about selection errors. Dominance deviations cause animals to breed different than their phenotypes indicate. Dominance deviations are like random environmental variations, in that they cannot be transmitted from parent to offspring. Epistatic variations are transmitted to a varying degree. Some part of whatever epistatically caused differences in the parents will show up temporarily in the offspring.

Accomplishment of small selection differentials or low heritability, or the combination of both, can act as road blocks to genetic improvement. Lush (1948) explains that selection differential can be small due to population uniformity, low reproductive rates and poor selection practices. Heritability may be small because of small genic variance, large environmental effects, dominance deviations of large magnitude, large epistatic variance, or the variance from non-linear interactions between environment and heredity may be large. Heritability cannot usually be changed by the breeder, thus the emphasis of this work will be to investigate different selection routines with specific levels of heritability.

Results of Selection Experiments

Various results from selection have been observed in beef cattle. However, it appears variation due to inbreeding is incorporated in many of the studies. Brinks (1965) reported increases of 5.8, 6.3 and 2.37 lbs. per year for final test weight, 196-day gain and weaning weight, respectively. Bulls were sequentially culled on the basis of weaning weight and score, 196-day gain, and in most instances a progeny test while females were sequentially culled on 18-month weight and score, fertility, age and progeny production. Cows were culled at 10 years or if they failed to produce a calf for 2 consecutive years. When these selection practices were applied his annual selection differential for final test weight and 196-day gain were 14.4 and 8.5 lbs., respectively, which accrued to 1.46 and 1.10

standard deviations above the mean for the respective two traits. Brinks selection also included a negative intensity against inbreeding of the calf and dam which were $-.20$ and $-.08$, respectively. However, inbreeding still increased at slightly less than 1.0% per year in the calves and caused detrimental effects on preweaning gain and weaning weight of bull calves. Postweaning gain was also decreased by inbreeding, the reported regression coefficient was -1.6748 .

Hoornbeck and Bogart (1966) reported no increases in performance of four inbred lines of beef cattle. Because a great deal of emphasis was placed on holding inbreeding to a minimum, selection differentials for the performance traits were not optimal, thus explaining in part why no increases were monitored.

Nelms and Stratton (1967) with Wyoming Herefords were able to obtain increases of 10.9 , $.05$ and 3.0 kg for final weight, average daily gain and 180-day weight, respectively, per generation. Final weight was the trait selected for with the average selection differential over 12 yr. being 2.41 kg per generation. Selection differential per generation for average daily gain and 180-day weight were $.07$ and 6.5 kg, respectively. The average generation interval reported was 4.29 yr. Birth weight was the only trait to exceed its selection pressure with a per generation increase of 1.2 kg compared to its selection differential of $.8$ kg. One can theorize this to happen if final weight and birth weight are genetically correlated plus the selection differential for birth weight is secondary, thus the expected change is not equal to heritability times secondary selection differential.

Chapman et. al. (1969) reported beneficial weight gains when selection was practiced on weaning weight and postweaning gain in beef cattle. Uniform selection differentials from year to year were accomplished for performance selected herds, but when yearling type score was the selection tool uniformity of selection differential for performance was lost. The two herds selected for rate of gain and weaning weight had significantly higher postweaning gain than the herd selected on type. In a later report on the same herds, Chapman et. al. (1972) concluded that rate of gain herd progeny were lower than weaning weight herd progeny in weaning weight performance, but both were superior to progeny from the type selected herd in postweaning average daily gain. Correlated responses in birth weight, weaning weight and yearling type score were realized when selection was for postweaning rate of gain. When weaning weight was the selection criterion, only birth weight responded in an upward manner. Chapman and his co-workers observed that when the absolute value of the genetic correlation was at least .4 then the direction of observed related response and the sign of the genetic correlation were in agreement.

Much investigation has been done using selection to improve swine and laboratory animals, thus only major articles will be reviewed to bring into perspective what selection can accomplish in other species. Dickerson et. al. (1954) summarized selection differentials and rate of performance improvement at seven state experiment stations cooperating in the Regional Swine Breeding Laboratory. Thirty-eight lines, which consisted of 4,521 litters, were included in the summary.

Inbreeding of varying degrees was practiced at most stations, thus the average inbreeding calculated for the dams and litters was 21 ± 7 and $24 \pm 7\%$, respectively. Dickerson reported the combined overall average 154-day weight selection differential for sires and dams from all reporting stations, which varied in their selection procedures, to be 14.9 lbs. The average age was 1.33 yr. for both sexes. For weight at 56-days the combined average selection differential for both sexes was 3.64 lbs. Although this amount of selection offered much opportunity for improvement, none was realized when data from four stations were analyzed. When linear regression of performance on time was calculated the mean change for 56-day weight was $-.41$ lb. and -4.0 lb. for 154-day weight. Dickerson and co-workers reported a -3.44 lb. change in 154-day weight per ten percent increase in inbreeding. A -2.8 lb. per year change in mean 154-day weight was still observed when corrections for inbreeding were made, indicating selection failed to improve genetic merit of lines being mildly inbred.

Hetzer et. al. (1956) reported that upward and downward selection on backfat thickness at a live weight of 175 lbs. produced genetic changes. In the Duroc breed after 7 generations of selection Hetzer observed an 18% reduction in backfat for pigs selected for low backfat and a 35% increase in backfat for those selected for increased backfat. The control Duroc group remained at the initial backfat thickness of 1.50 in., whereas low-fat selected were 1.22 in. and high-fat selected were 2.01 in. Hetzer (1963) also reported that the backfat selection brought about correlated changes in feed required per pound of gain

and carcass cutability. The control line required 3.13 lbs. of feed per pound of gain, whereas low-fat selected pigs consumed 3.07 lbs. per pound of gain while high-fat selected pigs needed 3.37 lbs. Low-fat selected pigs also showed increases in percent lean cuts while high-fat selected pigs decreased in there carcass cutability. The actual values for carcass cutability were 41.4, 37.0 and 39.2% for low-fat selected, high-fat selected and control pigs, respectively, which indeed show that as fat thickness decreases carcass cutability increases.

Dalton and Bywater (1963) conducted a selection experiment with mice in which they selected the whole litter of the litters that were high in either litter size or weight. Random mating was practiced, except to avoid litter mate matings. From first parity data they found no significant increase in either trait over 14 generations, however, the litter weight selected group was consistently above the litter size selected group and randomly selected group. In a later experiment, Dalton (1967) found that mice on two diets responded significantly to selection for growth. The mice were in a two-by-three factorial experiment in which one-half were placed on a diluted diet and one-half on a full-feed diet. Each diet group was split into thirds with the three subgroups being 1) selected for superior growth after weaning, 2) selected for inferior growth after weaning, and 3) randomly selected for use as controls. All lines, except for the superior growth line on dilute diet, were significantly different from the control line within each diet. After 13 generations of selection

the full-fed, superior growth line was 3.0 g heavier than the full-fed control line, 2.5 g heavier than the diluted diet, superior growth line and averaged 6.0 g heavier than both full-fed and dilute-fed inferior growth groups.

Rahnefeld et. al. (1963) in experimenting with mice found that mass selection increased postweaning rate of gain, which was measured from 18 to 42 days of age. After 17 generations of selection, the estimated amount of improvement for gain was 4.9 g, which was accomplished by total selection differentials of 36.28 g for males and 16.14 g for females. Rahnefeld reported the 4.9 g increase was about six times the additive genetic standard deviation, which was .89 g, and about 43% of the original mean growth.

Enfield et. al. (1966) in a selection experiment with *Tribolium Castaneum* found significant differences between selected and control groups when increase of pupa weight was the goal. Designation of parents was on an intra-half-sib family basis with the heaviest male and two heaviest females being selected from each half-sib family in his S population. The control population, C, was composed of individuals closest to the half-sib family mean. The average selection differential, after adjustment for differences in reproductive rate for the two S replicates, was 208.5 μ g. Response to selection was linear over 12 generations with the regression of the difference in mean pupa weight between S and the corresponding C on generation time being 60.3 ± 4.8 μ g and 61.8 ± 4.9 μ g for the first and second replicates, respectively. In 12 generations of selection no reduction in additive genetic variance was noticed.

Chapman (1951) summarized the effectiveness of selection in laboratory animals and discussed eight major points that he observed. The laboratory experiments indicated that with or without inbreeding selection has effectively produced changes in both the positive and negative direction over many generations. The effectiveness of back selection appeared to be dependent on number of generations of original selection preceding it in some cases but not others. Chapman observed that when crosses were made between individuals from positive and negative selected lines intermediate offspring were generally the result. In general, a constant amount of variation within selected lines has remained over the generations of selection. Correlated responses were observed and in one experiment a decrease in heritability occurred in later generations of selection. In most of the experiments Chapman reviewed, adequate amounts of variation were experienced, which allowed acceptable selection intensity to be practiced. However, in one experiment all of the phenotypic variance was due to environmental influences, which decreased the effectiveness of selection.

In a continuous selection for egg production experiment, Dempster et. al. (1952) found that with many mating systems the average flock production appears on the surface to have improved at a decreasing rate during the 16 years of selection. However, the second-degree regression coefficient was not statistically significant. Furthermore, it appeared improbable that response to selection had hit a plateau and possible that gains in relation to selection intensity may still be

obtained at approximately the rate symbolic of the early years of the improvement program.

Kyle and Chapman (1953) in looking at the effectiveness of selection for ovarian weight in mice found that expected progress was not obtained. The authors decided this discrepancy would disappear if a smaller individual heritability and/or a larger litter-environment variability were postulated. In the 14 generations of selection for high and low ovarian response, the results were interpreted as indicating little change in combined influence of additively genetic and litter-environment as sources of variation. Based on unweighted averages of all data, high groups were increased 29% and low groups decreased 23%, respectively, as compared to an expected increase and decrease of 34 and 35% for the two respective groups. Weighted values were equally far apart.

Selection and Improvement in Simulation Studies

Many studies have been done the last 17 years utilizing the Monte Carlo procedure developed by Fraser in the mid-1950's. In his first and second series of papers Fraser (1957a, 1957b) discusses the logic used by the computer to carry out the gene-by-gene simulation and how linkage can be incorporated to cause differences. Parameters used by Fraser were population size, selection intensity and degree of linkage. His study indicated linkage had no effect until the recombination frequency was tighter than .025. Fraser continued to expand his Monte Carlo approach but worked in areas that do not pertain to this investigation.

In 1965, Gill reported several findings in a Monte Carlo study in which a metric characteristic was determined by the genes at 40 loci equally spaced over eight chromosomes, with two alleles per locus and equal genetic effect at all loci. Gill (1965a) reported that restricted population size resulted in the accumulation of inbreeding effects even though it was not the studies purpose. His effective population sizes were 8, 12, 16 and 32 parents for which he considered many different gene action models with three of the nine models having conditional epistasis. Mating was done randomly.

After 20 generations the complete dominance, no epistasis model with population of 32 was significantly higher than other population sizes. The population with eight parents after 15 generations had regressed backwards because of inbreeding depression. With the over-dominance model very strong inbreeding effects in the small populations were quick to override the positive effects of selection and also resulted in negative regression of mean on generation number. In the additive-by-dominance, conditional epistatic model, instead of inbreeding causing a depression in the mean, it acted as an uplift.

Gill (1965b) in a later report pointed out the futility of predicting selection response based on infinite population size in graphic populations of realistic size. Whether the predictions are linear or asymptotic to the selection goal, random drift and selection have considerable influence in changing parameter values rather quickly.

Gill (1965c) further reported that selection in his work was effective in advancing the genetic mean with all models of gene action when the optimum genotype was homozygous. However, when the heterozygote was optimal, selection was ineffective in small populations under mass selection. Gill further elaborated that major differences in genetic means should be produced with different intensities of selection under models with a single peak of genetic merit or one maximum fixation state. In his investigation, when large amounts of dominance variance were present selection intensity brought about even greater differences in the genetic means. Important differences between actual and predicted selection differentials were observed in populations that had no environmental variance and a gene model involving dominance to a high degree. These two factors plus the fixation of many loci resulted in discontinuous phenotypic distributions after several generations of selection. Gill, in general, detected that deviations in amount of environmental variation between populations seem to be important in affecting the total response only when those differences existing are caused by rapid mean change because of intense selection.

A cause of bias in estimating components of variance in small populations was inbreeding rather than linkage disequilibrium. Gill (1966) reported selection increases the degree of inbreeding, especially in a population of restricted size. Linkage caused a high

degree of variability in degree of inbreeding, but could cause inbreeding level to become very high.

Utilizing an additive model, Parker et. al. (1969) reported on a 3^4 factorial simulation in which they investigated genetic correlation and response to selection. The four factors which has three levels each were genetic correlation between X and Y, intensity of selection for X, and environmental variation of X and of Y; these were considered in all combinations. Parker made no attempt to control the alteration in heritability over the 30 generations, which allowed changes in genetic parameters to occur when deviations in environmental variation were used.

Upon analyzing the data, Parker found an interaction between intensity of selection and heritability and a rapid decrease in genetic correlation requiring both intense selection and high heritability. When selection intensity became .2 genetic correlation was affected, becoming large only when heritability of the selected trait was high. Of course, this indicates that normal selection in our meat and milk producing species would cause little affect upon genetic correlations, for most of the traits we work with are, at the most, moderately heritable. In general, for mild selection initial genetic variance and covariance were maintained for the entire 30 generations of selection. Even with more intense selection genetic correlation remained near its initial level due to the fact that both genetic covariance and variance in the selected trait decreased together.

Parker reported that with truncation selection, phenotypic correlation decreased with respect to the unselected population. Because phenotypic correlation is a function of genetic and environmental correlations between traits plus heritability, a closer analysis had to be made to find what this reduction was due to. From graphical displays it was learned that truncation decreased genetic correlations, but the amount of reduction was a function of heritability rather than degree of truncation. As heritability increased genetic correlation in the selected offspring became less.

Using simulation methods, Ronningen (1969) experimented with maximization of improvement with progeny testing. In order to make progeny testing feasible as a means of genetic improvement, Ronningen pointed out that some of the following criteria should be met: 1) low heritability of the trait, 2) trait is sex limited, 3) trait is measurable only after slaughter, 4) generation interval is not increased greatly, 5) reproductive rate of the female is low and 6) males are used intensely through artificial insemination. Also in Ronningen's series of works he looked at progeny test stations sizes of 500, 1,000 and 2,000, heritability levels of .1, .3 and .5, three levels of maternal effects: 0, .1 and .2, and three sizes of full-sib groups: 1, 2 and 4. With a fixed mean, he used a random simulation model with the following elements random: additive genetic effects, non-additive genetic effects, permanent and temporary environmental effects.

When comparing selection based on individual record only (one-stage selection) to selection based on individual record and a progeny test of the individual (two-stage selection), Ronningen determined a 10 to 20% advantage in two-stage selection, provided generation interval was considered to be equal between one and two-stage methods and number selected was kept to a moderate level. The efficacy of two-stage selection increased as testing capacity increased; for example, the mean genetic improvement difference of two-stage compared to one-stage selection was 1.07, 1.10 and 1.13 for testing capacities of 500, 1,000 and 2,000, respectively. Deviations in heritability caused little effect, especially in group means. Ronningen further discussed that genetic response to selection was a function of the number selected and that the efficacy of two-stage selection decreased as the progeny group size increased.

Another affect selection caused, as reported by Ronningen (1970), was the skewing of the frequency distribution of both phenotypes and genotypes, with the latter being affected the greatest. Skewness increased as both heritability and selection intensity increased. As heritability got larger the tail of the normal curve representing the poorer genotypes got steeper, thus giving positive skewness. The tail of the normal curve representing better genotypic individuals was not affected to a significant degree by either heritability or selection intensity.

When Ronningen (1970) compared the efficiency of combined selection, i.e., performance testing combined with progeny testing,

to selection based on performance testing only the relative efficiency of combined to performance test only decreased as heritability increased. The average efficiencies for the heritability levels of .1, .3, .5 and .7 were 1.40, 1.16, 1.04 and .96, respectively. As expected, the greatest depression in efficiency came when heritability changed from low to moderate status. The reasoning used is that when heritability is low the basis for making the first selection is inaccurate, thus the information accumulated from progeny testing is more likely to increase the accuracy of predicting genic value.

Upon further analysis Ronningen found that the effect of common environment is small, but did seem to increase as heritability decreased and when number selected got smaller. Because of this the greatest error in ranking tested animals due to common environment was likely to happen when trait heritability was low. Also he found efficiency of combined selection decreased as the number of selected individuals increased. Due to this fact, plus previous mentioned findings, Ronningen recommended combined selection be used only when heritability is low and intensity of selection high.

Bereskin et. al. (1969) conducted a simulated swine selection experiment where two traits each were controlled by 28 pairs of genes. Twenty of the 28 pairs controlled both traits. He utilized three groups of which one, G-1, consisted of 16 replicates of one sire mated to 10 dams; group two, G-2, consisted of 8 replicates of two sires mated to 20 dams and group three, G-3, which consisted of 4 replicates of four sires mated to 40 dams. The heritability levels used were .12 for trait one and .34 for trait two.

When selection was employed on trait two, mean genotypic value for trait two was maintained in G-1, but increased at average rates of .25 and .50% per generation in G-2 and G-3, respectively. There was no indication of reaching a plateau by generation 10. Inbreeding, as one would expect, increased at drastic rates for G-1, as indicated by its coefficient of .76 at generation 11. Inbreeding for G-2 and G-3 reached .57 and .40, respectively. Bereskin observed uneven decreases in trait one in G-1, small decreases in G-2 for trait one and none in G-3.

Bereskin reported that additive variance was largely maintained because of direction of selection. Nonadditive variance was primarily responsible for maintaining within variance above the expected level in all groups for both traits. Random drift effectively increased the amount of between variance and was apparently the major factor in depressing and fixing the genotypes in G-1 for both traits. In general, phenotypic variation followed the same pattern of genetic variance. In other words, the principal factor accounting for differences between replicates within a group was random drift.

Later Bereskin (1972) reported on selection response and inbreeding depression. Inbreeding effects were largest in replicates of G-1 and smallest in those of G-3. For G-3, the accumulated effects from selection over 10 generations on the growth trait was 15.49 ± 2.33 units while inbreeding depression was -2.04 ± 0.10 units. The same values for G-1 were 10.68 ± 6.41 and -9.95 ± 1.28 units, which gave insight to what a restricted population size can do to improvement through selection.

Selection effects in Bereskin's additive model were two or three times the magnitude of any other models. Bereskin pointed out that for traits of medium inheritance, .15 to .35, substantial long-term genetic gains are possible even with inbreeding rates as high as in G-2 lines, where a six percent loss of heterozygosity occurred per generation. His average gains were .5% or more per generation in G-2 replicates. The response was contributed to continued availability of adequate additive genetic variance, despite inbreeding.

Mating Systems and Their Influence on Populations

Since the rediscovery of Mendelian genetics, there have been a vast multitude of mating systems developed for both plants and animals. Varied forms of inbreeding and outbreeding are the result of mating individuals because of their consanguinity or nonconsanguinity. Popular today is mating individuals which are either similar or dissimilar in a phenotypic character. This system, somatic resemblance assortative mating, can be either positive or negative, with negative many times being called corrective mating.

Mating systems based on consanguinity and phenotypic likeness have many differences and ramifications which will be discussed by reviewing ground work laid by Wright and Lush. The differences between assortative mating and consanguinity is three fold with one being that the phenotypic likeness may not be genic. Also, except for linkage, all gene pairs act independently of each other in consanguine mating and the number of loci does not affect the results, whereas in somatic assortative mating gene-by-gene similarity is

dependent on the number of loci. Lastly, somatic assortative mating does, while consanguinity does not, produce correlations between nonallelic genes which affect the same trait, thus affecting the variability of the population. Heritability has no effect on the genetic structure of the population in consanguine mating, but does in assortative mating. Indeed skill of mating becomes of utmost importance in somatic assortative mating because of results desired.

The problem with consanguine mating is the amount of inbreeding which can accumulate and cause performance depression. Small population sizes brought about consanguine mating and increases in inbreeding coefficients in simulation work done by Bereskin (1970) and Gill (1966). Dickerson (1949) reported close to a linear decline in performance with increased inbreeding for different strains of inbred hogs at experiment stations.

Nelms and Stratton (1967) found that in 302 Wyoming Hereford calves inbreeding caused a decrease in 180-day weight of .465 kg for each one percent increase in inbreeding coefficient. Final weight of the calf was not affected by inbreeding, nor did a low amount in the dams cause a depression in any traits. Hoornbeck and Bogart (1966) obtained results similar to Nelms and Stratton; in that, lower inbred male and female calves had greater suckling gains. Their mildly inbred calves had greater postweaning gain than non-inbred calves, but as inbreeding increased there was an indication of decreased performance. Inbreeding in the dams gave Hoornbeck and Bogart different results than Nelms and Stratton; that is, non-inbred dams had calves with higher suckling gains than inbred dams. Because of inbreeding depression Hoornbeck and Bogart realized no response from selection.

Brinks (1965) obtained similar results from inbred lines of Hereford cattle. The calves' and dams' average inbreeding coefficients were 16.1 and 11.7%, respectively, with the range for each in the 26 year period being 7.2 to 26.5% for calves and 3.1 to 22.7% for the dams. Calf and dam inbreeding had a detrimental effect on weaning weights and inbreeding of the calf also caused a decrease in post-weaning gain and final weight of selected bulls. For example, the arithmetic average partial regression of weaning weight on inbreeding of calf was -1.35 and -1.10 on inbreeding of the dam. Bull post-weaning, 196-day gain had a -1.675 partial regression coefficient on inbreeding of the calf and the partial regression coefficient for final weight was -2.296. Inbreeding of the dam was more detrimental in its effect on weaning weight of bulls than on heifers.

Somatic assortative mating is as Falconer (1960) describes it, when mated pairs tend to be of the same genotype more often than would occur by chance then positive assortative mating is taking place and if less often then the negative option is occurring. Somatic assortative mating can cause change in homozygosity, but because of the large number of gene pairs controlling production traits it is doubtful much change in homozygosity will occur. Wright (1921b) calculated that after 15 generations of perfect assortative mating with heritability equal to 1.0, perfect phenotypic correlation, gene frequency of .5 at each loci and the trait controlled by 10 gene pairs, one-third of the gene pairs would still be heterozygous as compared to the initial frequency of one-half. Under imperfect assortative mating (phenotypic correlation equal to .50) and other conditions not changed from above, the value is .444 at 15 generations and infinity.

The effects of assortative mating to random mating on population variance is of major importance in evaluating expected response to selection. Wright (1921b) calculated that when a trait is controlled by 10 factors with a phenotypic correlation between assortative mates of .75, there would be a 1.86 to 1.0 greater standard deviation than if random mating occurred. With perfect positive correlation the ratio is up to 4.47 to 1.0 with 10 factors. Wright further stated that if heterozygosis has been eliminated then the genic variance becomes equal to the number of factors controlling the trait. This is twice the value of the genic variance in the original random-bred population when heritability equals 1.0, regardless of the number of factors.

In Lush's (1948) review, the point is made that mating like to like phenotypes tends to bring together mates whose genes have similar effects but which need not be allelic to each other. He further comments that similarity between phenotypes can be great while the similarity of genotypes, gene by gene, may be drastically low. As the number of gene pairs controlling a trait increases, less and less of the phenotypic correlation comes from likeness in allelic genes and more comes from the non-allelic genes.

Positive assortative mating tends to increase the frequency of the genotypes at the two extremes and diminish the intermediate classes. Negative assortative mating acts in the opposite way; in that, the intermediate classes increase in frequency and the extremes become

fewer. Therefore, negative tends to lower the genic variance base, which lends to the system's other name, corrective mating.

The largest factor which determines the effectiveness of positive assortative mating is the closeness of correlation between the two mates genotypes. Lush (1948) explained that genetic correlation's magnitude cannot exceed the product of heritability in the narrow sense and phenotypic correlation between the two mates. Furthermore, he commented that dominance, epistasis and environmental effects tend to hold the genic correlation down because of their depressing effect on genic effects. Even though positive assortative mating can make a population more variable than the most inbreeding, Lush is quick to point out the difficulty in achieving proper assortative mating. Moderate values of correlation have distinct effects on the population variability. However, in order for positive assortative mating to make a population more variable than the most inbreeding, a heritability of .5 and a correlation larger than $\frac{n}{2n-1}$, where n is the number of gene pairs affecting a trait, must be available.

Positive assortative mating can be practiced only on traits that can be seen or measured. It is effective in increasing variance for certain characteristics only if they are highly heritable and controlled by a few genes. Li (1955) remarked in his conclusions that complete positive assortative mating should lead to complete homozygosis of a population but would be seldom accomplished under natural conditions due to imperfect assorting. Li continued that somatic resemblance

mating may lead to population genetic composition very different from that reached by inbreeding. Li concluded that if breeders could combine a system of inbreeding with positive assortative mating, the rate of genetic fixation for a phenotypic character would be greatly enhanced.

Experimentation with positive assortative mating in meat and milk producing species is not in the literature. However, a few experiments have been done with laboratory animals, some successful and some not. Blair et. al. (1961) reported highly significant differences for each generation due to mating systems and selection in *Tribolium Castaneum*. The descending rank of the mating systems for mean larval weight was: outbreeding, phenotypic assortative mating, random mating, phenotypic disassortative mating and inbreeding. The only significant change in population variance was with the inbred population. In a *Tribolium* study done by Wilson et. al. (1965), the average response of mass selected, assortatively mated lines was slightly more than the mass selected, randomly mated lines, though this difference was not significant. In mass selected lines, regardless of mating system, Wilson and co-workers observed a decrease in both phenotypic and genetic variance. Wilson et. al. (1966) in a later paper reported correlations obtained with their investigation. The phenotypic correlation between mates within line and replicate over the generations averaged .97, -.92 and -.06 for assortative, disassortative and random mating, respectively.

In an abdominal bristle study with *Drosophila melanogaster*, McBride and Robertson (1963) found assortative mating to increase the total population variance, however, not significantly. Of the 24 lines mated in a positive assortative fashion, 18 showed higher genetic variance. The authors credited the increased rate of response in early generations with assortative mating to an advantage in selection differential. McBride and Robertson further noticed that assortative mating was best with index selected lines; the index consisting of the animal's individual phenotype plus its family average.

Sutherland et. al. (1968) studied the effects of assortative and disassortative mating in comparison to random mating on six week weights in mice. Within each mating system, they practiced upward, downward and no selection to make a 3 by 3 factorial experiment. Their conclusions went along with previous laboratory animal work; that is, a small and insignificant advantage in genetic improvement was gotten for assortative over random mating. They further concluded, as had others, that only in cases of selecting with highly heritable characters would assortative mating be of economic advantage over random mating. Indeed, Sutherland's experiment, plus others, point out that the trouble of assortment may not be worthwhile, plus because of small differences realized, no great advantages in selection differential occurred.

Through out this section comparisons have been made between inbreeding, somatic assortative and random mating, but no formal definition or effects of the latter system have been given. The

formal definition given both by Falconer (1960) and Li (1955) for random mating is that, in the case of bisexual animals, any one individual of one sex is equally like to mate with any individual of opposite sex. "Panmixia" is sometimes used as a synonym of random mating.

Generally the Hardy-Weinberg Law is discussed whenever random mating is discussed. This law points out that with random mating, a sizable population, and no migration, mutation or selection, stability is gained with respect to both gene and genotype frequencies. Also the law points out that frequencies of genotypes in the progeny produced by random mating among the parents are determined solely by the gene frequencies among the parents.

Estimating Breeding Value

For many years breeding value estimation has been the never ending dilemma of progressive breeders. Usually, without realizing it, breeders tried to combine a few different types of available information into a crude mental index and used it as the basis of their selection. Today, with the advent of high speed computers, relatively complex and correctly weighted estimates of breeding values can be made in a phenomenal short period of time. However, before going into past literature and estimation methodology, definitions need to be brought forth.

Lush (1935) described breeding value as the average effects of the parents' genes on the mean genotypic value of their progeny. An individual's breeding value can be estimated from its own individual

record, or it can be estimated from progeny data or from a combination of both. If the sire is mated to a random sample of the population then his breeding value, expressed as a deviation from the mean, is twice the mean deviation of its progeny from the population mean with an infinite number of offspring per sire group raised in the same overall environment. The deviation is doubled because the individual contributes only one-half the genes to the progeny.

Falconer (1960) further defines breeding value in terms of average effects of genes which are the mean deviations from the population mean of individuals which received that gene from one parent; the gene received from the other parent having come at random from the population. In these terms, Falconer (1960, p. 121) defines breeding value of an individual as "... the sum of the average effects of the genes it carries, the summation being made over the pair of alleles at each locus and over all loci." However, such things as dominance, epistasis and other interactions cause errors in breeding value estimation. This lowers the accuracy of predicting a breeding value from own phenotypic performance or from a finite number of progeny. If the actual effects of a gene substitution upon the phenotype are sometimes larger and sometimes smaller than the average effect of that gene substitution in that population, the differences between the actual and average effects are due to epistatic or dominance deviations. If these two factors could be deleted from effective genotypic action the job of the animal breeder would be considerably simplified. But since dominance, epistasis and individual environmental effects make phenotypes deviated

from their breeding values, procedures of estimating breeding values from phenotypes need to be developed so maximum accuracy of predicting breeding values can be achieved. It is the breeding value of the animal that influences the productivity of its offspring.

Lush, in two papers (1935 and 1947), developed some of the early techniques in breeding value prediction by using either individual phenotype record, family merit or a combination of both. By use of a path diagram, Lush (1947) found that purely family selection would produce $[1+(n-1)r] / \sqrt{n[1+(n-1)t]}$ times as rapid progress as mass selection. The symbols used are: n for the number in the family, r for the intraclass correlation between breeding values of members of the same family, and t as the phenotypic counterpart of r . If t ever becomes as large as r^2 then family selection will produce less progress than mass selection. Lush (1947) diagrammatically shows the conditions necessary for mass selection to be more effective than family selection. Also he points out that large n improves effectiveness of family selection, but for family selection to be more effective than individual selection, family members must resemble each other genetically much more than they do phenotypically.

When individual phenotype and family merit were combined into one estimation of breeding value, Lush determined new relative effectiveness as $\sqrt{1 + \frac{(r-t)^2}{1-t} \cdot \frac{n-1}{1+(n-1)t}}$. In analyzing this type of selection, Lush explained that r and t must be very unequal if combination selection is to be more effective than mass selection alone. When r is greater than t , combining family information properly with individual record will increase the rate of genetic progress.

Furthermore, when t is much greater than r a similar increased effectiveness from combination selection will occur, however, in this case family merit will be given negative attention.

In a later section, Lush (1947) develops equations for predicting breeding value from individual phenotype and family average. Lush's equation was written:

$$\hat{G}-\bar{G} = \frac{A}{A+C+E} \left\{ \frac{1-r}{1-t} (P-\bar{P}) + \frac{r-t}{1-t} \cdot \frac{n}{1+(n-1)t} (Y-\bar{P}) \right\} \cdot \frac{A}{A+C+E},$$

is equal to the equation's net regression on individual phenotype; in that, A is the genic variance, C is the variance caused by differences between overall herd effects in the whole population, and E is variance caused by differences between individual environmental effects within the herd. When A , C and E are totaled they are equal to phenotypic variance. $\frac{1-r}{1-t}$, is the ratio of individual genetic variance within families to individual phenotypic variance within families, or the heritability of intra-family phenotypic differences. Lush explained later that, $\frac{n}{1+(n-1)t}$, is the ratio of variance among individual genotypes to the variance among actual family averages. The regression on family averages are automatically adjusted so that a difference between individuals and an equal difference between family averages will always be given importance inversely proportional to the variance of each. Increases of n from one to five will not double the regression unless t is less than .38 and will not triple it unless t is less than .17.

Lush in the same paper considered the individual as a deviation from its family average rather than from the whole population. He did

this by substituting $(P-Y+Y-\bar{P})$ for $(P-\bar{P})$ in the previous equation and then by separating the first two terms from the last two, expanding and combining common terms his new prediction equation became:

$$G-\bar{G} = \frac{A}{A+C+E} \left\{ \frac{1-r}{1-t} \cdot (P-Y) + \frac{1+(n-1)r}{1+(n-1)t} \cdot (Y-\bar{P}) \right\}.$$

His second regression coefficient has changed to become the ratio of additively genetic variance between family averages to phenotypic variance between family averages or simply the heritability of observed differences between family averages. Lush explained that in this form family average cannot be negative, but it can be extremely small if t exceeds r and if the genic variance is a small part of the individual phenotypic variance. As n gets large the regression moves toward r/t times heritability of individual differences. When the population consists of inbred but unrelated families r/t becomes large.

Lush (1948) summarized that conditions which make collateral relatives most useful are: 1) there are numerous sibs to be observed, 2) when the trait is sex limited, 3) when measurement requires slaughtering of the individual, and 4) the trait is an all-or-none thing. Of course, progeny testing could do all of these things and more, but it requires an increase in generation interval.

Whether the utilization of progeny testing is feasible, economically practical and theoretically sound is of major concern. The decision really to be made with progeny testing is whether to retain a sire or dam on the basis of their offspring. Naturally, if

one analyzes in this manner, time is required and many more individuals must have been similarly tested so selection can be practiced. Because the individual can produce many gametes sampling errors associated with Mendelian segregation can be reduced. However, other factors may lower the accuracy of progeny testing. Lush (1935) derived the correlation between the progeny average and the parents' breeding value and later revised it to the form as it appears in Lush (1948): $r_{GX} = r_{GP} \sqrt{\frac{n}{1+(n-1)t}}$. Because t is composed of both genetic correlation and other common events, one can find a great degree of inaccuracy in progeny testing if the common event component is large. Thus, to make progeny testing accurate, this latter term must be kept to a minimum or be appraised and discounted accordingly. Causes of high common event correlation, in many cases, is the common environment the progeny are in or if progeny are by related dams. If progeny by different sires are produced in different years and/or in different herds, accuracy of progeny testing is reduced. Lush (1948) concluded that if correlation from common events rises to .25, the progeny test cannot possibly average more accurate than mass selection. But if it is kept at zero, and heritability is .25, data on 5 progeny are identical to mass selection. If heritability is lower and/or number of progeny is greater selection by progeny testing will be more accurate than mass selection.

Number of progeny necessary for a highly accurate estimate of breeding value has been a question asked many times, but one that does not have a unique answer. In a study of Hereford progeny testing, Stanley and McCall (1945) could not come up with the number of progeny necessary for highly accurate estimation. However, in a similar study, Knapp et. al. (1942) partially answered the question. By analysis of variance, the pooled standard deviations between steers from the same sire was used in Knapp's study to determine what differences in efficiency of gain would be necessary to indicate significant differences in efficiency of feed utilization. In a diagram Knapp showed the necessary difference in efficiency of feed utilization when number of animals in each sire group vary. The results are that the information gained from each animal decrease drastically from 5 to 15 animals, with the sharpest decrease occurring between 5 and 10. That is, there was a rapid increase in information gained for each animal added, up to five, after that information gained decreased and over 15 progeny added very little to the accuracy and to what was already known. When Knapp compared the bulls to one another by the use of their first 8 steer progeny he found the mean difference necessary to find significant ($P \leq .05$) differences in efficiency of feed utilization

was 1.52 lbs. of gain per 100 lbs. total digestible nutrients consumed.

As mentioned previously, with the age of computers came the age of mathematical and statistical sophistication and animal breeding is no exception to that rule. Many different data items from various relatives are now commonly used to estimate breeding values. Indeed, part of this collateral data add accuracy to the prediction, whereas other data because of its limited quantity add little. Willham (1973) documented the type of computerized summary and calculations necessary to include own performance, paternal half sibs, maternal half sibs and average progeny performance. In Willham's example four linear equations were set up and then converted to the matrix form shown below.

$$\begin{bmatrix} 1/H & 1/4 & 1/4 & 1/2 \\ 1/4 & \frac{4+(N_1-1)H}{4N_1H} & 0 & 1/8 \\ 1/4 & 0 & \frac{4+(N_2-1)H}{4N_2H} & 1/8 \\ 1/2 & 1/8 & 1/8 & \frac{4+(N_3-1)H}{4N_3H} \end{bmatrix} \begin{bmatrix} B_1 \\ B_2 \\ B_3 \\ B_4 \end{bmatrix} = \begin{bmatrix} 1 \\ 1/4 \\ 1/4 \\ 1/2 \end{bmatrix}$$

In the left matrix the following symbolism was used: 1) N_1 , number of paternal half sibs; 2) N_2 , number of maternal half sibs; 3) N_3 , number of progeny; and 4) H , heritability of the trait for which breeding value is being estimated. The main diagonal contains the numbers for the relatives and the off diagonals contain the relationships among the relative group to the individual on the right hand side of the equal sign. The order of the individuals on the right hand side from top to bottom are the individual whose EBV is being

calculated, paternal half sibs, maternal half sibs, and progeny. The values on the right hand side are the relationships between the individual and his relatives. If a part of the data is missing, the row and column representing that data item are dropped. Thus the matrix is reduced in an upward and leftward fashion. Willham went on to explain that the solutions to these equations are best obtained when the left matrix is inversed and multiplied times the right hand side. Once the values for the B's are acquired the following formula is utilized to estimate breeding value:

$$EBV = B_1 \cdot \text{Individual Deviation} + B_2 \cdot \text{P.H.S. Average Deviation} + B_3 \cdot \text{M.H.S. Average Deviation} + B_4 \cdot \text{Progeny Average Deviation} .$$

The final value that can be calculated is accuracy, the correlation between the animal's actual breeding values and those estimated by the matrix process. It is calculated by taking the proper relationship values, which are on the right hand side of the equations, times the B values, summing them up and taking the square root of the total, thus the equation is: $\text{Accuracy} = \sqrt{B_1 \cdot 1 + B_2 \cdot \frac{1}{4} + B_3 \cdot \frac{1}{4} + B_4 \cdot \frac{1}{2}}$. This accuracy value simply gives a breeder an idea of how much confidence he can place on the breeding value estimate.

Deaton and McGilliard (1965) used methods similar to ones appearing in the last paragraph to combine and compare different combinations of information for milk production from Holsteins. Used in their selection index was individual record, dam's record, daughter's record, paternal half sib records, and maternal half sib

records. The accuracies ranged from .50, which was for an index utilizing only individual performance, to .68, which had individual performance, dam's record, three daughters' records, 100 paternal half sibs' records, and three maternal half sibs' records. The latter index had partial regression coefficients for the records as they were listed above of .16, .06, .19, .7 and .03, respectively.

After looking at many different combinations of data in indices, Deaton and McGilliard concluded that dam's record and maternal half sib's records added little to accuracy of estimation. They further concluded that paternal half sibs and daughters of a cow could substantially increase the accuracy. In particular, the workers noted that when number of paternal sibs was large, the potential for increasing accuracy was greater than for any other group of relatives.

Additional configurations were tried to evaluate the usefulness of more distant relatives, but if the cow's individual record was available these remote ancestors provided no information nor did they increase the accuracy of the index. However, when no individual record was available, the more distant relatives did have a small value. When Deaton and McGilliard calculated the correlation of a cow's index with an unselected daughter's record the average was .166, as compared to .140 for the correlation of the cow's own phenotype with her daughter's production. Thus, the index gave a 19% advantage in genetic gain over just using phenotype alone.

Nielsen (1974) investigated some features of national sire evaluation using 100 mock sires through the use of simulation. He looked at different options of reference and nonreference sires and variable number of progeny by each sire group. Four specific data structures were examined. Structure A had 10 reference sires and 90 nonreference sires with the latter having progeny in only one herd. The number of progeny by each nonreference sire was 10 and the number of progeny by reference sires, whose number varied from 5 to 10 in a herd, varied from 2 to 3 per sire. Structure B had 4 reference sires and 96 nonreference sires with the latter having 10 progeny all in one herd. Only 2 reference sires were used per herd and the number of progeny by each varied from 5 to 15. Structure C was the duplicate of B except there were twice as many progeny by each sire. Structure D was an undesigned structure which was used to simulate what might happen in field data. This data structure had more progeny per sire than the other structures thus leading to some of the results in the next paragraph.

The investigation also fit four data models of which one was a simple linear model with no sire by herd interaction, two models fit herd by sire interactions of 5 and 10% and the last model was used to simulate data where the coefficient of variation was constant over herds; i.e., there is more variance in a herd with a high mean than for a herd with a low mean. Rank correlations were calculated between the true values and the expected predicted difference values for sires. The approximate rank correlations between the expected

predicted differences and true breeding values of the sires were .40 for A, .50 for B, .75 for C and .80 for D. In Nielsen's study the sire evaluation is to compare herd sires against national reference sires and against other herd sires which were compared to the reference sires. Whereas the type of progeny test used in this research will compare sires within a herd and not across herds.

Estimates of Genetic Parameters

Heritabilities of Traits Studied

It is in general agreement among animal breeders that the heritability of weaning weight is low to moderate (.2 to .4). In works done by Carter and Kincaid (1959a), Wagnon and Rollins (1959), Shelby et. al. (1960), Pahnish et. al. (1961), Swiger et. al. (1962), Hamann et. al. (1963), and Brinks et. al. (1964) heritability estimates for weaning weight ranged from .43 to .69 for an average of .51. Taylor et. al. (1960) and Cunningham and Henderson (1965) estimated the heritability of gain up to weaning time as .36 and .50, respectively, for an average of .43. Estimates which ranged from .30 to .36 for an average of .32 came from studies done by Rollins and Wagnon (1956), Kincaid and Carter (1958), Blackwell et. al. (1962) for heifer calves, and Minyard and Dinkel (1965). Heritabilities which are thought to be close to the generally accepted low level have been produced by studies done by Knapp and Woodward (1951), Knapp and Clark (1951), Koch and Clark (1955), Brown (1958), Swiger et. al. (1961), Shelby et. al. (1963), Brown and Gacula (1964), and Pahnish et. al. (1964). Their estimates ranged from a high of .28 to a low of .10 for a mean heritability of .21. Heritability estimates in a similar range for steer calves were obtained by Carter and Kincaid (1959a), Pahnish et. al. (1961) and Blackwell et. al. (1962). Kincaid and Carter (1958) found an unadjusted heritability estimate for weaning weight to be .27. The average of all heritability estimates was .32.

In many studies done with laboratory animals maternal ability has had a very significant effect on WW and in some cases on post-weaning gain. Two papers showing such effects in mice were Young and Legates (1965) and Cox et. al. (1959). Postnatal maternal influence was found to account for 60% of the total variance in WW at 21-days. Hohenboken and Brinks (1971), Vesely and Robison (1971) and Deese and Koger (1967) have shown in analyses that maternal ability has a significantly positive effect on WW in beef calves. Koch (1972) in his review of studies in this area points out the correlation between milk production and gain of calves to weaning has ranged from .3 to .8. If the median of this range is used as the average correlation, slightly over 30% of the phenotypic variance could be accounted for by milk production alone. Koch arrived at 29 to 33% as the amount of phenotypic variation in gain from birth to weaning being accounted for by maternally related variation and covariation. Koch also found in studies that genetic and permanent environment components of maternal ability and covariance of individual and maternal effects accounted for 35 to 45% of the variation in gain from birth to weaning. Hohenboken and Brinks (1971) showed in Herefords that the heritability of maternal ability was .34 to .40.

The heritability for average daily gain after weaning is generally accepted as being fairly high. However, Knapp and Clark (1951) when regressing offspring on dam found the heritability estimate to be $.18 \pm .06$. Brown and Gacula (1964), on the other hand, found that their

three different methods of estimating heritability ranged from .80 to .96. Work done in 10 other studies ranged from .39 to .76. Carter and Kincaid (1959a) estimated heritability by three methods of which two were consistent. When using paternal half sib correlation estimates of .54 for females and .38 for males were obtained and .57 for females and .40 for males were realized with intrasire regression of offspring on dam. Regression of progeny average on sires gave an average estimate of .21. The nine estimates given in works done by Knapp and Clark (1951), Koch and Clark (1955), Shelby et. al. (1960), Swiger et. al. (1961), Blackwell et. al. (1962), Brinks et. al. (1962), Swiger et. al. (1962), Shelby et. al. (1963), and Brinks et. al. (1964) averaged .51. The 13 studies reviewed had an average heritability estimate of .51.

Not a great deal of work has been put forth in estimation of yearling weight heritability. Wagnon and Rollins (1959) found the heritability of 20 month weight to be 0.44 for 305 heifers in two herds. Blackwell et. al. (1962) found 18 month weight estimates of .34 for steers and .71 for heifers. The same paper presented the heritability of gain up to a year of age for both sexes as .32. In work done by Shelby et. al. (1960), 180-day weight and 196-day gain were added together and then an estimate of heritability for that figure was calculated as .55. The other studies surveyed fell between .32 and .50. Those estimating yearling weight heritability in this range include: Knapp and Clark (1951), Koch and Clark (1955), Swiger et. al. (1961), Brinks et. al. (1962), Brinks et. al. (1964) and Brown and Gacula (1964). The average of all yearling and long yearling weight estimates is .46.

Phenotypic, Genic and Environmental Variances
of the Traits Studied

Many studies have been conducted to estimate sources of variation in weaning weight, average daily gain and weight at approximately one year. However, as with much research the times and length of period for which these traits are measured are variable. Therefore, because of this, plus wide environmental differences, much variance occurs in the estimates occurring throughout the literature. Phenotypic variance for weaning weight is quite variable, ranging from a low of 1271 lbs. reported by Blackwell et. al. (1962) to a high of 3570 lbs. reported by Swiger and Hazel (1961). The greatest share of works report phenotypic variances below 2000 lbs., those included are: Knapp and Clark (1951), Koch and Clark (1955), Pahnish et. al. (1961), Blackwell et. al. (1962), Swiger et. al. (1962), Shelby et. al. (1963), Brinks et. al. (1964) and Pahnish et. al. (1964) in a later report. Brinks et. al. (1962) and Shelby et. al. (1960) earlier reported weaning variances of 2601 and 2862 lbs., respectively. The average phenotypic variance in the 11 reports cited was 2070 lbs.

From the preview of heritability estimates along with phenotypic variances, the genic variances look, as one would expect, inconsistent. The range is from 218 to 1231 lbs., with Shelby et. al. (1960) reporting the highest and Blackwell et. al. (1962) reporting the lowest. The average for nine studies reviewed was 530 lbs. The non-additive variance, which includes dominance, epistasis and environmental variance, from the same nine studies was calculated as the difference

between phenotypic and genic variance. When this was done the calculated average was 1540 lbs.

The studies determining variance components for average daily gain have not been as numerous. However, one consolation is that most of the studies lie within a fairly narrow range when looked at as variance in gain per day rather than variance over postweaning feeding phase. Studies reporting phenotypic variance between .075 and .100 are: Knapp and Clark (1951), Koch and Clark (1955), Carter and Kincaid (1959a), Shelby et. al. (1960), Blackwell et. al. (1962), Brinks et. al. (1962), and Swiger and Hazel (1961). Brinks et. al. (1964) later reported a small phenotypic variance of .031 for A.D.G. Also Shelby et. al. (1963) and Swiger et. al. (1962) reported smaller values which were .044 and .059, respectively. When the 10 studies review were averaged for phenotypic variance, it equaled .073. Genic variance reported are variable, however, most fall in the range of .03 to .05. Investigators reporting within this range were Koch and Clark (1955), Carter and Kincaid (1959a), Shelby et. al. (1960), Brinks et. al. (1962) and Swiger and Hazel (1961). The average of these five reports was .035. Brinks et. al. (1964) later reported a value of .014 which was in agreement with a value of .021 reported later by Shelby et. al. (1963). Swiger et. al. (1962) and Blackwell et. al. (1962) reported the highest genic variance values of .057 and .070, respectively. In the case of these latter two papers the heritability estimates were unrealistically high, thus discounting the validity of their genic variance estimates as being applicable to other beef cattle populations.

Scant information was found on variance estimates for yearling weight. Blackwell et. al. (1962) reported phenotypic variances of 2355 lbs. for steers and 1588 lbs. for heifers. The same author reported genic variances of 236 and 1122 lbs. for steers and heifers, respectively. When these two were averaged the genic variance was 679 lbs. and the phenotypic variance was 1971 lbs. Brinks et. al. (1964) and Koch and Clark (1955) reported similar values. Shelby et. al. (1960) and Swiger and Hazel (1961) had variance estimates that were twice as large as previous mentioned ones. Swiger and Hazel's estimates for phenotypic variance of yearling weight were 6438 lbs. and 3038 lbs. for genic. Shelby estimated phenotypic variance at 7845 lbs. and genic variance at 4315 lbs. In another review, Shelby et. al. (1963) estimated the phenotypic variance for final weight at 4963 lbs. and its genic counterpart at 3172 lbs. The average of all the studies, except for the last one mentioned, for yearling weight was 4310 lbs. for phenotypic variance and 2082 lbs. for genic variance.

Correlations Between Traits Studied

Only a few studies have made mention of the correlations which will be used in this study. Brinks et. al. (1962) and Brinks et. al. (1964) reported two sets of correlations which are in close agreement. In the first paper they reported correlations of .62, .67 and .59 for phenotypic, genetic and environmental correlations, respectively, between weaning weight and yearling weight. Brinks' second paper reported values of .73, .71 and .75 for phenotypic, genetic and

environmental correlations, respectively, between weaning weight and yearling weight. Shelby et. al. (1963) and Koch and Clark (1955) reported similar values to Brinks' two sets and when averaged with Brinks' the mean correlations for phenotype and genetic were .62 and .71, respectively. Blackwell et. al. (1962) reported correlations between weaning and 18 month-weight as .65 for phenotypic correlation, .16 for genetic correlation and .83 for environmental correlation. Their phenotypic, genetic and environmental correlations between weaning weight and 18 month gain were -.10, .08 and -.16, respectively.

Several authors have reported correlation values between weaning and average daily gain, however, they tend to be highly variable. For instance, Swiger (1961) reported the high genetic correlation between weaning weight and A.D.G. of .93 while Brinks et. al. (1964) reported the low of -.20. Other authors reporting values scattered across the whole range include: Koch and Clark (1955), Carter and Kincaid (1959b), Blackwell et. al. (1962), Brinks et. al. (1962), Swiger et. al. (1962), and Shelby et. al. (1963). When all eight of the reports were average the genetic correlation averaged out to be .33 while the phenotypic correlation average was .05.

Brinks in the two previously mentioned papers, along with Koch and Clark (1955) reported correlations between average daily gain and yearling weight. The average of these three papers for phenotypic, genetic and environmental correlations were .68, .71 and .68, respectively. Shelby et. al. (1963) reported higher correlations between average daily gain and final weight off of feed test. His phenotypic and genetic correlations were .86 and .96, respectively.

METHODS AND PROCEDURES OF SIMULATION

Introduction

The actual computer process of initiating a base parental population, simulating their offspring and offspring from matings in calf crops 2 through 10, storing and transferring data on local files from one program to another, collection of population data for analysis and soft-ware problems are indeed lengthy and complete discussion of each phase is too detailed and lengthy for this manuscript. Instead the programs utilized have been listed and put in loose-leaf notebook form and stored with the author and author's major professor. Thus, what follows in this section will be a brief documentation of how the populations were simulated.

A total of seven FORTRAN IV programs, made operational on the Michigan State University CDC 6500, were utilized to accumulate data from simulated populations to see if 1) random mating and phenotypic positive assortative mating were significantly different in the amount of genetic and phenotypic improvement they caused at three heritability levels; 2) two different sire testing procedures affect performance trait improvement; 3) different bull turnover rates significantly affect improvement in performance traits; 4) three contrasting heifer selection rates cause significant changes in the amount of performance improvement; 5) three variations in selection criteria bring about variation in trait improvement and which, if any, excels in yearling weight improvement; and 6) any two-way interactions exist between the independent variables.

BPAM and BTHS, two modified versions of the beef simulation program written by Drs. Gordon Thomson and Richard L. Willham at Iowa State University were used as the main programs to develop and carry out population characteristics. BPAM and BTHS incorporated extensive alterations of the aforementioned program to delete unnecessary printing and supplement the output with population parameters necessary to allow analysis of the fruitions selection and mating programs bring about. The two versions, BPAM and BTHS, were necessary to accommodate both within purebred herd testing of bulls and progeny testing of bulls within a commercial test herd. This required that two selection routines also had to be written. One selection routine was written to accommodate within purebred herd testing of bulls and the second accommodated progeny testing of purebred bulls in a commercial test herd while also maintaining selections within the purebred herd itself. A more detailed description of these two routines will follow in a later section.

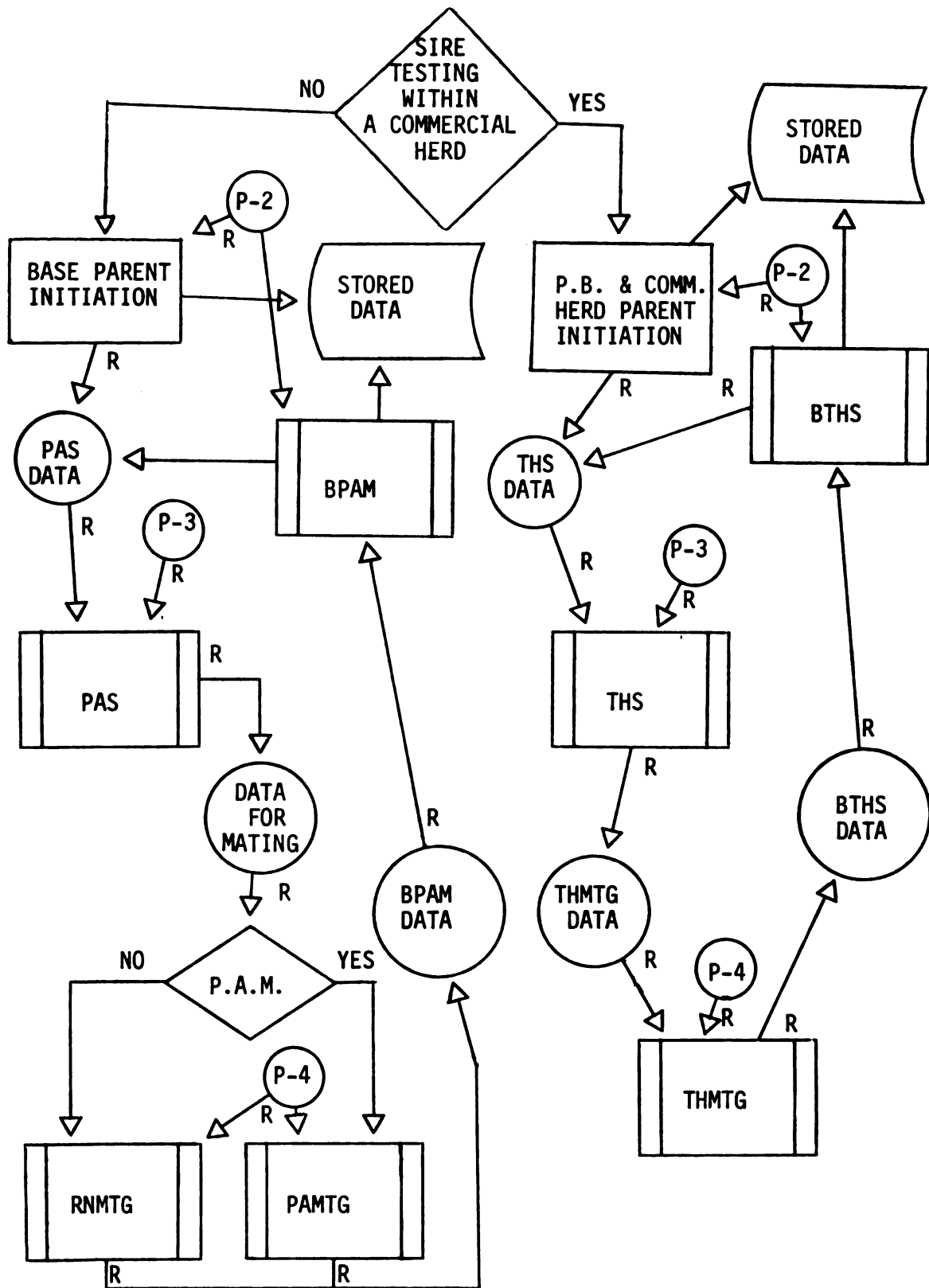
The investigation was setup to use random mating (RM) and positive assortative mating (PAM) in the purebred herd and RM in the progeny testing of bulls within a commercial test herd. In order to accomplish this two RM and one PAM programs had to be made operational. A brief description of each will follow in later sections.

All seven programs were compiled and stored on disk permanent file and on magnetic tape to accomplish easy access by control cards.

1

The flow chart in Figure 1 shows how the different programs were used when alternate options were chosen in simulating herds. Only one herd, a purebred herd, was initiated if the option of not progeny testing within a commercial test herd was chosen, whereas two herds, a purebred and a commercial test herd were initiated for the other case. After initiation of the herd was completed, selections and matings within the herd's population took place and were passed on to either BPAM or BTHS. The matings were carried out, offspring developed and information for selection supplied to the selection routines. The cycle of the three programs took place until nine selections and matings occurred.

FIGURE 1. FLOW CHART OF PROGRAMS UTILIZED TO SIMULATE BEEF HERD POPULATIONS.



With the use of control cards, the CDC 6500 created local files, P-2 through P-4, which contained parameter data that allowed the programs to function properly for specific types of data collection. If further information on parameter files or other description is needed, the program notebook should be consulted. The stored data file was made into a permanent file on disk and added to each time the simulation run was made. The other data files were local files which acted as go-betweens for the programs as they functioned in sequence. An R by the arrows going to and coming from the local files indicate they were rewound before being either written on or read from.

In the next section, Simulation of Herd Population, values which give a heritability of 40% for yearling weight (YW) will be used to show how base parents are initiated, their phenotypes formed and resulting offspring of a mating generated. These values plus the ones for the other heritability levels and how they are obtained will be discussed in the materials section. To present a numerical example in the next section, heritabilities of 19.7 and 59.1% for weaning weight (WW) and average daily gain (ADG), respectively, were used to make YW heritability 40%. The definitions and values, if they have any, for the abbreviations used in the next section are given in Table 1.

Simulation of Herd Populations

BPAM and BTHS had limitations which fixed maximum herd size at 90 cows and 9 bulls. In the initial calf crop 90 base

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cows and 9 base bulls were created for each herd. Then 10 cows were mated to each bull to produce 90 offspring. The biological model followed for the production of each offspring is found in Figure 2. The first calf crop production is the only time when parents are created, after that the individuals are created by simulating the mating of two individuals and the biological happenings diagrammed in Figure 2.

Throughout the 10 calf crops the cow herd size in both the purebred and commercial test herds was kept at a constant size of 90. The average death rate for cows and bulls was set at 5%. Determination of death in the cows, bulls and their offspring was by random number drawing. On the average 10% of the offspring died. Sex of the calves was also determined by random number drawing with 50% being each sex on the average.

As shown in Figure 2, base parents of the purebred herd and, when in use, commercial test herd had three breeding values created and stored with their herd identification. The three breeding values created by use of multiplication factors and standardized random normal deviates were genetic abilities for WW, ADG and maternal ability (MA). Also a permanent environmental effect for MA was created and stored for each female. The program was setup with no genetic correlation between WW and MA.

Formation of genotypes and phenotypes for base parents in the BPAM and BTHS was accomplished in the same manner for both sexes. Equations 1-3 show the creation of genotypes for WW, MA and

TABLE 1. ABBREVIATIONS, VALUES AND DEFINITIONS OF FACTORS USED IN FORMING GENOTYPES AND PHENOTYPES FOR SIMULATION OF HERD POPULATIONS SECTION.

Abbreviation	Value ^a	Definition
$G_{D \cdot D}, G_{D \cdot S}, G_{D \cdot O}$		Genic value for WW in dam, sire and offspring, respectively
$G_{M \cdot D}, G_{M \cdot S}, G_{M \cdot O}$		Genic value for maternal ability in dam, sire and offspring, respectively
$G_{F \cdot D}, G_{F \cdot S}, G_{F \cdot O}$		Genic value for ADG in dam, sire and offspring, respectively
$P_{W \cdot D}, P_{W \cdot S}, P_{W \cdot O}$		Phenotypic value for WW for dam, sire and offspring, respectively
$P_{F \cdot D}, P_{F \cdot S}, P_{F \cdot O}$		Phenotypic value for ADG for dam, sire and offspring, respectively
$P_{Y \cdot D}, P_{Y \cdot S}, P_{Y \cdot O}$		Phenotypic value for YW for dam, sire and offspring, respectively
$P_{M \cdot D}$		Phenotypic value for dams' maternal ability
SD, SF, SM		Genic Mendelian segregation for WW, ADG and maternal ability, respectively
$E(W), E(F), E(M)$		Random environmental effect on WW, ADG and maternal ability
$E(P)$	PESDW·RN(i)	Permanent environment on dams' maternal ability
CWG1 ^b	.04802	Factor required to produce genetic correlation between WW and ADG
CWG2 ^b	.18600	Factor required for total genic variance in ADG
CWW	21.21320	Factor required for genic variance in maternal ability
DGSDW	22.19234	Factor required for direct genic variance in WW

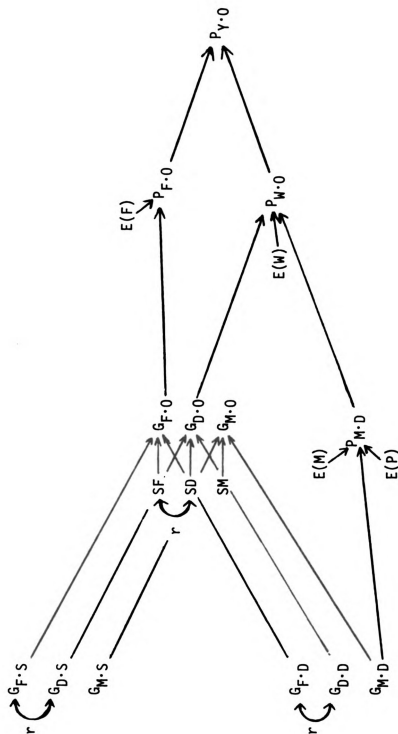
TABLE 1. -- Continued

Abbreviation	Value ^a	Definition
DESDW	26.11116	Factor required for direct environmental variance in WW
DESDG	.16000	Factor required for direct environmental variance in ADG
FESDW	27.52358	Factor required for direct environmental variance in maternal effect on WW
PESDW	15.07528	Factor required for permanent environmental variance in maternal effect on WW
HEW		Common herd environment for WW for one calf crop, equal to 10% of standardized random normal deviate times DESDW
HEF		Common herd environment for ADG for one calf crop, equal to 10% of standardized random normal deviate times DESDG
MMW	450	Mean value used for WW
MADG	2.50	Mean value used for ADG
NDGT	160	Number of days males and females are gain tested
RN(i)		Standardized random normal deviate (SRND) used to develop equations on pages

^aIf a value appears it is one necessary for a YW heritability of 40%.

^bSee Appendix A for calculation and explanation; both CWG1 and CWG2 are used both base parent initiation and calf crops 1 through 10.

FIGURE 2. DIAGRAM OF THE FACTORS INFLUENCING PERFORMANCE TRAITS IN SIMULATED ANIMALS.^a



^aAbbreviations and definitions of factors appear in Table 1.

ADG, respectively, for dams. Equation 4 shows the creation of the

$$\begin{aligned}
 (1) \ G_{D.D} &= 22.19234 \cdot RN(1) \\
 (2) \ G_{M.D} &= 21.21320 \cdot RN(2) \\
 (3) \ G_{F.D} &= .04802 \cdot RN(1) + (.186000 \cdot RN(3)) \\
 (4) \ E(P) &= 15.07528 \cdot RN(4) \\
 (5) \ P_{W.D} &= 450 + G_{D.D} + (26.11116 \cdot RN(5)) + (27.52358 \cdot RN(6)) \\
 (6) \ P_{F.D} &= 2.50 + G_{F.D} + (.16000 \cdot RN(7)) \\
 (7) \ P_{Y.D} &= P_{W.D} + (160 \cdot P_{F.D})
 \end{aligned}$$

permanent environmental effect on MA. Equations 5-7 show the calculations necessary to arrive at phenotypic expression for WW, ADG and YW, respectively, for dams. For all cases, the abbreviations and values are used as listed in Table 1. The correlation between $G_{D.D}$ and $G_{F.D}$ of .25 was produced through the use of the same standardized random normal deviate in equations 1 and 3. Along with the genotypes and phenotypes being stored, how each parent deviates from the herd mean for YW is stored. This individual deviation (IR) is used in a later program segment to calculate the estimated breeding value for YW (YW-EBV).

The procedure used to create animals after the base generation is shown in Figure 2. Half of the offsprings' genic value comes from each parent with appropriate Mendelian segregation being added. Because this path diagram develops the phenotype for only one individual, overall herd environmental effects on individual WW and ADG were omitted. As shown in Table 1, the common environment for

each individual in a herd-year group is 10% of the magnitude of direct environmental standard deviation for the trait times a standardized random normal deviate. There is one random draw for each calf crop.

The actual formulas used to calculate offsprings' genotypes and phenotypes are represented by equations 8-13.

$$(8) G_{D.O} = (G_{D.S} + G_{D.D})/2 + (\sqrt{.5} \cdot 22.19234 \cdot RN(1))$$

$$(9) G_{M.O} = (G_{M.S} + G_{M.D})/2 + (\sqrt{.5} \cdot 21.21320 \cdot RN(2))$$

$$(10) G_{F.O} = (G_{F.S} + G_{F.D})/2 + [\sqrt{.5} (.04802 \cdot RN(1) + .186000 \cdot RN(3))]$$

$$(11) P_{W.O} = 450 + G_{D.O} + (26.11116 \cdot RN(5)) + G_{M.O} + E(P) + (27.52358 \cdot RN(6)) + HEW$$

$$(12) P_{F.O} = 2.50 + G_{F.O} + (.16000 \cdot RN(7)) + HEF$$

$$(13) P_{Y.O} = P_{W.O} + (160 \cdot P_{F.O})$$

These formulas were utilized in forming progeny in all calf crops.

BPAM and BTHS were finitely developed to summarize and store data needed for YW-EBV calculations as described by Willham (1973). In particular, for the YW-EBV calculation the following four data items are used: (1) own performance expressed as a deviation from contemporary group (IR), (2) average performance of PHS as the average of the individual deviations and number of PHS, excluding the individual under consideration, (3) average performance of MHS as the average of the individual deviations and number of MHS, excluding the individual under consideration, and (4) average

performance of the individual's progeny expressed as the average of the individual deviations and the number of them. Due to programming difficulties PHS and MHS records are never updated once they are established. Indeed, added accuracy could be gained from more PHS data, but one progeny record adds to accuracy at twice the rate a PHS record does thus making half sib data update less essential. Progeny average was re-evaluated every time the individual produced another offspring. All items used in YW-EBV were expressed as deviations from the mean of the group in which they were produced. If a data item was missing then the row and column corresponding to that data item were dropped out of the simultaneous equations for YW-EBV. For instance, if only IR and PHS records were available for an individual the rows and columns corresponding to MHS and progeny average were dropped and only two B values, as described by Willham (1973), were estimated. The resulting YW-EBV would then be the two B values multiplied by their respective independent variables, IR and PHS.

BPAM and BTHS incorporated numerous modifications which allowed them to read from and write on local files in the computer were numerous. As diagrammed in Figure 1, information had to be passed onto the selection programs so correct selections could be made and the selected animals passed onto the mating programs. BPAM and BTHS wrote onto a local file the identification number, ADG and YW phenotypes and YW-EBV for the calves. In the case of individuals which are in production, progeny

averages for ADG and YW plus YW-EBV were also written onto the local file. Rewinding (R in Figure 1) of the local file was necessary before utilization by the selection programs could occur. In the case of reading the local file formed by mating programs, the BPAM and BTHS were altered to read the local file as card form images which the Thomson-Willham program currently utilizes for most classroom work.

Mechanics of Selection Programs

Two selection programs were developed to work in coordination with BPAM and BTHS. One selection program carried out the correct selections when only the purebred herd was used, while the other program carried out all the selections for the purebred and the commercial test herd when it was in use. Both selection programs used individual animal information read off the local file created by either BPAM or BTHS as shown in Figure 1, plus information from the parameter local file, P-3. P-3 specified which trait to select on and how many of each sex and age group were to be selected.

Selection of bull and heifer calves in the purebred herd when the commercial test herd was not utilized was based on either phenotypic expression for ADG or YW or the YW-EBV. Mature bull and cow selection in this instance was based on progeny records for ADG or YW or on YW-EBV which was revised each time individuals produced more progeny. The numbers selected will be discussed in the Parameter Values Used section.

When the commercial test herd was used, the selection program, test herd selection (THS), carried out more functions than the other selection

program, PAS. As with PAS, THS read in all sex and age classifications and ranked them via FORTRAN IV double do-loops based on the selection criteria read from P-3. Both THS and PAS selected heifer calves for the purebred herd based on their own performance records. These heifers were complemented with the highest ranking mature cows based on their progeny records or YW-EBV to make the breeding herd size 90 head. THS also kept the commercial test herd at 90 cows by replacing the dead mature cows with the highest yearling weight heifers.

Bull selections made by THS were more numerous and complicated in comparison to those described previously. Two stage selection took place before a bull was used in the purebred herd. The first of the two stages of selection came when the top 9 bull calves of the purebred calf crop were selected based on their own performance record or YW-EBV. These 9 performance tested bull calves were then randomly mated to commercial cows and progeny evaluated. After progeny evaluation in the Commercial test herd THS selected either 3, 4 or 6 of the 9 performance tested, progeny evaluated bulls to be used in the purebred herd. Selection of the performance tested, progeny evaluated bulls for the purebred herd was based solely on progeny average, except when YW-EBV was the tool used for selection. In this latter case, individual deviation from the herd mean for yearling weight, plus paternal and maternal half-sib performance and commercial progeny average yearling weights were incorporated into the breeding value estimate.

For two of the three bull selection options, selection of a portion of the bulls for the purebred herd was from bulls that had previously been used in the purebred herd. Therefore, the selection of these bulls was three stage. Firstly, they were originally selected on their own performance record or an estimate of their yearling weight breeding value before progeny evaluation in the commercial test herd took place. Secondly, the bulls were selected for use in the purebred herd based on progeny evaluation as previously described and thirdly, the bulls were selected for reuse in the purebred herd based on further progeny evaluation which had taken place in the purebred herd.

Mechanics of Mating Programs

Three mating programs were developed to accomplish the deeds of this investigation. RNMTG was a RM program utilized in the purebred herd only portion of the investigation. The program used in all cases where the design required PAM was PAMTG. THMTG was another RM program which besides RM the purebred herd also RM the 9 bull calves from the purebred herd with the 90 commercial test cows.

RNMTG and THMTG accomplished RM in the same manner, except that THMTG had to also RM the 9 purebred bull calves to 10 commercial test cows each. When the males and females were read in from the rewound local file created by the selection programs they were placed in two arrays, one for selected males and one for selected females. Each male and female was then assigned a value from the random number generator function within the computer. A FORTRAN IV double do-loop was then employed to rank the arrays in descending order according

to the assigned random numbers. In the purebred herd, the bull with the highest random number was assigned the 15 cows with the 15 highest random numbers, the bull with the second highest random number was assigned cows which ranked 16th through 30th by assigned random numbers and so on until cows ranking 76th through 90th were assigned to the bull with the smallest random number. The same tactics were used to accomplish RM of the 9 purebred bull calves to 10 cows each in the commercial test herd.

Accomplishment of PAM in the purebred herd was not as easy. Assorting of the animals was based on their own phenotypic expression. Even though the mature cows and bulls were selected on their progeny averages they were PAM on their own phenotypes as were bull and heifer calves, thus phenotypes had to be transferred with each individuals' identification number from the selection program to PAMTG. When PAMTG read in data from the local file created by PAS it created two arrays, one for males and one for females. Then based on mating criteria (i.e., whether to PAM on ADG, YW or YW-EBV as read from the local file P-4) PAMTG ranked, via double do-loops, the male and female arrays in descending order. PAMTG then assigned the first male with the first 15 females, the second ranking male with the second 15 females and so on until all 90 females had been assigned with the 6 selected males.

PARAMETER VALUES USED

Many objectives are meant to be evaluated in this investigation, however, the primary objective of this study is to evaluate the response of simulated populations to two sire testing procedures and to two mating systems. Two sire evaluation systems were chosen which would closely resemble what a moderate sized purebred beef herd might be able to accomplish. The first was an evaluation of sires within the purebred herd, while the second system utilized a commercial test herd to progeny test 9 bull calves before their use in the purebred herd. Naturally, the latter system requires a longer generation interval plus more capital investment in the way of 90 commercial cows.

The two mating systems under investigation are random and positive assortative mating. These were used as explained in the Method of Simulation section. It should be mentioned again, however, that only random mating was used when progeny testing of bulls was done in the commercial test herd.

Four other items were factorialized within the two sire evaluations and two mating systems. Three levels each of YW heritability and percent heifer calves saved were looked at, along with three combinations of young and old bulls saved plus selecting on either ADG, YW or YW-EBV. A discussion of the YW heritabilities will follow in a later section.

The three levels of heifer calves saved were 20, 50 and 80%. These three levels were chosen because they approximate the full range of selection intensities being used today plus these levels will

hopefully show advantages and disadvantages of generation turnover and selection intensity.

A total of 6 bulls was always used in the purebred herd, but three different combinations of young and old bulls were used to acquire this total. The three combinations were 0 old and 6 young, 2 old and 4 young, and 3 old and 3 young. Of course, the first of the three was used to find the effect maximum sire turnover rate might have on rate of improvement. The other two combinations were chosen to find what combination of young and old sire numbers would optimize selection intensity and accuracy, thus lending to maximum rate of improvement.

The selection traits in this project were chosen because of their interest to the author and his committee, plus large emphasis is currently being given to them by the purebred beef industry. In addition, it was of interest to investigate the impact YW-EBV would have on genetic improvement and how it would compare to other selection programs. As stated before the three data items used as selection criteria were ADG, YW and YW-EBV. Selection in the old bulls and mature cows for ADG and YW is based on progeny averages for the two traits. Whereas, selection of the bull and heifer calves is based on their own phenotype for the two traits. The only exception to this is when the bull calves are progeny tested in the commercial herd at which time they are selected on their progeny averages. Selection by YW-EBV calculation is accomplished in the same manner regardless of sex or age category, except for bulls progeny tested in the commercial herd. Because of great difficulty encountered in

transfer of data from program to program only the tested bull calves' individual deviation from herd contemporaries and average deviations of progeny was used in the YW-EBV calculation. The YW-EBV calculation for all other individuals utilized half sib data in addition to IR and average progeny deviation when it was available.

Three levels of YW heritability were chosen to cover the range of heritabilities cited in the literature. The three levels used in the simulation were 20, 40 and 60%. In developing the variance components of WW and ADG which would give the three levels of YW heritability, certain maximum values and ratios between various components were standardized. The total phenotypic variances for WW and gain from weaning to yearling time was set at 2500 and 1600, respectively. The latter, when put on a gain per day basis, had a phenotypic variance of .0625. Also set out was that heritability of ADG would not exceed 80%. The ratio between WW and ADG heritability would be a constant 1:3 ratio as long as heritability of ADG remained equal to or under 80%. But when YW heritability was set at 60%, the 1:3 ratio caused the 80% limit for ADG heritability to be exceeded, thus a 1:2 ratio was used.

As stated in a previous section, the genetic correlation between WW and ADG was set at .25. This was kept constant across the three YW heritability levels. Of course, the genic and phenotypic variances for YW were the summation of genic and phenotypic variances for WW and ADG plus two times the genic covariance between WW and ADG. The following two equations depict genic (1) and phenotypic

(2) variance, respectively, for YW, where

$$(1) \sigma_{G_Y}^2 = \sigma_{G_W}^2 + (160)^2 \cdot \sigma_{G_F}^2 + 2 \cdot 160 \cdot \sigma_{G_W G_F}$$

$$(2) \sigma_{P_Y}^2 = \sigma_{P_W}^2 + (160)^2 \cdot \sigma_{P_F}^2 + 2 \cdot 160 \cdot \sigma_{G_W G_F}$$

$\sigma_{G_W}^2$ and $\sigma_{P_W}^2$ are genic and phenotypic variances for WW, $\sigma_{G_F}^2$ and $\sigma_{P_F}^2$ are genic and phenotypic variances for ADG and $\sigma_{G_W G_F}$ is the genic covariance between WW and ADG. Naturally, as heritability of the traits increase so does the genic and phenotypic variance due to increased covariance.

Proper heritability levels for WW and ADG, which give the prescribed YW heritabilities, were gotten by trial and error method. The calculated heritability levels of WW and ADG, respectively, for YW heritabilities of 20, 40 and 60% were, 9.45 and 28.35%, 19.70 and 59.10%, and 39.25 and 78.50%, respectively. The expected genic and phenotypic variances, respectively, for the three heritability levels of 20, 40 and 60% were 853 and 4264, 1779 and 4441, and 2792 and 4665, respectively.

Once the proper WW and ADG heritabilities were determined it was decided to maintain constant ratios between the non-additive variance components in WW, for the direct genic variance for WW would vary a great deal over the different WW heritabilities. The six ratios between the other four variance components were as follows: (1) individual environmental to maternal genic, 2:1, (2) individual environmental to maternal permanent environmental, 3:1, (3) individual environmental to maternal temporary environmental, .9:1, (4) maternal genic to maternal permanent environmental, 1.4:1, (5) maternal genic

TABLE 2. COMPONENTS REQUIRED TO GIVE PRESCRIBED LEVELS OF YEARLING WEIGHT HERITABILITY.

Component ^a	YW Heritability					
	20%		40%		60%	
	Value	Percent ^b	Value	Percent ^b	Value	Percent ^b
DGSDW	15.37043	9.45 ^c	22.19234	19.70 ^c	31.32491	39.25 ^c
DESDW	27.72762	30.75	26.11116	27.27	22.71127	20.63
FGSDW ^d	19.60639	15.38	18.46337	13.64	16.05930	10.32
FESDW	29.22748	34.17	27.52358	30.30	23.93978	22.92
PESDW	16.00855	10.25	15.07528	9.09	13.11236	6.88
DGSDG ^e	.13304	28.35 ^f	.19209	59.10 ^f	.22159	78.50 ^f
DESDG	.21166	71.65	.16000	40.90	.11576	21.50
CWW	21.21320		21.21320		21.21320	
CWG1 ^g	.03326		.04802		.05540	
CWG2 ^h	.12880		.18600		.21455	

^aAbbreviations and definitions of components are given in Table 1.

^bPercent of total phenotypic variance.

^cHeritability in percent for WW.

^dAmount of WW variance due to genic variance in MA, value not used in BPAM or BTHS.

^eAmount of ADG variance due to genic variance, value not used in BPAM or BTHS.

^fHeritability of ADG.

^gFactor required to give genetic correlation between WW and ADG (See Appendix A).

^hFactor required to give prescribed genic variance in ADG (See Appendix A).

to maternal temporary environmental, .4:1, and (6) maternal permanent environmental to maternal temporary environmental, .3:1. The components with ratios to individual environmental variance (IE) were setup in the following equation to equal non-additive variance:

$$IE + IE/2 + IE/3 + 10 \cdot IE/9 = \text{Non-Additive Variance.}$$

The other components were found by using the ratios setup between them and IE. With these ratios the proper weightings for each variance component of WW was established and values calculated to obtain each level of YW heritability. The figures listed in Table 2 are multiplicative factors which were used in BPAM and BTHS programs to give the prescribed variances and heritabilities. The procedure for calculating CWG1 and CWG2 is given in Appendix A.

RESULTS AND DISCUSSION

The data presented in this section are from several analyses done on the calf crop information stored by the two modified versions of the Thomson-Willham program. The calf crop information, because of its volume, was stored on disk permanent file (and backed up with a data file on magnetic tape) for ease of handling, manipulation and incorporation into the Michigan State University computerized statistical software package. Through the use of short FORTRAN IV programs the large arrays of calf crop information were broken down to smaller data arrays, which were made into permanent files, and statistically analyzed. Analysis of variance procedure was done in two parts. One analysis procedure analyzed the data comparing the two mating systems, RM and PAM, and their four factorialized sources of variance, while the second analysis procedure analyzed the two sire testing procedures and their four factorialized sources of variance. The four factorialized sources of variance in both analyses were three levels of YW heritability, three bull combinations, three levels of percent heifer calves saved (PHCS) and three different selection methods. The magnitude of the two-way interactions was also evaluated in the analyses procedures.

The Effect of Main Sources of Variance

Mating Systems

Effect on Yearling Weight

Random mating (RM) and positive assortative mating (PAM), as used in this investigation, were not significantly different in the amount

of improvement they caused in YW over ten calf crops. Table 3 shows that RM populations were better than PAM populations for average calf YW in calf crop 4 (CC4). However, at calf crop 7 (CC7) and calf crop 10 (CC10) PAM populations averaged higher than RM populations. In the latter two calf crops, average progeny yearling weight for sires and dams was higher for PAM than RM. At CC10 the sires averaged 4.7 lbs. heavier in their progeny average for YW while dams averaged 4.1 lbs. heavier in their progeny average for YW with PAM, however, neither mating system was significantly different from the other for these two calculations.

PAM brought about an insignificant increase in phenotypic variance for calf YW. The probable reason why PAM does not increase the amount of genic or phenotypic variance is that the lower portion of the phenotypic distribution is continuously culled off. In CC10 phenotypic YW variance for PAM populations averaged 4528, while RM populations averaged 4336. The average expected phenotypic and genic variances for YW were 4457 and 1808, respectively. The difference in genic variance for calf YW was smaller, with PAM and RM variances equal to 2253 and 2132, respectively, at CC10. Because genic values and environment were not correlated one would not expect the difference between genic and phenotypic variances for the two mating systems to differ. However, chance alone could cause this much variation to occur between differences in the two mating systems for genic and phenotypic variance. Even though a highly variable population is not completely desirable, if the mating system creates greater variance in the breeding population more individuals in the upper extreme may be produced, thus enabling incorporation of animals into the breeding population which average higher in genic value. Also the breeder may be able to propagate a product of greater breeding

TABLE 3. ANALYSIS OF VARIANCE AND LIST OF MEANS FOR MAIN SOURCES OF VARIANCE IN MATING SYSTEM DATA FOR WW, ADG AND YW.

Source	Category	Calf Crop 4			Calf Crop 7			Calf Crop 10		
		WW	ADG	YW	WW	ADG	YW	WW	ADG	YW
Mating System	Sig.	.005	.151	.366	.046	.018	.788	.100	.005	.419
	RM	473.1	2.717	907.7	489.0	2.868	947.8	505.0	3.022	988.4
	PAM	468.7	2.731	905.6	485.0	2.897	948.6	501.2	3.063	991.2
YW	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	20%	464.1	2.629	884.8	474.7	2.713	908.8	482.2	2.791	929.9
	40%	470.1	2.740	908.6	482.7	2.906	947.7	500.5	3.071	991.9
Heritability	60%	478.3	2.803	926.8	503.6	3.028	988.1	526.5	3.264	1048.7
Bull	Sig.	.856	.401	.420	.228	.544	.379	.064	.309	.044
	0/6	471.0	2.725	907.0	486.4	2.873	946.1	501.3	3.029	986.0
	2/4	471.3	2.732	908.4	489.3	2.885	950.9	506.9	3.056	995.9
Combination	3/3	470.3	2.715	904.7	485.3	2.889	947.6	500.9	3.041	987.5
Percent Heifers Saved	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	20%	465.9	2.694	896.9	476.9	2.815	927.2	488.3	2.939	958.5
	50%	472.0	2.740	910.4	490.9	2.917	957.6	507.6	3.079	1000.3
Selection	80%	474.7	2.738	912.8	493.3	2.916	959.7	513.3	3.109	1010.7
	Sig.	<.0005	<.0005	.003	<.0005	<.0005	<.0005	<.0005	<.0005	.001
	EBV	476.7	2.716	911.3	498.3	2.860	956.0	516.7	2.977	993.1
Criteria	YW	478.5	2.679	907.2	500.1	2.813	950.2	521.4	2.964	995.7
	ADG	457.4	2.776	901.6	462.6	2.974	938.4	471.0	3.185	980.7

the breeder may be able to propagate a product of greater breeding value and possibly greater monetary value. However, these data do not support the theoretical ground work laid out in the review of the literature. Because PAM did not significantly stretch out the variance, increased selection intensity for YW was not possible. Due to this fact, significant increases in the improvement of YW were not made with PAM. Thus, as an adviser to breeders, one would not be warranted in suggesting the use of PAM, as used in the investigation, as a tool to accomplish significantly greater genic improvement in YW. One would have to state that the additional time and expense required to assortatively mate would not be rewarded economically with extra pounds of calf at a year.

When the correlations between mated individuals were analyzed and two-way interaction tables compiled, the phenotypic correlation between mates for YW selection and PAM were highly positive (+.88) and significantly ($P < .01$) different from the same correlation for RM, which was $-.06$. Indeed these two correlations would make one believe greater gains in YW improvement might be accomplished. However, when the genic correlations between mates for YW were analyzed the differences, although significant ($P < .01$), were small, $.16$ for PAM vs. $-.06$ for RM, thus again explaining why PAM did not give additional improvement in YW.

In retrospect, one would say PAM looks exciting in theory, but when it was actually practiced in this investigation additional rewards were not harvested, thus suppressing ones enthusiasm towards it.

Effect on Weaning Weight

The component parts of YW, WW and 160-day gain, reacted in opposite ways to the two mating systems. As presented in Table 3, a phenotypic significant difference in WW existed in CC4 and CC7 between the two mating systems. There was, however, no genic difference between RM and PAM in the three calf crops analyzed. Sire and dam direct genic values for WW were in total agreement with what was found for direct genic values in calves; in that, there were no significant differences found between RM and PAM. When the phenotypic and genic variances for WW were analyzed no significant differences between the two mating systems were found. In fact, RM caused more phenotypic variance in WW at CC10 (2506 vs. 2475), however, PAM caused slightly more genic variance (534 vs. 530) in WW at CC10.

When genic maternal ability for calves and parents were analyzed no significant differences were found between mating systems. However, the analysis did reveal that RM populations were continuously higher in direct genic value on WW and genic maternal ability in both the calves and parents, but that these differences narrowed as time elapsed.

Indeed to recommend PAM for greater improvement in WW would be one of poor judgment. Even though no direct selection was made on WW in this investigation, it is relatively safe to assume that PAM would not give additional improvement in WW. Indeed phenotypic correlation between mates will be high ($r > .85$), but the lower heritability of WW will cause lower genetic correlations to exist between mates, thus

lowering even further the possibility of more improvement through the use of PAM. Due to this fact, an even lower frequency of best-to-best matings would take place.

Effects on Average Daily Gain

Average daily gain for 160-days reacted more favorably to PAM than RM. As Table 3 shows PAM was significantly higher in genic ability and phenotype for ADG in CC7 and CC10. Sire and dam genic abilities for ADG followed the same significant pattern of those for calves. In CC10 the sires averaged .041 lbs. per day higher for PAM than RM and dams likewise, only the difference was .038 lbs. per day.

Because ADG was more highly heritable, the theoretical concepts of PAM took place. In CC4 and CC10 PAM caused significantly greater variance in both genic value and phenotype. At CC10 PAM had a 10.7% greater phenotypic variance and a 18.6% greater genic variance. Indeed these increases in variance gave PAM an advantage in selection differential. PAM was also substantially and significantly higher in both genetic and phenotypic correlation between mates in the three calf crops analyzed. When ADG selection in the two mating systems was compared very high phenotypic correlations existed between mates for ADG. The average phenotypic and genetic correlation between mates for the three calf crops for ADG selection in PAM were .90 and .30, respectively. The same two correlations for RM were .02 and .01, respectively. Because ADG was consistently higher in its heritability, greater genetic correlations occurred, thus allowing a higher frequency of best-to-best matings which acted to further stretch out the population variance.

Effect on Estimated Breeding Value

The two mating systems also caused hard to explain differences in EBV averages for calves, sires and dams. The average EBV for calves are presented in Table 5. Part of the difference in EBV average for the two mating systems may be due to the extra phenotypic variance in YW that PAM has over RM. Sire and dam EBV averages followed the pattern set by the calves, with the difference between the two mating systems increasing over time. At CC10 PAM sires and dams were 25 and 14% higher, respectively, in their EBV average. These differences in sire and dam EBV averages were not caused by differences in number of calves produced by each sire and dam. At CC10 the number of offspring per sire averaged 20.1 and 20.6 under RM and PAM, respectively, while cows averaged 4.2 and 4.1 calves under RM and PAM, respectively.

Even though mating system did effect EBV averages no harmful effect on its use seemed to have occurred. Thus it is safe to assume EBV will be useful regardless of mating system.

TABLE 4. ANALYSIS OF VARIANCE AND LIST OF MEANS FOR
MAIN SOURCES OF VARIANCE IN SIRE TESTING
DATA FOR WW, ADG AND YW.

Source	Category	Calf Crop 4			Calf Crop 7			Calf Crop 10		
		WW	ADG	YW	WW	ADG	YW	WW	ADG	YW
Sire	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
Testing	Within	473.1	2.717	907.7	489.0	2.868	947.8	505.0	3.022	988.4
	Commercial	466.3	2.672	893.9	480.3	2.799	928.2	492.6	2.932	961.8
YW	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
Heritability	20%	463.1	2.615	881.5	473.1	2.696	904.5	479.3	2.764	921.5
	40%	468.2	2.712	902.2	480.4	2.862	938.3	494.0	3.017	976.8
	60%	477.8	2.755	918.7	500.4	2.943	971.2	523.1	3.150	1027.1
Bull	Sig.	.362	.509	.226	.714	.587	.423	.332	.217	.094
Combination	0/6	468.8	2.689	899.0	483.5	2.825	935.5	496.8	2.966	971.3
	2/4	471.4	2.702	903.8	485.3	2.839	939.5	501.0	2.993	979.8
	3/3	468.9	2.692	899.6	485.1	2.837	939.0	498.7	2.973	974.2
Percent	Sig.	.002	.009	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
Heifers Saved	20%	465.5	2.674	893.3	477.2	2.789	923.5	487.9	2.912	953.7
	50%	472.1	2.698	903.8	488.1	2.855	945.0	503.9	3.002	984.1
	80%	471.5	2.711	905.3	488.6	2.856	945.6	504.7	3.018	987.5
Selection	Sig.	<.0005	<.0005	.011	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
Criteria	EBV	474.1	2.685	903.7	494.2	2.812	944.1	511.1	2.931	980.0
	YW	476.9	2.664	903.1	496.2	2.783	941.5	516.4	2.918	983.2
	ADG	458.2	2.734	895.6	463.6	2.906	928.5	469.0	3.082	962.1

TABLE 5. ANALYSIS OF VARIANCE AND LIST OF MEANS FOR
MAIN SOURCES OF VARIANCE FOR EBV IN MATING
SYSTEM DATA AND SIRE TESTING DATA.

Source	Category	CC4	CC7	CC10	Source	Category	CC4	CC7	CC10
Mating	Sig. RM	.030	<.0005	<.0005	Sire	Sig. Within	.633	.002	.428
System	PAM	1.93	1.87	1.92	Testing	Commercial	1.93	1.87	1.92
		2.25	2.50	2.99			1.86	1.39	1.79
YW	Sig.	<.0005	<.0005	<.0005	YW	Sig.	<.0005	<.0005	<.0005
Heritability	20%	2.51	2.84	3.22	Heritability	20%	2.40	2.48	2.84
	40%	2.44	2.78	3.27		40%	2.31	2.14	2.61
	60%	1.31	.94	.89		60%	.96	.27	.13
Bull	Sig.	<.0005	<.0005	<.0005	Bull	Sig.	<.0005	<.0005	<.0005
Combination	0/6	.31	.55	.71	Combination	0/6	.32	.58	.72
	2/4	2.59	2.52	3.01		2/4	2.34	1.91	2.39
	3/3	3.37	3.50	3.65		3/3	3.01	2.40	2.47
Percent Heifers Saved	Sig.	.015	.383	.355	Percent Heifers Saved	Sig.	.345	.016	.060
	20%	1.82	2.15	2.55		20%	1.75	1.35	1.62
	50%	2.35	2.35	2.55		50%	2.00	1.88	2.11
	80%	2.10	2.05	2.27		80%	1.92	1.66	1.85
Selection	Sig.	.012	<.0005	.001	Selection	Sig.	.004	<.0005	<.0005
Criteria	EBV	2.00	2.42	2.52	Criteria	EBV	1.84	2.02	2.32
	YW	2.40	2.49	2.89		YW	2.22	1.78	1.93
	ADG	1.87	1.64	1.97		ADG	1.62	1.09	1.32

Sire Testing Procedures

Effect on Yearling Weight

It is readily evident from data presented in Table 4 that progeny testing in a commercial test herd, as done in this investigation, proved to be unsuccessful at keeping pace in improvement of any trait when compared to progeny testing within the purebred herd. At CC10 the populations utilizing the commercial test herd were 97.3% as heavy as the other sire testing procedure. The same comparison at CC4 was 98.4%, pointing out that the difference between the sire testing procedures increases more rapidly in the first four calf crops because the second calf crop cannot be sired by selected sires. However, the difference between the two procedures continues to increase over all calf crops because of the increased generation interval testing in a commercial test herd brings about.

Effects on Weaning Weight and Average Daily Gain

The component parts of yearling weight reacted similarly to sire testing procedures. When the populations utilizing the commercial test herd were compared to sire testing within the purebred herd, it was found in CC10 that the former was 97.5 and 97.0% as heavy for WW and ADG, respectively. In calf crops 4, 7 and 10 sires in the commercial progeny testing runs were significantly ($P < .01$) lower in their direct genic values for WW, maternal ability (MA) and ADG than were sires in the purebred herd testing procedure. When the dams in

the two sire testing procedures were compared the differences were not as striking, but the populations utilizing the commercial test herd were significantly ($P < .01$) lower in dams' direct genic value for WW, MA and ADG.

In general, the progeny testing of bulls within a commercial test herd, as done in this investigation, would be fruitless when trying to accomplish greater improvement in the performance traits looked at in this study. Modifications to the system, such as: testing fewer bulls (i.e. increasing the first stage selection intensity), using a portion of the selected untested bulls in the purebred herd before their test is completed, or combining progeny test with individual performance, may give more advantageous results.

Yearling Weight Heritability

Effect on Performance Traits

In the three performance traits analyzed yearling weight heritability (YWH) usually accounted for the major portion of the total variance in each trait. As indicated in Tables 3 and 4, the means of different YWH levels always appeared to be significantly different from one another. This also appeared to be true for the genic values of the traits presented in Tables 3 and 4. The only exception to the above statement was genic maternal ability; in that, there was no significant difference in the amount of improvement made in genic MA under the three YWH levels.

In general WW, ADG and YW responded in a linear fashion to increases in YWH. However, WW tended to deviate from linearity due to a larger increase in its heritability when YWH went from 40 to 60%. As shown in Table 2, WW heritability increased from 19.70 to 39.25% when YWH increased from 40 to 60%, whereas, only a 10% increase in WW heritability was used between 20 and 40% YWH. Even though increases in heritability for ADG were about equal across the three YWH levels, the largest increase in amount of improvement made in ADG came between 20 and 40% YWH.

Effect on Estimated Breeding Value and Number of Offspring Per Parent

As explained in the Review of Literature, EBV are expressed as estimated genetic differences from the herd average at one particular time. Thus, the EBV do not give any relative genetic rankings among herds. However, for within herd comparisons, EBV can be used to compare individuals which do not greatly differ in age. Many sources which could significantly effect EBV as a predictor of breeding value have been imposed, but only the ones discussed in sections following have caused changes in EBV averages.

The highest level of YWH caused a highly significant depression in average EBV for calves. As Table 5 indicates, the highest YWH level is significantly lower than either of the lower levels of YWH for calves' average EBV. The 20% level of YWH consistently had the highest EBV average. Sires and dams were just the opposite in the

ranking of EBV averages by YWH level. In CC10 of the mating system analysis the average sire EBV for 20, 40 and 60% YWH were 17.3, 25.6 and 38.2, respectively, while average cow EBV for the YWH levels in the same analysis were 14.7, 24.5 and 34.8, respectively. The differences in EBV averages for sires and dams by YWH level in the sire testing analysis were almost the same as those previously mentioned and, therefore, will not be listed.

Level of YWH significantly ($P \leq .01$) affected the number of calves had by each sire and dam in CC7 and CC10. In the mating system analysis, the number of calves per sire for YWH levels of 20, 40 and 60% in CC10 were 21.3, 20.4 and 19.3, respectively. The number of calves per cow for the same YWH levels in CC10 were 4.3, 4.1 and 4.1, respectively. Although significance ($P < .01$) did exist in number of calves per sire or dam, it is doubted that these differences contributed to the differences seen in EBV averages for the three levels of YWH. One can speculate that an apparent contribution to the differences in average EBV for sires and dams as heritability increases is the higher correlation which exists between individuals and their relatives. But why calves differed from this is not known and cannot be explained.

Bull Combination

Effect on Performance Traits

The different combinations of untested bulls and progeny tested bulls (UT/PT) had no significant effect on the amount of genetic improvement made in YW over time. Even though Table 3 presented a

significant phenotypic difference for YW in CC10, a significant difference in YW genetic ability did not exist in that calf crop. The 2/4 bull combination appeared to bring about more phenotypic YW improvement, however, when the YW genetic abilities for each combination were investigated a nonsignificant difference was found. Although no phenotypic significant difference existed for WW, the 2/4 bull combination became significantly higher than either of the other bull combinations for direct genic value for WW at CC10. Table 3 and 4 further show that the 2/4 bull combination gave the highest averages for the three calf crops and three traits analyzed, with the exception of ADG in CC7 of the mating system analysis.

When the phenotypic variances of WW, ADG and YW were analyzed no significant differences were found between the bull combinations. In fact, the variances for all bull combinations were within one-fourth of one standard deviation for all three traits.

Effect on Estimated Breeding Value

As might be theorized, bull combinations significantly affected EBV average for the calf crop. Because selection of older bulls was based on progeny record, an automatic positive data item was incorporated into the EBV calculation of future offspring of the selected sires. Thus, most of the differences in EBV averages for bull combinations seen in Table 5 are likely due to the differences in PHS data incorporated into the EBV calculation for YW. The number of calves sired by each bull for the bull combinations 0/6, 2/4 and 3/3 in the mating system analysis were 13.5, 20.9 and 24.8, respectively.

Percent Heifer Calves Saved

Effect on Yearling Weight

Percent heifers saved caused more significant differences in the performance traits than any other entity investigated which can be controlled by a breeder. As percent heifer calves saved (PHCS) increased more improvement in YW was realized. Tables 3 and 4 show that most of the phenotypic improvement in YW caused by PHCS was when the replacement rate increased from 20 to 50%. Genetic ability for YW reacted exactly as phenotypic expression did to PHCS, with significance ($P < .01$) existing in the same ranking for the three calf crops analyzed.

Different levels of PHCS also caused significant ($P < .01$) differences to occur in phenotypic and genic variances in CC7 and CC10. In CC10, the 20% level of PHCS had 6 and 15% more phenotypic variance than the 50 and 80% levels, respectively. The same comparison for genic variance was 16 and 28%. This result could be explained by the fact that only the top 20% of the heifer calves are included in the mating population, thus creating a subunit of females in the herd which phenotypically average 1.4 standard deviations above the herd mean. With a 20% replacement rate 8.1 heifer calves will be put into the breeding population each year. With a 5% death loss in cows this allows the culling of only 3.6 cows per year, which is only 4.2% of the 85.5 cows subject to culling. Thus the cows after culling average less than .1 of a standard deviation above the herd mean, therefore, explaining why the substantial differences in variances occurred with the different replacement rates.

Effect on Weaning Weight

The component parts of YW, WW and ADG, were affected in the same way by the different levels of PHCS. Switching PHCS from 20 to 50% accounted for most of the improvement in WW caused by increasing the percent heifers saved. In the three calf crops analyzed, the 80% saving rate was, at the most, 5.7 lbs. heavier in WW than the 50% rate and usually less than 2.0 lbs. heavier. Direct genic value for WW was the highest for the herds incorporating 50 and 80% saving rates, but these two were not significantly different from one another. Level of PHCS did not significantly effect the amount of phenotypic or genic variance in WW.

PHCS proved to have a major effect on improvement of genic maternal ability. The data in Table 6 show that increased heifer saving rates improved MA. However, a leveling off occurred in the mating system analysis and a nonsignificant depression in the sire testing analysis occurred when PHCS changed from 50 to 80%. From the slight improvement gained, it appears the added expense of developing, breeding and calving out an additional 30% of the heifers could not be made economically feasible. This fact will be even more evident when the unadjusted weaning weights for bull calves are compared.

Effect on Average Daily Gain

The effects of PHCS on ADG were similar to what happened for WW. There was no significant difference between 50 and 80% heifer saving rates for phenotypic expression or genic value. Indeed, the

TABLE 6. CALF AVERAGE FOR GENIC MATERNAL VALUES
IN MATING SYSTEM DATA AND SIRE TESTING DATA.

Source	Category	Mating System Analysis			Sire Testing Analysis		
		CC4	CC7	CC10	CC4	CC7	CC10
Percent Heifers Saved	Sig.	.052	.007	.031	.083	.023	.046
	20%	2.3	4.5	8.2	1.5	4.2	6.9
	50%	3.8	8.9	12.5	4.0	8.2	11.4
	80%	5.2	10.0	13.3	4.0	7.6	10.1
Selection Criteria	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	EBV	5.0	10.8	14.4	4.7	9.0	11.9
	YW	7.8	12.7	19.4	6.1	12.0	16.3
	ADG	-1.5	-.1	.1	-1.4	-1.1	.2

TABLE 7. BULL CALF AVERAGE FOR UNADJUSTED WEANING WEIGHT
IN MATING SYSTEM DATA AND SIRE TESTING DATA.

Source	Category	Mating System Analysis			Sire Testing Analysis		
		CC4	CC7	CC10	CC4	CC7	CC10
Percent Heifers Saved	Sig.	<.0005	.002	<.0005	<.0005	<.0005	.003
	20%	455.4	467.2	468.6	456.8	467.8	467.1
	50%	447.8	465.7	481.7	448.2	462.5	477.4
	80%	442.0	458.2	477.7	438.5	454.9	470.0
Selection Criteria	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	EBV	454.6	475.4	490.4	452.7	471.9	484.8
	YW	455.3	476.4	492.5	454.1	473.5	487.0
	ADG	435.4	439.4	445.1	436.8	439.7	442.7

TABLE 8. BULL CALF AVERAGE FOR UNADJUSTED YEARLING WEIGHT
IN MATING SYSTEM DATA AND SIRE TESTING DATA.

Source	Category	Mating System Analysis			Sire Testing Analysis		
		CC4	CC7	CC10	CC4	CC7	CC10
Percent Heifers Saved	Sig.	.074	.001	<.0005	.008	.132	<.0005
	20%	886.0	917.8	938.2	883.0	915.2	932.5
	50%	886.0	932.3	974.8	879.6	918.6	957.8
	80%	880.0	924.9	975.5	872.9	911.7	952.7
Selection Criteria	Sig.	.006	<.0005	.012	.037	<.0005	<.0005
	EBV	888.6	933.2	967.6	881.9	922.4	953.8
	YW	884.5	926.2	965.7	879.8	918.0	953.3
	ADG	878.8	915.6	955.2	873.7	905.0	939.9

TABLE 9. MEANS AND SIGNIFICANCE VALUES OF EBV AND
YW BREEDING VALUES FOR SIRES AND DAMS IN
MATING SYSTEM AND SIRE TESTING DATA.

Source	Selection Criteria	Mating System Analysis			Sire Testing Analysis		
		CC4	CC7	CC10	CC4	CC7	CC10
Mean of Sires' EBV	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	EBV	27.9	29.3	30.2	25.8	25.2	26.0
	YW	26.5	26.4	29.3	25.0	22.0	23.1
	ADG	19.1	18.6	21.5	17.4	15.6	17.2
Mean YW Breeding Value for Sires	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	EBV	947.4	986.5	1025.5	924.8	968.1	1005.4
	YW	930.7	978.4	1028.0	923.2	965.9	1009.1
	ADG	923.7	967.0	1011.6	913.9	949.0	990.1
Mean of Dams' EBV	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	EBV	19.2	26.7	31.0	19.1	26.1	30.1
	YW	16.1	22.3	25.2	15.7	21.6	23.9
	ADG	12.0	15.6	17.9	11.2	14.7	16.4
Mean YW Breeding Value for Dams	Sig.	<.0005	<.0005	<.0005	<.0005	<.0005	<.0005
	EBV	887.0	927.5	965.4	884.1	919.4	953.2
	YW	884.1	924.4	966.7	881.5	918.8	955.3
	ADG	878.3	913.5	954.5	876.1	907.3	942.8

additional heifers saved over 50% in this study gave no beneficial result in the way of increased improvement in ADG. However, both 50 and 80% saving rates were significantly higher in phenotypic and genic value averages than the 20% saving rate.

When the phenotypic and genic variances for ADG were analyzed the results were parallel to those obtained for YW. In the mating system analysis data at CC10, the 20% saving rate had 19% more phenotypic variance and 34% more genic variance than 50 and 80% PHCS. In CC7 the differences were also significant, but not as large. There were no significant differences in CC4 for these two variances.

Effect on Unadjusted Weaning Weight and Yearling Weight

Both analyses in Table 7 show that 20% heifer saving rate was superior in its average unadjusted WW for bull calves in CC4 and CC7 when compared to either 50 or 80% saving rates. However, by CC10 enough additional improvement in direct genic value for WW and MA occurred in the 50 and 80% saving rate populations so that their unadjusted WW averages were superior to the 20% replacement rate. Table 8, which gives the means for unadjusted YW, shows a different reaction to heifer saving rates. Because ADG is not adjusted for age of dam effect, the additional improvement which was made in ADG with the two higher PHCS levels made up for the unadjusted WW depression which occurred in the earlier calf crops. As presented in Table 8, the 80% PHCS level was inferior to 50% on all but one occasion for bull calves.

Heifer calves responded exactly as bull calves did to the three levels of PHCS for both unadjusted WW and YW. But the unadjusted WW for heifer calves was on the average 10% less than bull calves due to adjustment to a common sex basis. Naturally, this 10% difference at weaning time was carried through to the unadjusted YW.

Effect on Generation Interval

Even though PHCS had no significant effect on average calf EBV in the three calf crops analyzed, it did effect the generation interval. As PHCS decreased, the generation interval increased due to a greater number of years the cows were left in production. At CC10 in the mating system analysis, 20, 50 and 80% heifer saving rates averaged 6.1, 3.7 and 2.8 calves per cow, respectively, and in the sire testing analysis the same respective averages were 6.1, 3.6 and 2.8. The overall mean number of offspring per cow for both analyses and the three PHCS levels was 4.2. From the above figures, one can easily calculate an estimated turnover rate for the females. It is equal to the average number of offspring per cow, plus 10% of that value to allow for calf death loss, plus 1.0, which corrects the cows' age to what will happen under normal production schemes, as females in the simulated populations reproduce at one year of age. Therefore, from this method the turnover rates in the mating system data were 7.6, 5.1 and 4.1 years, respectively, for 20, 50 and 80% PHCS.

Even though selection differentials for heifers in the lowest saving rate would be much larger than the other two rates, the selection differential on the mature cows would be extremely small.

Because of this, plus the low turnover rate, the depression in adjusted yearling weights with the low PHCS should be of no surprise. Indeed at the low heifer saving rate one is not taking advantage of the genetic reach one made when the selection of their sires was done. From this data one would not recommend a low heifer saving rate, for it would be wasteful of the genetic trend brought about by the intense selection for the sires. As stated previously, putting 80% of the heifers back into the breeding herd would not be economically feasible because of the additional expenses and small amount of additional improvement made with this larger array of heifers. It is this investigator's estimate that somewhere between 50 and 65 percent heifer calves saved will maximize genetic improvement without an intolerable number of actual pounds lost due to the age of dam adjustment.

Selection Criteria

Effect on Yearling Weight

The selection methods utilized in this investigation highlighted what might be predicted and also brought out problems which may need to be resolved with future research. Tables 3 and 4 show that in this study the most improvement in YW came when selection was made on YW itself or the estimate of its breeding value, EBV. EBV selection consistently gave greater improvement in YW through CC7, but by CC10 YW selection caused heavier weights to occur, although EBV and YW selection never appeared to be significantly different from one another in the three calf crops analyzed. Table 9 presents why these two

selection methods may have switched in their order as time progressed. In all three calf crops of the mating system analysis, EBV selection had the highest sire and dam average for EBV. However, CC10 data in that analysis show that YW selection gave parents which had superior genetic ability for YW. In the sire testing analysis these same differences were even larger. Also to be noted from Table 9 is that cows averaged as high in EBV as sires, even though the intensity of selection was much greater for sires. This indeed points out that a serious bias in female EBV may be occurring; in that, as years go by their individual deviation from herd mean is not readjusted and the records for calves produced in the early part of a cows' production are included in the EBV calculation as deviations from means that are below the genetic mean of the herd at the time the dams are selected. Thus, the EBV of selected females is biased upward in herds that are improving rapidly from one calf crop to the next.

When ADG selection was compared to EBV and YW selection it averaged significantly ($P < .01$) lower in YW improvement. The reason for this is the slow improvement in WW.

Selection criteria caused no significant change in the amount of phenotypic or genic YW variance. EBV selection did, however, consistently give populations with the most phenotypic and genic YW variance.

Effect on Weaning Weight

ADG selection gave slower improvement in YW than either EBV or YW selection. The main cause of this slower improvement was the

extremely slow correlated improvement in direct genic value for WW. Tables 3 and 4 show that by CC4 YW and EBV selected populations averaged approximately 20 lbs. higher than ADG selected populations in their WW performance. Of course, the main reason why this is occurring is that WW is a component part of YW. When selection is practiced on either YW or EBV a great deal more selection pressure is placed on direct genic value for WW than when selection is by ADG. Also suffering heavily when ADG selection is employed is MA. Since no correlation existed between ADG and MA, the latter neither increased nor decreased as ADG increased (Table 6). Due to the large deficit these two aspects summed up to, selection by ADG did not result in substantial enough improvement in ADG over YW and EBV selection to make it a competitive way to optimize improvement in YW.

The greatest amount of correlated improvement in genic value for WW was when YW selection was practiced (Table 3 and 4). However, YW and EBV selection appeared not to be significantly different. Selection criteria affected genic value for MA the same way it did phenotypic and genic values for WW. YW selection, as seen in Table 6, gave the largest improvement in genic value for MA, while EBV selection improved it at a slower rate and ADG selection caused no change.

Selection criteria brought about no significant changes for either phenotypic or genic variances in WW. In CC4 and CC7, YW selection was lower in its phenotypic and genic variance than the other two selection criteria, but in CC10, YW selection was intermediate in its variances.

Effect on Average Daily Gain

As should be expected, ADG selected populations had the greatest amount of improvement in ADG. In the mating system analysis (Table 3), ADG selected populations at CC10 averaged .22 lbs. per day higher than EBV and YW selected populations, while in the sire testing analysis (Table 4), ADG selected populations averaged .16 lbs. per day higher than those selected on EBV and YW. Without doubt, if ADG is the single, utmost important trait to improve in the beef industry, then selection by ADG or by an estimated breeding value of it is the route one should follow to the highest degree. However, as previously mentioned, ADG selection will not bring about optimum improvement in yearling weight because of its downfall in increasing performance up to weaning time. EBV and YW selection did not differ significantly in their improvement rates for ADG.

As with the previous performance traits, selection criteria did not affect the amount of phenotypic or genic variance in ADG.

Effect on Unadjusted Weaning and Yearling Weights

Unadjusted WW for bull and heifer calves responded to selection criteria exactly as adjusted WW did. Even though YW and EBV selection appear not to be significantly different from one another in unadjusted WW, Table 7 shows that YW selected populations were consistently higher than EBV selected populations. YW and EBV selected populations were significantly ($P < .01$) superior in unadjusted WW performance when compared to ADG selected populations. This last statement also held true for unadjusted YW, thus making YW and EBV selection the most desirable for improving actual weight at one year of age.

Effect on Estimated Breeding Value

Selection criteria had a major impact on calf crop averages for EBV. As Table 5 presents, EBV and YW selection in both the mating system and sire testing analyses gave consistently higher calf crop averages for EBV than did ADG selection. The way YW and EBV selected populations ranked in EBV average differed for the two analyses. In the mating system analysis, YW selected populations were higher in EBV average than those using EBV selection, whereas in CC7 and CC10 of the sire testing analysis, EBV selected populations were higher than those selected by YW methods. When EBV averages for sires and dams were analyzed the same pattern of events that were described above occurred. It is likely a lower correlation between ADG and estimated breeding value for YW existed, thus causing ADG selection to average lower in calf crop EBV. At this time, the relevance of this to genetic improvement is indeed questionable.

Selection criteria had a highly significant ($P < .01$) effect on the number of offspring per sire and dam. The number of calves per sire and dam in both analyses averaged higher for EBV selection than for either ADG or YW selection. The average number of calves per sire for EBV, YW and ADG selection in the mating system analysis were 22.0, 19.4, and 19.6, respectively, while in the sire testing analysis the same respective averages were 22.5, 18.1 and 18.5. The two analyses averaged the same for number of calves per cow, with EBV, YW and ADG selection averaging 4.4, 4.1 and 4.0, respectively. Indeed it appears that selection by EBV will tend to keep a cow in the breeding herd for

close to a half year more than YW or ADG selection. This further emphasizes the point made earlier about the bias in EBV calculation for older cows; in that, the cows' individual deviation from the herd mean and the performance of offspring in past calf crops for YW tends to bias the EBV upward, thus making the retention period for females in the breeding herd longer.

General

In short, it appears that either EBV or YW selection will maximize improvement in most of the performance traits. Although only small differences exist between EBV and YW selection, most of these lie in favor of YW selection, thus making it slightly more favorable in maximization of performance improvement. If modifications to individual deviation from herd mean could be employed, EBV selection may show up as a more desirable tool for selection. However, when the deviation from the herd mean for an old animal is considered to be equal to an individual deviation from the current herd mean, serious biases result and consequently inaccurate culling of animals takes place.

Interactions Between Main Sources of Variance

Mating System and Yearling Weight Heritability

When the analysis of the mating system data was done this interaction appeared to affect both ADG and EBV. For ADG, mating system did not interact with YW heritability (YWH) in CC4, but the level of significance was .037 for CC7 and .025 for CC10. The same

interaction was significant in CC7 and CC10 for genic value for ADG. Table 10 shows that the interaction in ADG occurs because PAM responds better to the highest heritability level for YW. For YWH levels 20 and 40%, ADG was equal in both mating systems, however, with 60% YWH, ADG averaged .07 lbs. per day higher in PAM than RM. This interaction was also noted in CC10 of the analysis of genic value for ADG variance. At the 60% level of YWH, PAM had 28% more genic variance than RM at the same heritability, whereas at the other two levels RM and PAM were within 10% of one another.

In CC4 and CC10, mating system significantly ($P < .01$) interacted with YWH for calf crop EBV average. Table 11 shows that when YWH increased from 40 to 60% a much greater reduction in EBV average occurred with the RM populations than with PAM populations. To properly explain why this situation developed, an investigation of the component parts used in calculating EBV would be required. Because these data items were not collected no solution will be offered, but the fact that the same significant ($P < .05$) interaction existed in the three calf crops analyzed for sire and dam EBV averages will be added to strengthen the evidence that there was an interaction between mating system and YWH. The relevance of this to performance trait improvement and the ramifications it may have are unknown at this time. However, it is an occurrence which breeders should be aware of, but one which will have no major impact on improvement programs. The EBV is not an end to a mean, but an aid, which, when properly put into perspective, can be extremely helpful in the selection of superior genetic stock within a population. It is pertinent for breeders to

TABLE 10. ADG MEANS FOR MATING SYSTEM AND YW HERITABILITY SUBCLASSES.

		20%	40%	60%	Marginal Means
RM	CC4	2.63	2.74	2.78	2.72
	CC7	2.72	2.90	2.99	2.87
	CC10	2.78	3.07	3.22	3.02
PAM	CC4	2.63	2.74	2.82	2.73
	CC7	2.71	2.92	3.06	2.90
	CC10	2.80	3.08	3.31	3.06
Marginal Means	CC4	2.63	2.74	2.80	2.72
	CC7	2.71	2.91	3.03	2.88
	CC10	2.79	3.07	3.26	3.04

TABLE 11. EBV MEANS FOR MATING SYSTEM AND YW HERITABILITY SUBCLASSES.

		20%	40%	60%	Marginal Means
RM	CC4	2.66	2.34	.78	1.93
	CC7	2.70	2.42	.49	1.87
	CC10	2.86	3.00	-.09	1.92
PAM	CC4	2.37	2.54	1.85	2.25
	CC7	2.97	3.15	1.38	2.50
	CC10	3.58	3.54	1.87	2.99
Marginal Means	CC4	2.51	2.44	1.31	2.09
	CC7	2.84	2.78	.94	2.18
	CC10	3.22	3.27	.89	2.46

remember that different selection intensities, turnover rates and YWH levels can cause major changes to occur in population means for EBV.

Sire Testing and Yearling Weight Heritability

This interaction occurred in CC10 for both ADG and YW. The significance level for both performance traits was .016. Table 12 shows why in CC10 this significant interaction occurred in ADG and YW. The interaction was caused by a greater increase in both ADG and YW as YWH increased for the case of within purebred herd sire testing than for sire testing in a commercial test herd. At the low level of heritability, progeny testing within the purebred herd proved to be below its expected value based on the marginal means. When the YWH was 60%, within purebred herd sire testing exceeded its expectation and sire testing within a commercial test herd fell short of its expectation. Indeed these results back up what has been theorized; that is, as heritability of the trait increases, there is less advantage in progeny testing of males before their inception into the purebred herds.

Sire Testing and Percent Heifer Calves Saved

The interaction of these two independent variables occurred in YW and unadjusted YW. For the former trait, the interaction was significant ($P \leq .01$) in CC10, while it was significant ($P < .05$) in both CC7 and CC10 for unadjusted YW. The interaction was the result of

TABLE 12. ADG AND YW MEANS IN CALF CROP 10 FOR SIRE TESTING AND YW HERITABILITY SUBCLASSES.

	ADG	20% YW	ADG	40% YW	ADG	60% YW	Marginal ADG	Means YW
Within	2.78	928.6	3.07	991.1	3.22	1045.5	3.02	988.4
Commercial	2.74	914.5	2.97	962.4	3.08	1008.6	2.93	961.8
Marginal Means	2.76	921.5	3.02	976.8	3.15	1027.1	2.98	975.1

TABLE 13. YW AND UNADJUSTED YW MEANS IN CALF CROP 10 FOR SIRE TESTING AND PERCENT HEIFER CALVES SAVED SUBCLASSES.

	YW	20% U.YW	YW	50% U.YW	YW	80% U.YW	Marginal YW	Means U.YW
Within	960.0	939.1	1000.1	973.5	1005.1	970.2	988.4	960.9
Commercial	947.4	925.9	968.1	942.1	970.0	935.3	961.8	934.4
Marginal Means	953.7	932.5	984.1	957.8	987.5	952.7	975.1	947.6

within purebred herd sire testing responding to increased heifer saving rates more than sire testing within a commercial test herd (Table 13). The difference between sire testing within the purebred herd and in the commercial test herd was less at 20% PHCS than at 50 or 80% PHCS.

The two interactions reported on sire testing, indeed, reinforce the thinking that in order for extensive progeny testing of future sires to be warranted, heritability of the trait must be low and heifer saving rates limited because of costs or facilities necessary for maintaining the replacements before their inception into the productive herd.

Yearling Weight Heritability and Selection Criteria

Interaction between these independent variables occurred consistently in WW, ADG and unadjusted WW in both analyses and in all three calf crops analyzed. This interaction also occurred for MA in CC7 and CC10 of the mating system analysis. Mating system analysis data are presented in Table 14 to show that ADG selected populations did not respond as much to YWH increases as EBV and YW selected populations responded. CC4 and CC7 data were the same as CC10, only the degree of difference was not as great. As should be expected, unadjusted WW for bull and heifer calves responded in the exact manner adjusted WW did.

This interaction was highly significant ($P < .01$) for ADG in both mating system and sire testing analyses for the three calf crops

TABLE 14. WW AND MA MEANS IN CALF CROP 10 FOR YW
HERITABILITY AND SELECTION CRITERIA FOR
MATING SYSTEM DATA.

	EBV		YW		ADG		Marginal	Means
	WW	MA	WW	MA	WW	MA	WW	MA
20%	488.0	11.9	497.7	22.5	461.0	-2.3	482.2	10.7
40%	514.5	20.9	516.8	18.5	470.2	-.4	500.5	13.0
60%	547.7	10.5	549.8	17.2	481.9	3.2	526.5	10.3
Marginal Means	516.7	14.4	521.4	19.4	471.0	.1	503.1	11.3

TABLE 15. ADG MEANS FOR THE INTERACTION OF YW
HERITABILITY WITH SELECTION CRITERIA
FOR MATING SYSTEM DATA.

		EBV	YW	ADG	Marginal Means
20%	CC4	2.64	2.60	2.65	2.63
	CC7	2.71	2.68	2.74	2.71
	CC10	2.76	2.77	2.85	2.79
40%	CC4	2.71	2.71	2.80	2.74
	CC7	2.87	2.83	3.02	2.91
	CC10	2.99	2.99	3.24	3.07
60%	CC4	2.80	2.73	2.88	2.80
	CC7	3.00	2.93	3.16	3.03
	CC10	3.18	3.14	3.47	3.26
Marginal Means	CC4	2.72	2.68	2.78	2.72
	CC7	2.86	2.81	2.97	2.88
	CC10	2.98	2.96	3.19	3.04

investigated. Table 15, with data from the mating system analysis, shows ADG selection gave more improvement in ADG than either EBV or YW selection as YWH increased. It is of interest to note that EBV and YW selection were almost identical in the amount of improvement they caused in ADG at all levels of YWH. Data from the sire testing analysis for this interaction were a replicate of mating system data, except the results of ADG selection were not as drastically different from EBV and YW selection.

Yearling Weight Heritability and Percent Heifer Calves Saved

These two independent variables interacted to a significant degree in YW ($P < .01$) and ADG ($P < .05$) in the three calf crops analyzed. However, this interaction was significant only in the mating system analysis. Table 16 shows that linear increases in improvement occurred across PHCS levels with YWH levels of 20 and 40%. But, with the 60% level of YWH, a leveling off occurred in ADG and YW when PHCS changed from 50 to 80%.

Significance of this interaction in WW was sporadic with no set pattern occurring in the parts comprising the makeup of WW. The interaction was significant in CC7 and CC10 for direct genic value of WW, but significant for WW phenotype only in CC7. Significance ($P < .05$) for MA occurred only in CC4 and this was due to a negative response as PHCS increased with the heritability level at 60%, whereas with the other YWH levels MA increased as PHCS increased. Direct genic value and phenotypic averages for WW responded to increases

TABLE 16. ADG AND YW MEANS FOR YW HERITABILITY AND PERCENT HEIFER CALVES SAVED IN MATING SYSTEM DATA.

		20%		50%		80%		Marginal Means	
		ADG	YW	ADG	YW	ADG	YW	ADG	YW
20%	CC4	2.62	880.6	2.63	884.1	2.64	889.6	2.63	884.8
	CC7	2.67	895.0	2.72	909.7	2.75	921.6	2.71	908.8
	CC10	2.72	907.3	2.80	932.3	2.85	946.9	2.79	928.9
40%	CC4	2.68	893.7	2.76	910.3	2.78	921.7	2.74	908.6
	CC7	2.81	923.7	2.94	953.5	2.96	965.7	2.91	947.7
	CC10	2.94	956.6	3.10	999.4	3.17	1019.7	3.07	991.9
60%	CC4	2.78	916.3	2.83	936.9	2.80	927.1	2.80	926.8
	CC7	2.96	963.0	3.09	1009.4	3.03	992.0	3.03	988.1
	CC10	3.15	1011.4	3.33	1069.1	3.31	1065.5	3.26	1048.7
Marginal Means	CC4	2.69	896.9	2.74	910.4	2.74	912.9	2.72	906.7
	CC7	2.81	927.2	2.92	957.6	2.92	959.7	2.88	948.2
	CC10	2.94	958.5	3.08	1000.3	3.11	1010.7	3.04	989.8

TABLE 17. ADG MEANS FOR YW HERITABILITY AND BULL COMBINATIONS IN MATING SYSTEM DATA.

		0/6 ^a	2/4	3/3	Marginal Means
20%	CC4	2.64	2.61	2.63	2.63
	CC7	2.69	2.70	2.75	2.71
	CC10	2.77	2.78	2.83	2.79
40%	CC4	2.73	2.74	2.15	2.74
	CC7	2.90	2.90	2.92	2.91
	CC10	3.05	3.10	3.06	3.07
60%	CC4	2.80	2.84	2.77	2.80
	CC7	3.03	3.05	3.00	3.03
	CC10	3.27	3.29	3.23	3.26
Marginal Means	CC4	2.72	2.73	2.72	2.72
	CC7	2.87	2.88	2.89	2.88
	CC10	3.03	3.06	3.04	3.04

^aFirst number indicates the number of progeny tested sires utilized and the second number indicates the number of untested bulls.

in YWH and PHCS in the same manner. For YWH levels 20 and 40%, WW increased as PHCS increased, however, at 60% YWH, WW increased when PHCS increased from 20 to 50% and then leveled off.

The interaction was the same in all three calf crops for ADG. Increases in ADG phenotype and genic value were realized as PHCS increased with the lower two YWH levels. However, when YW was 60% heritable, the 50% heifer saving rate was superior to the 80% rate as presented in Table 16.

Yearling Weight Heritability and Bull Combination

The only trait influenced by this interaction was ADG in the mating system analysis. The significance of this interaction for ADG phenotype in CC4, CC7 and CC10 was .018, .045 and .069, respectively. For genic value the significance levels for the same three calf crops were .012, .068 and .049, respectively. Table 17 shows that at low YWH more improvement in ADG is made when more progeny tested bulls are incorporated into the breeding system. However, at the highest YWH, the use of fewer progeny tested bulls enhanced the rate of improvement. This supports the theory of keeping generation interval at a minimum when heritability of the trait is high, thus causing the accuracy of breeding value estimation based on own performance to be at a high level.

Selection Criteria and Percent Heifer Calves Saved

Significance ($P < .05$) for this interaction occurred only in ADG for the mating system data. As might be expected, this interaction

occurred because ADG selection responded to the levels of PHCS to a greater degree than EBV and YW selected populations. With EBV selection, the average improvement in ADG, when saving rate went from 20 to 80%, was .08 lbs. per day. YW selection also had an average improvement rate of .08 lbs. per day in ADG, but ADG selected populations averaged .20 lbs. per day improvement in ADG as heifer saving rate went from 20 to 80%. It was noted from the analysis, that of the .20 lbs. per day improvement, 87% occurred when PHCS increased from 20 to 50%.

General

In brief, many interactions between the independent variables occurred, but in most instances there was simply a change in the differences among responses to the major effects. Thus, major changes in the ranking of cases in the independent variables were seldom. The only change in ranking monitored by a significant interaction effect was between YWH and bull combinations. In this case, as YWH increased a faster turnover rate in bulls became more desirable for greater genetic gains in ADG.

CONCLUSIONS

It is pertinent that a breeder of any purebred livestock be competent in aspects of animal breeding which he can control. This investigation was set up to include different alternatives which could be used by breeders of beef cattle. Indeed, at the outset of the investigation it was known that certain options would not maximize genetic improvement, however, inclusion of them was deemed necessary if perspectives for the other options were to be established. Even though this simulation is not exactly parallel to production schemes occurring today, it is thought that results obtained in this study can be used as guidelines to steer a breeder from unnecessary wrong practices, which might jeopardize his long-term goals of performance improvement.

When the two mating systems, random mating (RM) and positive assortative mating (PAM), were compared, few advantages were found in favor of PAM. PAM populations were significantly lower than RM populations in average phenotype and direct genic value for weaning weight (WW) in the three calf crops analyzed. However, PAM did cause significantly greater gains in genetic improvement for average daily gain (ADG). But the .04 lbs. per day for 160 days was not great enough to overcome the WW deficit which PAM populations suffered, thus not giving PAM populations significantly superior performance at one year of age.

When phenotypic and genic variances were compared for the two mating systems, it was found that PAM caused significantly more

phenotypic and genic variance to occur in ADG than RM. However, there was no difference between the two mating systems in the amount of variance for either WW or yearling weight (YW). These facts point out that a purebred breeder should not spend a great deal of time in assorting his breeding population. However, the results still pointed out that proper evaluation of breeding values are necessary for optimization of genetic improvement.

The use of a commercial test herd to progeny test performance tested bull calves before their use in the purebred herd proved to be fruitless in this investigation, especially when yearling weight heritability rose above 20%. When a trait is measurable and moderate to high in heritability, as were the traits (ADG and YW) in this investigation, then the use of mass selection proved to give greater genetic improvement than requiring a progeny test on bulls before they are used. Possibly by incorporating performance tested bull calves in the sire ranks before progeny test data is available will make a modified progeny testing method more competitive than the system utilized in this study.

The combinations of performance, progeny tested (within the purebred herd) and performance, non-progeny tested bulls were not significantly different in the amount of improvement they caused in genetic ability for WW, ADG and YW. However, in practically all calf crops analyzed the combination of two performance, progeny tested and four performance, non-progeny tested bulls was highest for phenotypic average of WW, ADG and YW, thus giving partial evidence that the fastest possible bull turnover rate is not the best for optimization

of genetic improvement. Different bull combinations caused no changes in genic or phenotypic variance to occur.

One of the major findings in this study was the tremendous impact heifer retention rate had on the improvement of genetic ability for the measured performance traits. The 50 and 80% levels of percent heifer calves saved (PHCS) caused significantly greater genetic and phenotypic gains in all performance traits investigated when compared to the 20% level. The levels of PHCS with the lowest selection differentials gave more genetic and phenotypic gains than did the PHCS level with the highest selection differential. In most cases, the 80% level was not significantly different from 50% PHCS, thus not warranting the extra expenses involved in saving an additional 30% of the heifers. The superiority of the 50 and 80% PHCS populations was especially pronounced in the averages for genic maternal ability.

The weaning weights and yearling weights, not adjusted for the age of dam effect, were compared for the three levels of heifer saving rate. In the data analyzed, the 20% level was higher than 50 and 80% levels in unadjusted WW through calf crop 7. However, by CC10 the greater improvement in direct genic value for WW and maternal ability caused the 50 and 80% levels of PHCS to exceed the 20% level in unadjusted WW. The 50 and 80% heifer saving rates were also superior to 20% PHCS for unadjusted YW because of the greater genetic gains made in ADG.

As was expected, PHCS levels had a major effect on generation interval. The average cow age for 20, 50 and 80% PHCS were 7.6, 5.1 and 4.1 years, respectively.

In evaluating the effect on WW the data show that the EBV and YW selected populations were 45.7 and 50.4 lbs. heavier, respectively, than ADG selected populations in average calf WW for calf crop 10 of the mating system data. The same figures for the sire testing data were 42.1 and 47.4 lbs., respectively.

Selection of the basis of ADG had no significant effect in genic maternal ability, while selection for EBV or YW significantly increased genic maternal ability by calf crop 4. ADG selected populations were significantly superior in ADG improvement to those populations utilizing EBV and YW selection. Selection criterion, however, did not significantly affect the amount of phenotypic or genic variance in ADG.

EBV selection increased the number of years a cow stayed in production. This was due to the fact that individual deviation from the herd mean for a cow at the time she was a calf was used as a constant in her EBV calculation, along with, paternal and maternal half sib average performance and progeny performance if available. The average genetic ability of a herd increased with each new calf crop, but the individual deviations for the older cows were still taken as deviations from the mean of their calf crop which was lower than for cows in later calf crops.

Many interactions occurred between the independent variables. The seven interactions reported on were the following: mating system and yearling weight heritability (YWH), sire testing and YWH, sire testing and PHCS, YWH and selection criteria, YWH and PHCS, YWH and bull combination, and selection criteria and PHCS. All but one of

the significant interactions reported were of the type where the differences among the means due to one main effect increased as the level of another main effect changed. Thus, few changes of the rankings of the means occurred. The only interaction which had a switch in the ranking of the means was bull combination and YWH. When YWH was low more improvement in ADG was made when more progeny tested bulls were incorporated, whereas with the highest YWH, the use of fewer progeny tested bulls enhanced the rate of improvement.

In general, the interactions were not alarming in their effect on performance improvement. Five of the seven interactions involved YWH, which, as every breeder should know, cannot be significantly altered or controlled, thus lowering the importance of those interactions involving it. The two interactions not involving YWH were simple increased response as another source of variance changed.

SUMMARY

The data used in this study were collected from the simulation of approximately 295,000 animals. A biological model was used to simulate the performance of animals based on genic effects from the parents, Mendelian sampling and environmental effects. All selection and mating decisions were accomplished by the use of different computer programs.

Two different mating systems, random mating and phenotypic positive assortative mating, were compared, along with two bull testing procedures, testing within the purebred herd and testing within a commercial test herd. Also included as independent variables in the study were three levels of yearling weight heritability, 20, 40 and 60%, three different bull combinations, 0 progeny tested and 6 non-progeny tested, 2 progeny tested and 4 non-progeny tested, and 3 progeny tested and 3 non-progeny tested, three levels of percent heifer calves saved, 20, 50 and 80%, and three selection criteria, EBV, YW and ADG. When selection was on YW and ADG, the bull and heifer calves were selected on their phenotypic expression, however, the older bulls and cows, which had produced offspring, were selected totally on progeny averages.

Traits investigated in the study were phenotypic and genic means and variances for weaning weight, average daily gain and yearling weight for calves, sires and dams. Also included in the array of data items summarized were EBV averages for calves, sires and dams, plus progeny means for sires and dams and average number of offspring per parent. Genetic and phenotypic correlations between mated parents

for average daily gain and yearling weight, plus the correlation between EBV's of mated parents were analyzed.

The analysis of variance was done in two parts. One procedure analyzed the two mating systems and the four factorialized sources of variance, while the second procedure analyzed the two sire testing procedures and the four factorialized sources of variance.

Random mating (RM) and phenotypic positive assortative mating (PAM) were not significantly different in the amount of improvement they caused in YW over ten calf crops. PAM caused an insignificant increase in phenotypic and genic variance for calf YW. The phenotypic correlation for YW between mated individuals was .88 for PAM populations, as compared to -.06 for RM populations. Even though the difference in YW genetic correlation for the two mating system was still significant ($P < .01$), it was much smaller, .16 for PAM versus -.06 for RM.

Superior genetic and phenotypic gains in ADG were made with PAM over RM. At calf crop 10, PAM populations averaged .04 lbs. per day higher than RM populations in ADG. Furthermore, PAM caused significantly greater variance in both genic values and phenotypes than RM at calf crops 4 and 10. The average phenotypic and genetic correlations between mates for the three calf crops for ADG selection in PAM were .90 and .30, respectively, while in RM populations the same respective figures were .02 and .01.

PAM was significantly higher in its EBV average for calves, sires and dams. At calf crop 10, PAM populations were 56% higher in their

calf EBV averages, however, this seemed to have no detrimental effect on the use of EBV as a selection tool for improvement of yearling performance.

Sire testing within a commercial test herd, as done in this investigation, was inferior to sire testing within the purebred herd for genetic improvement of all performance traits monitored. At calf crops 4 and 10, the populations utilizing the commercial test herd were 98.4 and 97.3%, respectively, as heavy as the other sire testing procedure at yearling time. In calf crop 10, the populations utilizing the commercial test herd were 97.5 and 97.0% as heavy for WW and ADG, respectively, when compared to testing within the purebred herd.

The means for the three levels of yearling weight heritability (YWH), for all performance traits monitored, appeared to be significantly different from one another. Genic maternal ability was the only trait which was not affected by YWH. WW, ADG and YW responded in a linear fashion to increases in YWH.

The highest level of YWH caused an unexplainable significant depression in average EBV for calves. The average EBV for sires and dams was affected just the opposite by YWH. In calf crop 10 of the mating system analysis, the average sire EBV for 20, 40 and 60% YWH were 17.3, 25.6 and 38.2, respectively, while cows averaged 14.7, 24.5 and 34.8, respectively, for the same YWH levels.

The different bull combinations tested in this study caused no significant change in the amount of genetic improvement made in YW over time. However, data were presented to show that the combination

of 2 progeny, performance tested and 4 non-progeny, performance tested bulls gave the highest averages for the three calf crops and three traits analyzed, with the exception of ADG in calf crop 7 of the mating system analysis. The 2/4 bull combination became significantly higher than either of the other bull combinations for direct genic value for WW at calf crop 10. No significant differences were found in phenotypic variances for WW, ADG and YW for the different bull combinations investigated.

The heifer saving rate had a positive effect on YW improvement as percent retained increased. Fifty and 80% heifer saving rates were significantly ($P < .01$) greater in YW improvement than the 20% retention rate. Switching the percent heifer calves saved (PHCS) from 20 to 50% accounted for most of the improvement in WW caused by keeping more heifers in the breeding population. Direct genic value for WW was the highest for the herds incorporating 50 and 80% replacement rates. However, level of PHCS had no effect on phenotypic or genic variance in WW.

As PHCS increased, the genic maternal ability increased, however, a leveling off occurred in the mating system analysis and a non-significant depression in the sire testing analysis occurred when PHCS changed from 50 to 80%.

The two higher levels of PHCS did not differ significantly from one another in the amount of ADG improvement, however, both were significantly superior to 20% PHCS in phenotypic and genic value averages. The 20% saving rate had 19% more phenotypic variance and 34% more genic variance than 50 and 80% PHCS at calf crop 10 of the mating system analysis.

The unadjusted WW was higher for the 20% PHCS level through calf crop 7. However, by calf crop 10 enough improvement in direct genic value for WW and maternal ability occurred in the 50 and 80% saving rate populations so that their unadjusted WW averages were superior to the 20% level. The unadjusted YW averages were significantly higher for 50 and 80% levels of PHCS than for 20% at calf crop 7.

PHCS levels had a major effect on the generation interval. At calf crop 10 in the mating system analysis, 20, 50 and 80% heifer saving rates averaged 6.1, 3.7 and 2.8 calves per cow, respectively, which gave calculated cow turnover rates of 7.6, 5.1 and 4.1 years, respectively, for 20, 50 and 80% PHCS.

Selection by YW or EBV caused the most improvement in YW. EBV selection consistently gave greater improvement than YW selection through calf crop 7. But by calf crop 10, YW selection gave heavier calf YW, however, neither was significantly different from the other.

A possible, serious bias in female EBV was pointed out. The EBV of a selected female is biased upward in herds that are rapidly improving in performance. This occurs because the females' individual deviation from herd mean was not readjusted, plus the fact that the records for calves produced in the early part of a cows' productive life are included in the EBV calculation as deviations from herd means that are below the herd genetic mean at the time of dam selection.

YW selection caused the greatest amount of correlated improvement in genic value for WW. However, it was not significantly greater than

EBV selection in either phenotype or genic value for WW. YW selection also gave the greatest amount of improvement in genic maternal ability, with EBV selection slightly below it.

ADG selection caused the greatest improvement in ADG to occur. ADG selected populations for both analyses averaged .19 lbs. per day higher than EBV and YW selected populations. EBV and YW selected populations did not differ significantly in their improvement rates for ADG.

Many interactions between the independent variables occurred, however, five of the seven discussed in the thesis involved yearling weight heritability (YWH). One of these was the interaction of mating system and YWH for ADG in calf crops 7 and 10. For YWH levels 20 and 40%, ADG was equal in RM and PAM, however, with 60% YWH, ADG averaged .07 lbs. per day higher in PAM than RM.

Sire testing interacted with YWH in calf crop 10 for both ADG and YW. A greater increase in both ADG and YW occurred as YWH increased for the case of within purebred herd sire testing than for sire testing in a commercial test herd. Sire testing also interacted significantly with PHCS for YW and unadjusted YW in calf crop 10. The interaction was the result of within purebred herd sire testing responding to increased PHCS levels more than sire testing within a commercial test herd.

YWH interacted significantly with selection criteria in WW, ADG and unadjusted WW in both analyses and in all three calf crops analyzed. Also it occurred for genic maternal ability in calf crops

7 and 10 of the mating system analysis. The cause of the interaction was that ADG selected populations did not respond as much to YWH increases as EBV and YW selected populations for traits mentioned. This interaction also occurred in the mating system analysis for ADG. ADG selection gave more improvement in ADG than either EBV or YW selection as YWH increased.

The interaction of YWH and PHCS was significant for YW and ADG in all three calf crops of the mating system data. Improvement increased linearly across PHCS levels with 20 and 40% YWH, however, with the 60% level of YWH, a leveling off occurred in ADG and YW when PHCS changed from 50 to 80%. Significance of the interaction, with the same action as described in the previous sentence, occurred in genic value for WW in calf crops 7 and 10, but only in calf crop 7 for WW phenotype.

The final independent variable YWH interacted with was bull combination. This interaction influenced ADG in the mating system analysis. At low YWH more improvement in ADG was made when more progeny tested bulls were incorporated into the breeding system. However, at the highest YWH level the use of fewer progeny tested bulls enhanced the rate of improvement.

The last interaction discussed was between selection criteria and PHCS. It was significant for ADG in the mating system data. EBV and YW selected populations had an average improvement in ADG of .08 lbs. per day when PHCS increased from 20 to 80%, while ADG selected populations improved .20 lbs. per day as PHCS went from 20 to 80%.

APPENDIX A

Method of Calculating CWG1 and CWG2

CWG1 and CWG2 are multiplicative factors used in BPAM and BTHS to give a genetic correlation of 0.25 between WW and ADG. CWG1, as used in this simulation, is equal to the covariance between WW and ADG at the specified heritabilities divided by the genic standard deviation for WW. CWG2 is then equal to the square root of the genic variance in ADG minus CWG1 squared.

What follows next will be a step-by-step display of how CWG1 and CWG2 were calculated when heritability of yearling weight was equal to 0.2. First formulas and then a numerical example.

FORMULAS:

$$1) \sigma_{WW,ADG} = \gamma_{WW,ADG} \cdot \sqrt{\sigma_{WW}^2 \cdot \sigma_{ADG}^2}$$

$$2) CWG1 = \sigma_{WW,ADG} / \sigma_{WW}$$

$$3) CWG2 = \sqrt{\sigma_{ADG}^2 - (CWG1)^2}$$

NUMERICAL EXAMPLE:

$$1) \sigma_{WW,ADG} = 0.25 \cdot \sqrt{(15.37043)^2 \cdot (.13304)^2}$$

$$2) CWG1 = 0.51123 / 15.37043$$

$$3) CWG2 = \sqrt{(.13304)^2 - (.03326)^2}$$

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