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Cynthia M. Wood
Iowa State University

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APPLICATION OF MIXED MODEL METHODOLOGY TO THE EVALUATION OF PERFORMACE TESTED BOARS

Iowa State University  

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Application of mixed model methodology
to the evaluation of performance tested boars

by

Cynthia M. Wood

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Animal Science
Major: Animal Breeding

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Signature was redacted for privacy.

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For the Graduate College

Iowa State University
Ames, Iowa

1986

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>LITERATURE REVIEW</td>
<td>2</td>
</tr>
<tr>
<td>Test Stations</td>
<td>2</td>
</tr>
<tr>
<td>Parameter Estimates</td>
<td>5</td>
</tr>
<tr>
<td>Methodology</td>
<td>5</td>
</tr>
<tr>
<td>Selection index</td>
<td>5</td>
</tr>
<tr>
<td>Mixed models</td>
<td>7</td>
</tr>
<tr>
<td>Models</td>
<td>9</td>
</tr>
<tr>
<td>Accuracy</td>
<td>10</td>
</tr>
<tr>
<td>Fixed effects</td>
<td>12</td>
</tr>
<tr>
<td>Common environmental effects</td>
<td>13</td>
</tr>
<tr>
<td>Genetic ties</td>
<td>15</td>
</tr>
<tr>
<td>Use of the relationship matrix</td>
<td>15</td>
</tr>
<tr>
<td>Application of mixed models to swine evaluation</td>
<td>19</td>
</tr>
<tr>
<td>MATERIALS AND METHODS</td>
<td>20</td>
</tr>
<tr>
<td>Test Station Survey</td>
<td>20</td>
</tr>
<tr>
<td>Parameter Estimates</td>
<td>21</td>
</tr>
<tr>
<td>Animal Model with Relationships</td>
<td>23</td>
</tr>
<tr>
<td>Measure of Variability</td>
<td>26</td>
</tr>
<tr>
<td>Changes in Accuracy Due to Estimation of Fixed Effects</td>
<td>27</td>
</tr>
<tr>
<td>Designs</td>
<td>29</td>
</tr>
<tr>
<td>Programs</td>
<td>33</td>
</tr>
<tr>
<td>RESULTS AND DISCUSSION</td>
<td>34</td>
</tr>
<tr>
<td>Parameters</td>
<td>34</td>
</tr>
<tr>
<td>Numbers of Animals</td>
<td>36</td>
</tr>
<tr>
<td>Unrelated boars</td>
<td>36</td>
</tr>
<tr>
<td>Families</td>
<td>38</td>
</tr>
</tbody>
</table>
### iii

<table>
<thead>
<tr>
<th>Topic</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Degree of Relationship</td>
<td>40</td>
</tr>
<tr>
<td>- Full-sibs versus half-sibs</td>
<td>44</td>
</tr>
<tr>
<td>- Multiple family ties within station</td>
<td>44</td>
</tr>
<tr>
<td>Ties Across Tests</td>
<td>49</td>
</tr>
<tr>
<td>- Analysis of multiple stations</td>
<td>49</td>
</tr>
<tr>
<td>- Half-sib ties</td>
<td>51</td>
</tr>
<tr>
<td>- Paternal half-cousin ties</td>
<td>56</td>
</tr>
<tr>
<td>- Full-sib ties</td>
<td>63</td>
</tr>
<tr>
<td>- Accuracy of sire evaluations</td>
<td>69</td>
</tr>
<tr>
<td>Sources of Error</td>
<td>73</td>
</tr>
<tr>
<td>- Consequences of using the wrong model</td>
<td>73</td>
</tr>
<tr>
<td>- Fixed effects</td>
<td>74</td>
</tr>
<tr>
<td>Recommended Designs</td>
<td>78</td>
</tr>
<tr>
<td>- Central test stations</td>
<td>78</td>
</tr>
<tr>
<td>- On-farm performance programs</td>
<td>80</td>
</tr>
<tr>
<td>- Sire evaluation</td>
<td>80</td>
</tr>
<tr>
<td>CONCLUSIONS</td>
<td>82</td>
</tr>
<tr>
<td>Summary of Findings</td>
<td>82</td>
</tr>
<tr>
<td>- Design parameters</td>
<td>82</td>
</tr>
<tr>
<td>- Influence of heritability</td>
<td>82</td>
</tr>
<tr>
<td>- Number of boars</td>
<td>82</td>
</tr>
<tr>
<td>- Genetic relationships</td>
<td>83</td>
</tr>
<tr>
<td>- Designing relationship ties</td>
<td>84</td>
</tr>
<tr>
<td>BIBLIOGRAPHY</td>
<td>85</td>
</tr>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>93</td>
</tr>
<tr>
<td>APPENDIX A. TEST STATION SURVEY RESULTS</td>
<td>95</td>
</tr>
<tr>
<td>APPENDIX B. SUMMARY OF LITERATURE ESTIMATES OF PHENOTYPIC AND GENETIC PARAMETERS FOR AVERAGE DAILY GAIN, BACKFAT PROBE AND FEED EFFICIENCY</td>
<td>105</td>
</tr>
<tr>
<td>APPENDIX C. GENERATION OF RELATIONSHIP MATRIX INVERSES REQUIRED FOR DESIGNS</td>
<td>122</td>
</tr>
</tbody>
</table>
LIST OF TABLES

Table 1. Number of pens by breed, number of animals per pen and relationships among pigs in central test stations 21

Table 2. Composite literature estimates of phenotypic and genetic parameters for average daily gain, backfat probe and feed efficiency 23

Table 3. Data structure designs employed to evaluate mixed model methodology 32

Table 4. Expected correlations between true and estimated breeding values calculated for evaluation of individual performance records, multiple trait selection index and best linear unbiased prediction of average daily gain and backfat probe 35

Table 5. Comparison of average accuracy of evaluation for different distributions of individual boars 37

Table 6. Accuracy of prediction for boars within stations, accounting for degree of relationship 41

Table 7. Average prediction error variances of average daily gain and backfat probe for full-sib boars tied by sires within stations 46

Table 8. Prediction error variance of average daily gain and backfat for boars with sire ties across families, within tests 48

Table 9. Average prediction error variances of average daily gain and backfat probe for boars in tests tied by half-sibs 54

Table 10. Comparison of accuracy of evaluation of full-sib boars with varying number of sire ties across stations 55

Table 11. Percent change in accuracy relative to untied stations for full-sibs tied across stations by sires (half-sib ties) 57
<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table 12</td>
<td>Average prediction error variances of average daily gain and backfat probe for boars in tests tied by half-cousins</td>
<td>61</td>
</tr>
<tr>
<td>Table 13</td>
<td>Comparison of accuracy of evaluation of full-sib boars tied across stations by half-cousin ties</td>
<td>62</td>
</tr>
<tr>
<td>Table 14</td>
<td>Average prediction error variances of average daily gain and backfat probe for boars in tests tied by full-sibs</td>
<td>63</td>
</tr>
<tr>
<td>Table 15</td>
<td>Accuracy of evaluation for full-sibs tied across stations by littermates (full-sib ties)</td>
<td>67</td>
</tr>
<tr>
<td>Table 16</td>
<td>Percent increase in average accuracy of evaluation when full-sib, half-sib or half-cousin ties are added across stations</td>
<td>68</td>
</tr>
<tr>
<td>Table 17</td>
<td>Average prediction error variances of evaluations for sires of boars</td>
<td>70</td>
</tr>
<tr>
<td>Table A1</td>
<td>Number of pens tested, by breed</td>
<td>96</td>
</tr>
<tr>
<td>Table A2</td>
<td>Entry requirements</td>
<td>102</td>
</tr>
<tr>
<td>Table B1</td>
<td>Estimates of heritability for average daily gain</td>
<td>106</td>
</tr>
<tr>
<td>Table B2</td>
<td>Estimates of heritability for backfat</td>
<td>108</td>
</tr>
<tr>
<td>Table B3</td>
<td>Estimates of heritability for feed to gain ratio</td>
<td>111</td>
</tr>
<tr>
<td>Table B4</td>
<td>Estimates of phenotypic variance for average daily gain</td>
<td>113</td>
</tr>
<tr>
<td>Table B5</td>
<td>Estimates of phenotypic variance for backfat</td>
<td>114</td>
</tr>
<tr>
<td>Table B6</td>
<td>Estimates of phenotypic variance for feed to gain ratio</td>
<td>114</td>
</tr>
<tr>
<td>Table B7</td>
<td>Estimates of phenotypic correlation between average daily gain and backfat</td>
<td>115</td>
</tr>
<tr>
<td>Table B8</td>
<td>Estimates of genetic correlation between average daily gain and backfat</td>
<td>115</td>
</tr>
</tbody>
</table>
Table B9. Estimates of phenotypic correlation between average daily gain and feed to gain ratio 116

Table B10. Estimates of genetic correlation between average daily gain and feed to gain ratio 117

Table B11. Estimates of phenotypic correlation between backfat and feed to gain ratio 119

Table B12. Estimates of genetic correlation between backfat and feed to gain ratio 120

Table B13. Summary of literature estimates of heritabilities, standard deviations and correlations 120
LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1</td>
<td>Average accuracy of evaluation of average daily gain as influenced by number of families and half-sib family size</td>
<td>39</td>
</tr>
<tr>
<td>Figure 2</td>
<td>Influence of degree of relationship on accuracy of evaluation of backfat for varying number of families</td>
<td>43</td>
</tr>
<tr>
<td>Figure 3</td>
<td>Average accuracy of evaluation of average daily gain as influenced by number of families and full-sib family size</td>
<td>45</td>
</tr>
<tr>
<td>Figure 4</td>
<td>Average accuracy of evaluation of average daily gain measured on boars with or without half-sib ties across stations</td>
<td>52</td>
</tr>
<tr>
<td>Figure 5</td>
<td>Average accuracy of evaluation of average daily gain measured on full-sib boars in different size families, with one half-sib tie across stations</td>
<td>53</td>
</tr>
<tr>
<td>Figure 6</td>
<td>Average accuracy of evaluation of average daily gain measured on full-sib boars with or without half-cousin ties across stations</td>
<td>59</td>
</tr>
<tr>
<td>Figure 7</td>
<td>Influence of family size on average accuracy of evaluation of average daily gain measured on full-sib boars tied by half-cousins across stations</td>
<td>60</td>
</tr>
<tr>
<td>Figure 8</td>
<td>Influence of family size on average accuracy of evaluation of average daily gain measured on boars with full-sib ties across stations</td>
<td>65</td>
</tr>
<tr>
<td>Figure 9</td>
<td>Average accuracy of evaluation of average daily gain for boars with or without full-sib ties across stations</td>
<td>66</td>
</tr>
<tr>
<td>Figure A1</td>
<td>Locations of central swine testing stations in the United States, 1985</td>
<td>104</td>
</tr>
</tbody>
</table>
INTRODUCTION

Although mixed model methodology was developed more than 25 years ago, and has been refined and applied extensively in the dairy and beef cattle industries, the swine industry in the United States has been slow to adopt its use. For many years, the overall economic situation, the low value per animal, compared to that of a calf, and the relatively fast progress made in the reduction of backfat by simpler methods precluded the use of anything more complicated or more expensive than classical selection indexes first developed in the mid-forties. In recent years, results of mixed model analyses of swine data have been reported in increasing numbers, but very little is known about their particular properties when varying amounts of information are available.

This dissertation addresses two aspects of the application of mixed model methodology to the evaluation of performance tested boars. First, it explores the influence of a variety of genetic relationship matrices on the accuracy of solutions. Secondly, it combines those results with literature information to establish guidelines for exploiting the data structure to increase accuracy of swine evaluation.
LITERATURE REVIEW

Test Stations

A brief history of central testing of swine was presented by Robison (1982). The concept was developed first by the Danish in 1907, as part of an effort to win a share of the British bacon market. Test stations were started in many other countries soon after, and until the development of the backfat probe by Hazel and Kline (1951), served primarily as evaluation centers for family selection. The present set of swine testing stations in the United States began operating in 1954 at Ohio State University and in 1956, the station opened in Ames, Iowa (Robison, 1982).

Presently, the primary emphasis is on performance of individuals for average daily gain (ADG), backfat (BF) and feed efficiency (FE), which is measured as feed/gain on pens of full- and/or half-sibs. Loin eye area may be measured, but is not recommended for use in indexes (USDA, 1981b).

Steane (1983), in an address to British producers, listed three types of relevant information which must be available in order to profit from genetic improvements. They were:

1) the genetic differences between suppliers (corporate and nucleus, or seedstock);
2) identification of the rate of genetic gain;
3) how to obtain genetic stock.

Central test stations can help provide answers in all these areas.
Robison (1982) stated that one purpose of central test stations was to provide a uniform environment which allowed tested animals to express their true genetic merit. This also could allow evaluation of genetic differences between represented herds. Other goals he listed were providing tested boars to commercial producers to decrease the genetic "lag" time between superior seedstock herds and their commercial customers and education of seedstock breeders. These are very similar to functions listed in the Beef Improvement Federation Guidelines (USDA, 1981a).

Recently, interest in central testing has been declining. It is an expensive exercise, and lack of organization and strong leadership has led to a perception of little progress (Miller, 1983), although Blanchard (1986) cited several studies showing improvement in traits of economic interest. Also encouraging was an Ohio survey (Isler, 1984), in which 34% of those individuals responding indicated test records were the major reasons for deciding where to buy boars.

Robison (1982) recommended the following steps to bolster performance testing of swine.

1) Use commercial farms for estimating genetic differences among elite herds.
2) Incorporate on-farm tests with central tests.
3) Organize central tests within breed.
4) Test only progeny of tested parents.
5) Recognize that test stations are only one part of any scheme for pig improvement.
The second step may be quite important, as Roberts and Curran (1981) reported that genetic correlations between farm and station results, based on an index of traits, were in general less than .30. However, they also indicated that similar aggregate genotypes were being selected. Pfeiffer (1984) recommended centralized testing because of the variations between test stations and farms of origin. On the other hand, Standal (1977) reported results which seemed to indicate a genotype x environment interaction between station and farm effects, and concluded that stations are of limited use for improvement of the commercial pig.

As current procedures are set up, results from central tests are useful only within location, year and season (USDA, 1981a). In order to carry out some of the above recommendations, more recent technology must be used. Willham (1982) outlined suggestions, based on years of experience in the dairy and beef industries, for use of artificial insemination and mixed model methodology to increase genetic progress in the swine industry by combining sources of information through genetic ties. Mabry and Benyshek (1984) outlined a National Central Test Young Sire Evaluation Program which could utilize test station information in a program to improve genetic progress, rather than as a merchandising tool. The first step consists of evaluating sires across stations. The second step will incorporate the centrally collected information with on-farm performance tests to further enhance the usefulness of estimated breeding values.
Parameter Estimates

Genetic improvement of livestock depends on the resemblance among relatives. Parameters such as heritability, genetic correlations, phenotypic correlations and environmental correlations are used by the geneticist to capitalize on the likeness among relatives. By applying methodologies which employ estimates of these parameters to maximize the probability of correctly selecting the best breeding stock, genetic progress also is maximized.

In order to investigate the role of central test stations in the improvement of pigs in the United States, a thorough knowledge of parameters involved is necessary. A search of the literature was conducted and estimates of pertinent parameters were compiled and summarized. These composite estimates are in Table 2 in Materials and Methods.

Methodology

Selection index

This method, first applied to animal breeding in the 1940s, has long been the method of choice in swine breeding and is recommended by the National Swine Improvement Federation (USDA, 1981b). Properties of index selection were described by Hazel (1943) and enlarged upon by others (Henderson, 1973; Young, 1984). Reasons for use of indexes include:
1) the correlation between the index and the underlying aggregate genotype is maximized;
2) a single value is used to rank animals for any number of economically important traits;
3) it maximizes genetic progress per year;
4) it gives unbiased results;
5) it allows evaluation of individuals through use of relatives, by properly weighting the information;
6) linear combinations of the solutions retain the above properties.

In addition, an index can be very helpful in predicting relative merits of alternative selection programs (Henderson, 1973).

As pointed out by Hazel (1943), however, disadvantages are present as well. Possible violations of underlying assumptions include:

1) economic values are subject to change over time and/or distance;
2) there may be genetic differences among herds (stations);
3) management differences may cause standard deviations to vary across herds (stations);
4) sampling errors of the genetic constants tend to be larger than wished;
5) as selection progresses, relationships among parameters may change, causing the need for reconstructing the indexes.
Mixed models

In his classical paper, Henderson (1973) addressed many of these points and clearly outlined the differences among best predictors, best linear predictors (selection index) and best linear unbiased predictors (BLUP). He noted that the primary disadvantage of indexes was that fixed effects were assumed to be known without error, and that if generalized least squares estimators of fixed effects were used in selection indexes, then the solutions were BLUP. He also addressed specific areas in which mixed models are advantageous:

1) means are not required, and only ratios of the variances are needed. The ratios are functions of heritability and appear fairly robust to errors of estimation;

2) large sets of multiply-classified data with potentially many subclasses and unbalanced data give rise to problems under selection index conditions;

3) methods have been derived which adjust for bias due to selection on records as well as for prior knowledge;

4) differences among subgroups can be accounted for, allowing estimation of genetic trends.

Originally applied to dairy cattle AI data (Henderson, 1973), mixed models have been used extensively in the beef industry (Winrock International, 1983) and numerous variations on the original sire evaluation model have been developed (Henderson, 1973; Pollak et al., 1977; Berger, 1983; Blair and Pollak, 1984). A review of topics
pertaining to methods of sire evaluation is found in Thompson (1979),

Due to differences in biology, as well as industry, pigs do not lend themselves as easily to mixed model evaluation. Being born into litters, sheer numbers become overwhelming, and added to that is the problem of analysis of common environmental effects. As Willham (1982) noted, heterosis has played a large role in improving the commercial market pig and heritabilities of most performance traits are high enough to permit direct selection among individuals. Together, these factors have slowed the adoption of techniques used routinely by the beef and dairy industries. Recently, however, reports have been published in the United States (Carlson et al., 1984) and Canada (Hudson and Kennedy, 1985a,b) which indicate swine geneticists are beginning to use mixed models.

Computational difficulty was often cited as a reason not to use mixed models, but as Young (1984) pointed out, phenotypic and genetic matrices required for selection indexes also can be extremely complex if very many sources of information are included. In general, it appears that advantages of mixed models outweigh those of indexes, in terms of flexibility, efficiency, and increased accuracy of breeding value estimations. Some questions which still need answers, however, were listed by Johnson (1984):

1) What is the cost in computing time and record processing?
2) What are the effects of sources of bias on estimates and their accuracy?
3) How do procedures of estimation affect selection decisions?

4) What are the differences in predicted genetic gain for each method?

Models

Three subgroups of models can be recognized. These are:

1) sire evaluation, in which breeding values of sires are estimated based on progeny performance (e.g., AI bulls);

2) repeated records, in which individuals are evaluated on their own and/or progeny records, measured over time (e.g., lactation records); and

3) animal model, in which individual performance is used to evaluate breeding value (e.g., performance testing of potential herd bulls).

Henderson (1973) first delineated the basic ideas for these models, along with possible selection models and multiple trait evaluation. Since then, a number of researchers have expanded on his ideas and have added variations to the theme (Arnason, 1982; Benyshek, 1984; Henderson, 1984; Wilson et al., 1985). All of the models may encompass the use of relative information, and hence tend to overlap. Equivalent models (Blair and Pollak, 1984) may also be written to lessen computations. Sire evaluation has become accepted in the beef industry and the dairy industry has seen great improvement in milk production over the years (Mirende and Van Vleck, 1985) through use of sire evaluation.
Accuracy

Measures of variability are crucial for comparison of alternative models (Henderson, 1975a), as well as being guides to the reliability of results. With selection indexes, the correlation between the index and aggregate genotype is used (Hazel, 1943), since it is directly related to expected genetic change. In the case of BLUP, prediction error variance (PEV) is a convenient measure (Henderson, 1975a), since it is the product of the inverse of the left-hand side coefficient matrix and the residual error variance and is a measure of \( E(u - \hat{u})^2 \), where \( u \) represents the true breeding values of the animals being evaluated. Under conditions outlined by Henderson (1973), this is minimized, giving the best predictor in the class of linear unbiased predictors. More analogous to selection index, BLUP also maximizes the correlation between the true and estimated breeding values, which is the classical animal breeding definition of accuracy.

The expression for accuracy

\[
\rho_{u\hat{u}} = \sqrt{1 - \frac{V(u - \hat{u})}{\sigma_G^2}}
\]

may be derived from known mixed model properties (Henderson, 1973), as shown by Berger (1983). The formula demonstrates that accuracy is a direct function of PEV. Arnason (1984) noted the term is dependent on the heritability, quantity and distribution of the information, and degree of relationship among the animals. Keown (1974) compared
different sire models and found the most important aspect was inclusion of off-diagonal elements in the coefficient matrix, although inclusion of groups to obtain more homogeneous genetic subpopulations also was important.

Schaeffer and Wilton (1975) indicated that 100 to 150 progeny per sire were required to obtain an acceptable standard error of prediction (SEP). They noted that SEP reflects the number of progeny per sire, number of herd-year x sire interactions, distribution of progeny over herd-years and number of progeny of other sires. Their analysis did not include the relationship matrix.

Carlson (1980) reported mean PEV in the analysis of swine test station information and he concluded that using an animal model with relationships resulted in much larger decreases in PEV relative to an animal model without relationship information. In addition, ADG had larger percent reductions in PEV than BF since its heritability was lower.

When large systems of equations are involved, approximations to PEV must be used. If relationships are incorporated into the left-hand side coefficient matrix, however, approximations of PEV may be biased because the equations may not be diagonally dominant (Wilmink and Dommerholt, 1985). They noticed the effect in particular with bulls having many daughters and few direct comparisons.
Fixed effects

The primary difference between selection index and mixed model solutions is the absence or presence, respectively, of fixed effects (Henderson, 1973). Derivation of selection index properties was predicated on knowledge without error of both first and second moments (mean and variance) of the distribution. BLUP requires knowledge only of the ratio of variances (second moments).

Inclusion of fixed effects in the model must be weighed carefully. As Henderson (1975a) noted, ignoring fixed effects which are of some importance leads to biased solutions, albeit lower PEV. Inclusion of trivial effects, however, may cause equations to misbehave (especially if subclass numbers are small), in addition to increasing PEV. If the magnitude of the fixed effects in question can be estimated reasonably well, the bias caused by their exclusion can be calculated. In the usual case, however, there is no way to tell which effects can be excluded safely and consideration should be limited to cases involving small numbers (Henderson, 1975a).

In addition, Schaeffer and Wilton (1975) noted that if only one sire is represented within a herd-year, effective progeny number is zero, so those herd-years can be deleted prior to analysis. Ojala et al. (1985) carried the process a step further by examining the effect of subclass size and varying numbers of progeny on solutions. Assuming sires were unrelated, accuracy increased with increasing progeny number; as subclass size increased, the calculated correlation
between true and predicted breeding values approached or reached its expectation for each progeny number. Although loss of subclasses due to single observations was a problem, increasing the subclass size to three observations provided acceptable solutions.

Chauhan (1985) compared three methods of defining herd-period-season effects. By treating herd-period or herd alone as fixed effects, the effective daughter number was reduced to 4/5 and 2/3, respectively, of that obtained when herd-period-season was fixed. He noted that this would be particularly effective in situations where small subclass numbers cause loss of a large amount of information.

Multiple trait mixed models were derived using principles of multiple trait index selection (Henderson and Quaas, 1976). Due to their complexity, limited use of them has been made, although Arnason (1982, 1984) outlined a method of transforming the correlated structure to allow for single trait analysis in horses.

**Common environmental effects**

In one respect, swine evaluation is quite different from either dairy or beef, in that progeny are born into litters. This offers the opportunity associated with greater contemporary numbers (Pirchner, 1983) but also brings the problems associated with the extra correlation between littermates which causes them to be more alike than expected. Lush (1945) described $c^2$ as "the variance caused by whatever fraction of the environmental, epistatic, and dominance deviations are alike for members of the same family, but vary from one family
to another."

The presence of such effects, if ignored, can severely limit improvement in accuracy of progeny tests (Pirchner, 1983); yet accounting for the effect in design and analysis can be extremely difficult as well. Thus, use of paternal half-sibs has become the method of choice, especially in progeny testing (Berger, 1983).

With the inherent ability to handle large unbalanced data sets, and with correct partitioning of the model, mixed model methodology offers the possibility of accounting for common environment effects (Henderson, 1973). He suggested treating $c^2$ as an interaction term and using an equivalent model. Kennedy et al. (1985) fit a random litter effect to estimate variance components by which at least part of $c^2$ was estimated. Carlson (1980) noted that pen effects appeared important in data collected from five stations over nine year-seasons, but he chose not to fit the effect because of probable confounding with dams, among other things.

In order to measure $FE$, littermates and/or half-sibs must be housed together, or all pigs fed separately. The single test station measuring $FE$ on an individual basis is in the process of changing to pen-based measurement (Cleveland, E. 1985. University of Georgia, personal communication). If indirect selection for $FE$ is practiced, half- or full-sibs could be assigned randomly to pens to help reduce $c^2$ (Falconer, 1981). To further complicate matters, however, Falconer (1981) also pointed out that competition may cancel out some of the
effects due to common environment by decreasing the within-sib variance. Another strong argument for penning relatives together is the fear of disease.

Genetic ties

Schaeffer (1975) noted that sire-herd subclasses are connected if differences between all possible pairs of sires are linearly estimable and if differences between all possible pairs of herds are linearly estimable. In general, genetic ties are the links by which animal breeding data are connected into larger subsets, providing more information with which to estimate breeding values. However, determining which subclasses are connected by genetic ties, and how strongly, can be a formidable task in large data sets (Searle, 1971; Fernando et al., 1983). In specific cases, genetic ties have been defined in different ways. Carlson (1980) defined a tie as any nonzero genetic relationship between two animals, and he used percent of filled cells to evaluate the extent of ties present in his data set. Wilson (1982) specified three kinds of ties: reference (AI) sire; genetic relationship; and chain tie, in which herd-year-seasons with no animals in common were tied through other seasons which had animals in common with the untied seasons.

Use of the relationship matrix

Resemblance among relatives is the phenomenon on which animal breeding is based. Lush (1935) pointed out that breeding value can
be estimated from three sources: pedigree, individual performance, and progeny performance. It stands to reason, then, that incorporation of relative information can improve estimation of breeding values. It also is well-known, however, that relative information is more helpful in some cases than others. For instance, Lush (1945) showed that family selection is more efficient for lowly heritable traits with low repeatability, while mass (individual) selection is more efficient for medium to highly heritable traits, assuming of course, that the traits were measurable in both instances. In some cases (sex limited traits), relative information is all a geneticist has available. Pirchner (1983) summarized results which showed that in progeny testing, relative information is more valuable for lowly heritable traits, and that for traits with heritability greater than .40, selection on individual performance is more efficient in any case.

Falconer (1981) also pointed out that if sib information is available, parent information adds little. Quaas et al. (1979) showed that the maternal grandsire (MGS) model could be used to approximate the effect of the cow by using the relationship matrix (A) from the males in the pedigree. Wilson (1982) investigated the effect of different types of relationships on the accuracy of beef sire evaluations and found that a bull/sire/MGS pedigree was equivalent to a bull/sire/dam pedigree when the dam had two progeny. When the dam had four records, however, it took 400 progeny records on the MGS to provide the same information. He also compared PEV resulting from
ties provided by reference sires, as well as direct and indirect contemporary group ties. Results indicated the possibility of eliminating the need to use reference sires in beef sire evaluations, although field data needed to be analyzed to provide a definitive answer.

Henderson (1973) gave examples of how relationship matrices could be incorporated into evaluations, but it was not until he published a simple method of calculating the inverse (Henderson, 1975b, 1976) that use of relationships became cost effective. From simulations as well as field data analysis, researchers have reported increases in accuracy of evaluation for dairy, beef and swine by inclusion of relationship matrices (Kennedy and Moxley, 1975; Pollak et al., 1977; Jensen, 1980; Carlson et al., 1984; Kemp et al., 1984). Carlson (1980) summarized such studies by noting that the relationship matrix reduced PEV by differing amounts depending on the model and relationships involved, but Arnason (1984) noted that inclusion of the complete relationship matrix is the optimal utilization of information available.

Henderson (1975c) demonstrated the use of relationships in intra-herd evaluation, pointing out that inclusion allowed use of more records; permitted combination with AI information; and more efficiently accounted for genetic and environmental trend than did grouping. He also showed that use of the relationship matrix eliminates culling bias and bias due to selection of dams on previous records. There is
indication (Pollak and Quaas, 1981) that use of the complete relation­ship matrix replaces the need for genetic grouping in order to estimate genetic trend and selection.

In an application to a sire model, Henderson (1975d) noted that inclusion of relationships among sires increased accuracy of prediction for sires and did not lessen the suitability of the coefficient matrix for iterative solutions, since the relationship matrix was relatively sparse. Inclusion of some dam information also helped increase accuracy, especially for those sires with few or no progeny; accounted for genetic trend and genetic differences among herds; and allowed earlier evaluation of sires.

Pimland (1983) explored properties of equations which included the relationship matrix. A sire/MGS model was developed which required fewer assumptions about randomness of mating than a sire model (without relationships) and under which preferential mating could be practically ignored. He showed how effective number of daughters increased as more male ancestors were included in the equations through \( A \), by deriving the regression coefficients of the sire solutions.

Kennedy (1982) suggested inclusion of groups in addition to relationships for use in evaluating pigs, however, since relationships rarely are known completely. Berger (1983) summarized work which suggested grouping be based on type of selection practiced, with con­struction of the model such that selection occurs within groups.
Application of mixed models to swine evaluation

Carlson et al. (1984) employed the animal model to evaluate more than 9,000 records accumulated during nine seasons of tests in five central swine testing stations. For the analysis, they assumed the heritability of each trait was the same for all breeds. Their use of the relationship matrix allowed evaluation of sires as well, although they had no records themselves.

Kennedy (1982) presented possible models (sire-dam and animal) for evaluating swine using mixed model methodology, and applications are reported by Hudson and Kennedy (1985a). They evaluated five Canadian breeds of pigs separately, using both central and on-farm performance records for days to 90 kg and backfat. From a simultaneous estimation of genetic parameters (Kennedy et al., 1985), they concluded use of single trait evaluation would be easier, as well as safer, since the genetic correlation between the two traits was low, and little information on the error structure was available. In Sweden, Lundeheim and Eriksson (1984) used mixed models to estimate genetic trends in the Yorkshire and Landrace populations, as did Hudson and Kennedy (1985b) in Canada.

A pilot program for evaluating young sires is underway in Georgia (Mabry and Benyshek, 1984) and Blanchard (1986) used mixed models to evaluate the sale price of centrally tested Hampshire boars. All of these reports have addressed present test programs and not structure for future programs. This thesis will explore possible designs to maximize accuracy of evaluation.
MATERIALS AND METHODS

Test Station Survey

In order to acquire a basis from which to work, a telephone survey of 32 central swine testing station managers was conducted in June, 1985. Two questions were of interest, although many people volunteered additional information, and several mailed packets of material, all of which proved very helpful. The questions were:

1) What are entry requirements, e.g., number of animals, relationships and sexes?
2) How many pens of each breed were tested in the past two seasons?

Information from the current and most recent (two or three) tests was used in tabulating results from the 26 stations responding. The ranges and means for number of pigs per pen, number of pens per breed and the genetic relationships among pigs were calculated and are presented in Table 1. Of the remaining six stations, two were closed, one was not currently testing pigs, and three did not have the information at hand. Details of the survey results are in Appendix A. These numbers were used as guidelines in setting up the various combinations of parameters used for the simulated test station examples investigated.
Table 1. Number of pens by breed, number of animals per pen and relationships among pigs in central test stations

<table>
<thead>
<tr>
<th>Total number of pens, by breed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breed</td>
</tr>
<tr>
<td>-----------------</td>
</tr>
<tr>
<td>Berkshire</td>
</tr>
<tr>
<td>Chester</td>
</tr>
<tr>
<td>Duroc</td>
</tr>
<tr>
<td>Hampshire</td>
</tr>
<tr>
<td>Landrace</td>
</tr>
<tr>
<td>Poland China</td>
</tr>
<tr>
<td>Spot</td>
</tr>
<tr>
<td>Yorkshire</td>
</tr>
</tbody>
</table>

Number of animals per pen

<table>
<thead>
<tr>
<th>Animals</th>
<th>Stations</th>
<th>Relationships among penmates</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>5</td>
<td>Half-sibs</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
<td>Pull-sibs</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>Either</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>Two litters maximum</td>
</tr>
</tbody>
</table>

Average = 3

Parameter Estimates

The performance index recommended by the National Swine Improvement Federation (USDA, 1981b) includes average daily gain (ADG), backfat (BF) and feed efficiency (FE) measured as the ratio of feed to gain.
Parameters pertaining to these traits include the phenotypic and genetic standard deviations and correlations, as well as heritabilities. Estimates from the literature were summarized using medians, modes and weighted averages. Weighted averages were obtained using guidelines provided by Hutchens and Hintz (1981). Duplicate reports of estimates from the same data set were not included. The numbers of animals used to obtain estimates were used as weighting factors, when available. Other reports were included in the composite estimate, but were not given as much weight. Medians and modes were not weighted. Also included were the ranges and standard errors. These summaries then were used to develop designs for evaluation of performance tested boars. Table 2 contains the composite estimates, while Appendix B has summaries of the results.

Heritabilities for ADG and BF were determined to be .40 and .50, respectively, while the composite for PE (.25) is lower than previously thought (USDA, 1981b). Of considerable interest are the genetic correlations among FE, ADG and BF. It appears that indirect selection for FE may be almost as good as direct and considerably less expensive (Bereskin and Steele, 1985; Christian and Wood, 1985). The absence of a genetic correlation between ADG and BF also suggests the use of single trait mixed models as opposed to a multiple trait model with its correlated variance structure (Hudson and Kennedy, 1985a).
Table 2. Composite literature estimates of phenotypic and genetic parameters for average daily gain, backfat probe and feed efficiency

<table>
<thead>
<tr>
<th>Trait</th>
<th>ADG</th>
<th>BF</th>
<th>FE</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADG</td>
<td>.40</td>
<td>0</td>
<td>-.60</td>
</tr>
<tr>
<td>BF</td>
<td>.15</td>
<td>.50</td>
<td>.30</td>
</tr>
<tr>
<td>FE</td>
<td>-.60</td>
<td>.20</td>
<td>.25</td>
</tr>
</tbody>
</table>

* Upper triangle = Genetic correlations; Diagonal = Heritability; Lower triangle = Phenotypic correlations.

b ADG = Average daily gain; BF = Backfat probe; FE = Feed/gain.

Animal Model with Relationships

Because boars in test stations are potential herd sires, and because individual performance records for moderate to highly heritable traits are available, an animal model would seem to offer more advantages than the more traditional sire model by evaluating boars being tested. In addition, by including the genetic relationship matrix (A), sires with no performance records of their own can be evaluated, while sires with records can contribute to the evaluation of their progeny.

The model used in this study assumed breeds were analyzed separately, and that the only fixed effect was due to station-season. The only random variable in the model was breeding value. Common environmental effects (c²) were ignored in order to keep the designs
as simple as possible, and because very few estimates of the common environmental variance were available. Any genetic trends among stations should be accounted for by inclusion of relationships (Pollak and Quaas, 1981). The traits ADG and BF were analyzed separately, based on information from the literature suggesting a genetic correlation close to zero (Table 2). FE was ignored, since genetic correlations between it and the other two traits appear to be relatively large and favorable (Table 2).

The model used for animals with records was

$$Y_{ij} = s_i + b_{ij} + e_{ij}$$

(1)

where $Y_{ij}$ = observation of the $j^{th}$ boar in the $i^{th}$ station-season,

$s_i$ = fixed effect due to the $i^{th}$ station-season ($i = 1, 2, ..., p$), plus the underlying mean common to all observations,

$b_{ij}$ = random effect due to the $j^{th}$ boar in the $i^{th}$ station-season ($j = 1, 2, ..., n$), and

$e_{ij}$ = residual random error associated with the observation on the $j^{th}$ boar in the $i^{th}$ station-season.

The general representation of a mixed model in matrix notation is

$$y = X\beta + Z\gamma + e.$$

(2)

For the specific case of an animal model which includes both animals with records and related animals with no records,

$y$ is an $n \times 1$ vector of observations;
X is an n x p incidence matrix and Z is an n x n identity matrix relating observations to animals which made them;

is a p x 1 vector of unknown fixed effects;

u is a t x 1 vector of random breeding values equal to u1, which is an n x 1 vector representing animals having records, plus u2, which is a (t-n) x 1 vector for related animals with no records;

and e is an n x 1 vector of random residual errors.

\[
\begin{pmatrix}
Y \\
u \\
e
\end{pmatrix} = \begin{pmatrix}
X \beta \\
0 \\
0
\end{pmatrix}, \quad \text{and} \quad V \begin{pmatrix}
Y \\
u \\
e
\end{pmatrix} = \begin{pmatrix}
V \sigma_G^2 & 0 \\
0 & \sigma_G^2 \\
0 & 0
\end{pmatrix},
\]

where \( V = \sigma_G^2 + \sigma_e^2 \), A = genetic relationship matrix and \( Z = I_n \).

If the ratio of the residual variance to the additive genetic variance (\( \sigma_e^2/\sigma_G^2 \)) is known, Henderson's (1973) mixed model equations may be written as follows:

\[
\begin{pmatrix}
X'X & X'Z & 0 \\
Z'X & (Z'Z & 0) \\
0 & 0 & 0
\end{pmatrix} + A^{-1} k \begin{pmatrix}
\hat{\beta} \\
\hat{u}_1 \\
\hat{u}_2
\end{pmatrix} = \begin{pmatrix}
X'y \\
Z'y \\
0
\end{pmatrix},
\]

where \( k = \sigma_e^2/\sigma_G^2 = (1-h^2)/h^2 \)

and \( 0 \) represents rows and columns of zeros required to include evaluation of animals with no records which are related to animals with records, through A.

Station-season effects were absorbed on a station-by-station basis and \( A^{-1} \) was built directly using Henderson's (1975b) method. This resulted in
\[
\begin{bmatrix}
(Z'MZ & 0) + A^{-1}\kappa
\end{bmatrix}
\begin{bmatrix}
\hat{u}_1 \\
\hat{u}_2
\end{bmatrix}
= \begin{bmatrix}
Z'MY \\
0
\end{bmatrix}
\tag{4}
\]

where \( M = I_n - X(X'X)^{-1}X' \).

Examples of the \( A^{-1} \) required for the designs used are in Appendix C.

Measure of Variability

Henderson (1975a) defined the "best" evaluation method as the one which in the class of linear unbiased predictors has minimum prediction error variance. It has been shown (Henderson, 1973) that the mixed model solutions have these properties, and that the minimum variance is measured by the variance of prediction error on \( \text{Var}(u-u) \).

There are two reasons this measurement is useful.

1) It is easy to calculate if the inverse of the left-hand side coefficient matrix can be obtained directly, since

\[
\text{Var}(u-u) = C_{22}^{22}, \text{ where }
\]

\[
\begin{bmatrix}
X'X & X'Z \\
Z'X & Z'Z + I_n\kappa
\end{bmatrix}
= \begin{bmatrix}
C_{11}^{11} & C_{12}^{12} \\
C_{21}^{21} & C_{22}^{22}
\end{bmatrix}
\tag{5}
\]

in general.

2) It is directly related to accuracy, which in animal breeding is defined as the correlation between the estimated and true breeding values. This can be seen using identities derived by Henderson (1973), as shown by Berger (1983):
Var(\(\hat{u}\)) = Cov(\(u, \hat{u}\)) = Var(\(u\)) - Var(\(u-u\)).

Thus \(r_{uu} = \left(\frac{\text{Cov}(u, \hat{u})}{\sqrt{Var(u)Var(\hat{u})}}\right)^2 = \left(\frac{\hat{\text{Var}(u)}}{Var(u)}\right)^2 = \frac{\hat{\text{Var}(u)}}{Var(u)} = 1 - \frac{\text{Var}(u-u)}{Var(u)},\)

and \(r_{uu} = \sqrt{1 - \frac{\text{Var}(u-u)}{\sigma^2}}.\) \(\text{(6)}\)

This is the criterion by which the designs in this study were compared to determine which are optimum under present testing conditions, as well as to provide ideas for more efficient use of existing facilities and for guidelines in future planning of performance testing of pigs.

**Changes in Accuracy Due to Estimation of Fixed Effects**

To reduce cost of computation, if the number of fixed effects in a mixed model is large, they may be absorbed into the random variables by rewriting the fixed effect equations in terms of \(u\). If solutions to fixed effects are desired, they may be obtained by backsolving. Either way, solutions for \(u\) will be the same. An efficient way to handle the calculations in this study was to absorb the fixed effects on a station-by-station basis.

The results of estimating fixed effects may be seen by comparing selection index equations to mixed model equations. Let

\[
[Z'Z+I_nk][\hat{u}] = [Z'y]
\]  \(\text{(7)}\)
be the set of equations (1) under the conditions of selection index, in which fixed effects are known without error, no further estimates of \( \beta \) are required and relationships are not included. Henderson (1973) explained, in detail, the differences between index (best linear predictions) and mixed model (best linear unbiased predictions) solutions. The solutions to (7) are a function of the identity matrix, augmented on the diagonal by the ratio of residual to additive genetic variances.

In the case of BLUP, as well as least squares, some of the available information must be used to estimate \( \hat{\beta} \). This can be observed in the set of absorbed mixed model equations for observations within a single fixed effect,

\[
[(Z'Z - Z'X(X'X)^{-1}X'Z) + \frac{1}{n}I][\hat{u}] = [Z'y - Z'X(X'X)^{-1}X'y],
\]

which for the animal model (4) is

\[
[I_n - J_n(1/n) + \frac{1}{n}I][\hat{u}] = [y - J_n(1/n)y],
\]

where \( J_n \) is an \( n \times n \) matrix of ones and \( Z = I_n \).

If \( n \) and \( k \) are equal, the diagonal elements of the coefficient matrix in (9) will be smaller than those in (7), and the off-diagonal elements will change to nonzero numbers, resulting in larger diagonal elements in the inverse and a larger prediction error variance (Van Raden, 1984).

One way of determining exactly how the inclusion of \( \beta \) will influence the prediction error variance is by looking at the estimator of one fixed effect:

\[
\hat{\beta} = L'y.
\]
where \( L' = (X'V^{-1}X)^{-1}X'V^{-1} \), \( V^{-1} = \left( ZAZ'\sigma_G^2 + \text{I}_n \sigma_e^2 \right)^{-1} \) and \( A = \text{I}_n \).

The elements of the row vector \( L' \) will be proportional to the amount of information (from genetic relationships) available on the observations belonging to the particular fixed effect. Note that

\[
V(\hat{\beta}) = (X'[I_n - Z(Z'Z + \text{I}_n k)^{-1}Z']X)^{-1} = (X'X)^{-1}(\sigma_G^2 + \sigma_e^2).
\]

This effect due to \( \hat{\beta} \) is found in solutions to \( \hat{u} \) (12) and the prediction error variance (13), since (10) is included as

\[
Z'\hat{X}\hat{\beta} + (Z'Z + \text{I}_n k)\hat{u} = Z'Y
\]

\[
\hat{u} = (Z'Z + \text{I}_n k)^{-1}[Z'Y - Z'X\hat{\beta}]
\]

\[
= (Z'MZ + \text{I}_n k)^{-1}Z'MY
\]

in the former case, and

\[
\text{Var}(u - \hat{u}) = [(Z'MZ + \text{I}_n k)^{-1}]\sigma_e^2
\]

in the latter.

**Designs**

Data structure designs (Table 3) were developed by simulation, using parameter estimates from the literature. Since a direct inverse
of the coefficient matrix was desired, numbers of pens, stations and total number of animals were kept small, but in a manner consistent with information from the station survey.

Designs examining relationships included animals with no genetic ties, half-sib families and full-sib families. Family size (number of sibs) varied from 1 in the case of unrelated boars to 8 for half-sibs. This last design is reflective of a possible progeny test using half-sibs, while family sizes of 2, 3 and 4 are commonly found in test station situations (Table 1).

Numbers of families were constrained by total number of animals involved, but 16 families was the average size of test groups; 5 families and 25 families represent two extremes. The number of unrelated animals was based on the total number of animals in the multiple-member families.

Ties across stations are of interest since comparison of boars in different tests is then possible. From the structure of swine data as seen in the survey results, full-sib families were used in tying stations together. A genetic tie is defined as a relationship between animals in different families through a common relative. Number of ties is based on the number of sets of animals so tied.
Table 3. Data structure designs employed to evaluate mixed model methodology

<table>
<thead>
<tr>
<th>Relationships</th>
<th>Family size</th>
<th>Number of families</th>
<th>Ties across stations</th>
<th>Number of ties</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>1</td>
<td>10,15,20,32,40, 48,50,64,75, 100,128,200</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>Half-sibs</td>
<td>2,3,4,8</td>
<td>5,16,25</td>
<td>None</td>
<td>None</td>
</tr>
<tr>
<td>Full-sibs</td>
<td>2,3,4</td>
<td>5,16,25</td>
<td>Half-sib Half-cousin Full-sib</td>
<td>0,1,2,3,4,5</td>
</tr>
</tbody>
</table>

Types of ties include:

1) sire (half-sib) ties, in which litters in different stations have the same sire;

2) paternal grandsire (paternal half-cousins) ties, in which sires of litters in different stations are confounded with station, but are tied across stations because they are half-sibs; and

3) full-sib ties, generated by assigning members of a litter to different stations.

Also of interest was the question of how additional ties of the same kind would affect accuracy. Therefore, within each type of tie, number of ties was varied.

For each of these designs, ADG and BF were evaluated. In addition
to individual prediction error variances (and accuracies) for individual boars, sires, dams (in some cases) and paternal grandsires (as applicable), average PEV were calculated for each class of animals.

**Programs**

The programs required for generation of coefficient matrices and the resulting PEV were written in FORTRAN. From literature estimates (Table 2), error variances were calculated for ADG and BF, and the variance ratios (k) were obtained from the heritabilities. After the animal equations with station-season absorbed were built, constants needed to adjust the equations for information from the relationship matrix were added to the appropriate elements of the coefficient matrix. That matrix was inverted using an IMSL routine and PEV were calculated from the diagonal elements of the inverse. Once all \( \text{Var}(u-u) \) had been accumulated for each class, the average was calculated.

Debugging of the programs was accomplished by setting up small examples by hand and using existing software (SAS) to perform necessary matrix manipulations. Results were printed out, but also written on tape for future use.
RESULTS AND DISCUSSION

Parameters

Heritabilities of the two traits under consideration were assumed to be .4 and .5 for ADG and BF, respectively. In classical animal breeding experiments, it has been shown (Lush, 1945; Pirchner, 1983) that information from relatives is more useful for lowly heritable traits. Table 4 contrasts correlations between true and estimated breeding values using three methods of evaluation. It is readily apparent that as more sources of information are added, the correlation becomes more complex. Ranking of animals on single trait performance records for ADG has a correlation of .63, while that of BF is .71. However, covariances between ADG and BF, as well as FE, are ignored. If the producer is interested in selecting for both traits, he must decide on a weight for each measurement.

A selection index weights information according to phenotypic and genetic covariances and economic values as well as heritability, giving producers a single index value on which to rank animals for selection. This value maximizes accuracy of selection if the weighting factors are correct (Hazel, 1943; Henderson, 1973). Unfortunately, these vary from population to population and the economic values may vary from farm to farm. The fact that selecting for multiple traits may slow genetic progress can be seen by comparing correlations for single traits and an index formulated for ADG and BF, with FE as a correlated trait (Table 4).
Table 4. Expected correlations between true and estimated breeding values calculated for evaluation of individual performance records, multiple trait selection index and best linear unbiased prediction of average daily gain and backfat probe

<table>
<thead>
<tr>
<th>Method of evaluation</th>
<th>Formula</th>
<th>Correlation</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>Individual performance record</td>
<td>$r_{uu} = h^2$</td>
<td>ADG = .63246</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>BP = .70711</td>
<td></td>
</tr>
<tr>
<td>Multiple trait selection index</td>
<td>$r_{uu} = \sigma_i / \sigma_H$</td>
<td>.589</td>
<td></td>
</tr>
<tr>
<td>Best linear unbiased prediction</td>
<td>$r_{uu} = \sqrt{1 - \frac{V(u-u)}{\sigma_G^2}}$</td>
<td>ADG: .60 to .70</td>
<td>BP: .67 to .75</td>
</tr>
</tbody>
</table>

\[ a_h^2_{ADG} = .40; \ h^2_{BP} = .50. \]

\[ b_I = 100 + 177(ADG-ADG) - 167(BF-BF). \] FE is carried as a correlated trait (Christian and Wood, 1985).

\[ c \] Values varied by number and distribution of animals, as well as the relationship among those animals. These represent the extremes found in this study.

Best linear unbiased predictions (BLUP) of breeding values may account for the same genetic information as selection indexes, but usually differ in that total numbers of animals as well as relatives included are important. Also, fixed effects are fitted in addition to predicting breeding value (Henderson, 1973). Economic weights are left up to the breeder.
As expected, results from this study indicate that, all else being equal, BLUP accuracies will be higher for traits with higher heritability, since the smaller $\sigma_e^2$ relative to $\sigma_G^2$, the smaller $V(\hat{u} - \hat{\mu})$ will be. However, depending on number of animals per fixed effect, and degree of relationship, and their interaction, the accuracies may be lower than that due to ranking on individual performance (Table 4). Specific instances are highlighted under appropriate sections of Results and Discussion.

Numbers of Animals

Unrelated boars

Increasing total number of animals within fixed effects is advantageous, as seen by writing out the absorption of fixed effects into the animal equations on the left-hand side. Assuming an animal model and a single fixed effect, the absorbed equation for the $i^{th}$ animal with a record is

$$[(1-1/n) + \sum_{j\neq i} (-1/n) + \sum_{j\neq i} (a_{ij}k)\hat{u}_j] = y_i - \bar{y}. \quad (14)$$

Since $\lim_{n \to \infty} 1/n = 0$, the more animals in a subclass, the more accurate the evaluation. At the limit, the fixed effect is known without error and can be substituted for the estimator obtained under BLUP, giving selection index values (Henderson, 1973). Table 5 contains results from a simple comparison of unrelated individuals, the only change
Table 5. Comparison of average accuracy of evaluation for different distributions of individual boars

<table>
<thead>
<tr>
<th>Distribution</th>
<th>Average accuracy of evaluation</th>
<th>Average daily gain</th>
<th>Backfat</th>
</tr>
</thead>
<tbody>
<tr>
<td>10 boars in each of two stations (n=20)</td>
<td>.59948</td>
<td>.67082</td>
<td></td>
</tr>
<tr>
<td>10 boars in each of five stations (n=50)</td>
<td>.59948</td>
<td>.67082</td>
<td></td>
</tr>
<tr>
<td>10 boars in each of eight stations (n=80)</td>
<td>.59948</td>
<td>.67082</td>
<td></td>
</tr>
<tr>
<td>40 boars in each of two stations (n=80)</td>
<td>.62500</td>
<td>.69857</td>
<td></td>
</tr>
</tbody>
</table>

\[ a_{u|u} = \sqrt{1 - \frac{\text{Var}(u-u)}{\sigma_g^2}} \]

being in the number of animals per test. By redistributing 80 animals from 10 in each of eight stations to 40 in each of two, PEV was reduced 4.9% for ADG and 6.9% for BF. Increasing the total number of animals by adding more stations did not affect accuracy when the stations were untied. The increases were small because heritability is high. Increasing numbers of animals by tying stations together is discussed later.

In an evaluation of class size relative to number of progeny, Ojala et al. (1985) found that three observations per subclass were sufficient for sire evaluation assuming sires were unrelated. Fewer than three resulted in unacceptable loss of information. Progeny numbers, however,
ranged from 20 to 320. Taking a different view, Chauhan (1985) compensated for small subclass numbers by treating portions of the effect due to herd-period-season as random. This decreased the effective number of daughters necessary to achieve a given level of accuracy, as Henderson (1975a) predicted.

Families

When family structure is considered, the effect of increasing numbers of pigs becomes more complicated. Numbers now must be distributed between more and/or larger families. With unlimited test space, the ideal situation would be larger, more numerous families. However, practically speaking, the opportunity to place one more boar in a pen (or replace a barrow with a boar) or to remodel or reorganize an existing station is more likely than being able to build larger ones.

Another method to increase numbers is to incorporate on-farm tests with central tests. This has the added appeal of testing boars based on their relatives' market performance, as there is some indication that the traits measured in the station are not those being marketed at the packing plant (Standal, 1977; Roberts and Curran, 1981). This is a long-term goal, however, and is not ready for implementation. Therefore, discussion centers around the idea of limited numbers in a finite set of central test stations. The following discussion uses half-sibs, but the situation is similar for full-sibs.

Figure 1 illustrates the differences in accuracy for varying numbers of half-sib families as family size increases. The graph is for ADG, but
Figure 1. Average accuracy of evaluation of average daily gain as influenced by number of families and half-sib family size
BF is very similar. It is apparent that accuracy will improve for smaller families faster than for larger families as family size increases (e.g., an increase in total numbers is more beneficial when numbers are low to begin with), since the change is proportionately smaller for the latter. To account for adjustment of station-season, almost 48 half-sibs (16 families of 3 pigs) are needed to equal the accuracy of individual performance records on ADG; four half-sibs in each of 16 families (64) are required for BF. Comparing distribution of numbers within and across families, increases in accuracy from 32 pigs (2 sibs in 16 families) to 40 pigs (8 sibs in 5 families) to 48 pigs (3 sibs in 16 families) for example, are not linear (Table 6).

Past 16 families, the slopes of the lines move towards zero, while the differences in family size remain parallel. Therefore, if test size is small, the first priority is to increase number of families; when that is maximized or reaches approximately 15, attention should turn to increasing family size. A two-pronged attack on the problem could include reorganizing tests to achieve more uniformity (like State and National breed tests) and concurrently rewriting entry requirements to fill pens most efficiently.

Degree of Relationship

Full-sibs have on the average 1/2 of their genes in common, while half-sibs share only a 1/4 of their genes in common and unrelated animals have no genes in common. Therefore, the accuracy of breeding
Table 6. Accuracy of prediction for boars within stations, accounting for degree of relationship

<table>
<thead>
<tr>
<th>Degree of relationship</th>
<th>Family size</th>
<th>Number of families</th>
<th>Number of boars</th>
<th>Accuracy&lt;sup&gt;a&lt;/sup&gt;</th>
<th>ADG</th>
<th>BP</th>
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</thead>
<tbody>
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<td>.67082</td>
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</table>

<sup>a</sup>ADG = Average daily gain; BF = Backfat.
value estimates made from records on full-sibs should be higher than corresponding values estimated for half-sibs, which would be expected to have more accurate estimates than individuals. However, in situations involving small numbers per subclass, the presence of nonzero off-diagonal elements may have a detrimental effect. Using average prediction error variance, this is shown in Table 7. The reason can be found by inspection of the equation for obtaining the inverse of a positive definite submatrix (14).

\[
P = \begin{pmatrix} \hat{p}_{11} & \hat{p}_{12} \\ \hat{p}_{21} & \hat{p}_{22} \end{pmatrix}, \quad P^{-1} = \begin{pmatrix} \hat{p}_{11} & \hat{p}_{12} \\ \hat{p}_{21} & \hat{p}_{22} \end{pmatrix}^{-1}
\]

and \( \hat{p}_{11} = [\hat{p}_{11} - \hat{p}_{12} \hat{p}_{22} \hat{p}_{21}]^{-1} \). (15)

If \( \hat{p}_{11} \) is a scalar, then the quantity \( (\hat{p}_{12} \hat{p}_{22} \hat{p}_{21}) \) is dependent on the number of animals, and the magnitude of the off-diagonal elements relative to the diagonals of \( \hat{p}_{22} \). This is similar to the weighting process used to determine \( \beta \), and is data dependent, as shown in Figure 2. When the matrix loses diagonal dominance, as is the case with small numbers and close ties, the inverse is different than expected. In fact, there appears to be a quadratic response, with extremes at both ends providing higher accuracy than those in the middle. In the case of unrelated animals, the matrix is diagonally dominant; on the other end of the scale, the matrix becomes blocks of
Figure 2. Influence of degree of relationship on accuracy of evaluation of backfat for varying number of families

GROUP CODE = NUMBER OF ANIMALS
1: N=4  2: N=10  3: N=20  4: NO FIXED EFFECTS
diagonal and off-diagonal elements which are close to being equal, resulting in "block" dominance. The minimum point for accuracy is a function of the number of fixed effects (as they influence the diagonal elements) and degree of relationship.

**Full-sibs versus half-sibs**

Focusing on full-sib and half-sib relationships, full-sib relationships result in higher accuracy than for half-sib boars. Comparing Figure 1 with Figure 3, the result can be seen graphically. Under the assumption of no $c^2$, the addition of extra full-sibs has more than double the impact of adding the same number of half-sibs. When tests are as large as 25 families, two full-sibs contribute almost as much information as six half-sibs, if families are independent.

**Multiple family ties within station**

The next logical progression is the presence of ties among multiple families within a station-season. This is representative of the situation which occurs when a sire has more than one set of littermate progeny on test at the same time. While not frequent in central tests, this will occur more often in an on-farm performance program.

As previously suggested, these designs with large numbers of ties tend to increase average PEV. From the average PEV in Table 7, it can be seen that the situation definitely is worse for smaller tests and marginally so for the trait with higher heritability (BF).

Closer inspection of individual PEV for boars reveals why the
AVERAGE DAILY GAIN

Figure 3. Average accuracy of evaluation of average daily gain as influenced by number of families and full-sib family size.
Table 7. Average prediction error variances of average daily gain and backfat probe for full-sib boars tied by sires within stations

<table>
<thead>
<tr>
<th>Number per family</th>
<th>Total number of sires</th>
<th>Number of sires</th>
<th>Prediction error variance</th>
<th>Average daily gain</th>
<th>Backfat probe</th>
</tr>
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Table 7. (continued)

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<th>Number per family</th>
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</table>

averages behave as they do. Table 8 contains PEV for individual boars. In each design, two subsets of PEV were generated, based on the pattern of ties. With small numbers of ties, the subsets consisted of boars with direct ties and boars with no ties. When the number of ties grew large enough, the two subsets contained boars with multiple ties and those with single ties. For example, in a test consisting of five pens, one sire tie resulted in two litters having one PEV (.0037767) and the other three having another (.0036982). When these five litters were sired by two boars, however, the first subset consisted of three litters from one sire; the second contained the two litters sired by the second boar. In other words, all litters were tied directly with at least one other and some were tied more tightly than others.

Several points can be made from Table 8. First, increasing ties among animals increased PEV in all cases investigated except the large (25 family) test. In that instance, the design with the fewest sires resulted in a slightly lower PEV than the one with five more sires.
Table 8. Prediction error variance of average daily gain and backfat for boars with sire ties across families, within tests

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<td>3</td>
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<td>0.0031764</td>
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</tbody>
</table>

\textsuperscript{a}In the case of very few sires, this column contains prediction error variances for boars with multiple ties.

\textsuperscript{b}In the case of very few sires, this column contains prediction error variances for boars with single direct ties.
However, the variance still was higher than the cases with fewer sire ties. This pattern followed the one discussed earlier, but was much harder to detect since the designs contained more variables. Having more animals within a family helped alleviate the pressure some, as did increasing the number of families within a test. The 75 animals present in 25 families of three littermates each had the lowest PEV. As noted previously, evaluation of BP, with its higher heritability, resulted in lower PEV than ADG, and more dramatic changes occurred in the smaller sized tests.

Ties Across Tests

Analysis of multiple stations

Analyzing untied station-seasons as one data set is analogous to analyzing stations separately, since the coefficient matrix is a block diagonal matrix. The only advantage may be computational efficiency, if the data sets are small. In larger data sets, separate analyses would be more cost effective and analyzing station-seasons together may give the impression that the data are comparable.

Among the advantages of tying stations using genetic relationships are:

1) use of relative information to help predict breeding values;
2) solutions are comparable across station-seasons, so boars can be compared;
3) animals (e.g., parents) with no records can be evaluated;
4) an equivalent reduced animal model may be written to increase computational efficiency.

Disadvantages include

1) more complex programming for extremely large data sets;
2) higher cost.

Reports to date all have been favorable regarding the inclusion of genetic relationships. Henderson (1975c,d) demonstrated how inclusion of sire relationships improved accuracy of evaluation; Pollak and Quaas (1981) examined the possibility of eliminating groups by using the complete relationship matrix to account for genetic differences among herds and genetic trend. The relationship matrix played a crucial role in development of the reduced animal model as well (Blair and Pollak, 1984). Designed ties such as reference AI sires in beef have proven useful, though recent work suggests naturally occurring ties might be sufficient (Wilson, 1982). In Carlson's study (1980), greater increases in accuracy were obtained by using an animal model, compared to literature reports based on a sire model, if relationships were included in both.

Results of designs using three kinds of ties (sire or half-sib, paternal grandsire or half-cousin, and full-sib) are presented and discussed. These ties were used to connect three hypothetical stations of varying sizes (5, 16 and 25 families). The average test size based on the test station survey was 16 pens (Appendix A). Five pens were chosen as an arbitrary extreme and some of the recommendations made
by Robison (1982) suggested 25-pen tests could be a reality in the future. The ties chosen are either representative of the purebred swine industry today, wherein sons of popular sires produce the boars being tested in central stations (half-cousin); the traditional sire evaluation model (half-sib); and the possibility of more closely tying neighboring evaluation stations on a regional basis (full-sib).

Half-sib ties

A half-sib tie is defined here as litters located in different station-seasons having the same sire. Number of boars per litter was varied as number of ties changed to provide some idea of how these factors varied together. Table 9 contains average PEV of individual boars. The sparseness of the large matrix led to the expected results; as number of ties increased, the average PEV gradually declined.

Individual PEV carried to three significant digits are in Figure 4. Boars in tied stations can be compared to those in stations with no ties and are clearly evaluated more accurately. Even boars in small tests have a higher accuracy than that obtained from ranking on individual performance. This increase in accuracy for those boars with ties is what increases the average for the whole test. Comparison of Figure 4 with Figure 5 demonstrates that tying smaller families will increase accuracy as much as increasing family size. For example, 15 animals (5 families of 3 full-sibs) with no ties to other stations have almost the same accuracy (.62298) as 10 animals with a tie to the other two stations (.62290). Note, however, that both accuracies are
Figure 4. Average accuracy of evaluation of average daily gain measured on boars with or without half-sib ties across stations
Figure 5. Average accuracy of evaluation of average daily gain measured on full-sib boars in different size families, with one half-sib tie across stations.
Table 9. Average prediction error variances of average daily gain and backfat probe for boars in tests tied by half-sibs

<table>
<thead>
<tr>
<th>Number per family</th>
<th>Total number</th>
<th>Number of sires</th>
<th>Number of ties</th>
<th>Average prediction error variance</th>
<th>Average daily gain</th>
<th>Backfat probe</th>
</tr>
</thead>
<tbody>
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</table>

Three stations with 5, 16 and 25 pens.

lower than obtained by ranking on individual performance, because of fitting the fixed effect.

When the accuracies are carried out five significant digits, the equations behaved similarly to the smaller data sets (Table 10). Again, the results are data dependent, but in general, for a fixed sample size, animals with direct ties had lower accuracies of prediction than those with no ties. However, the increase in accuracy of evaluation of untied animals in the same test more than compensated for the small decrease in the accuracy for closely related boars. The end result was the observed increase in average accuracy. In the case of very small numbers of animals, the connections with larger groups
Table 10. Comparison of accuracy of evaluation of full-sib boars with varying number of sire ties across stations

<table>
<thead>
<tr>
<th>Number of ties</th>
<th>Number of pens</th>
<th>Accuracy</th>
<th>Accuracy</th>
<th>Accuracy</th>
<th>Accuracy</th>
</tr>
</thead>
<tbody>
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<td></td>
<td>Average daily gain</td>
<td>Backfat probe</td>
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<td>Indirect</td>
</tr>
<tr>
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<td>Direct</td>
<td>Indirect</td>
<td>Direct</td>
<td>Indirect</td>
</tr>
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<td>Three full-sibs per family</td>
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</table>

*Direct = boars with direct ties; Indirect = test mates of boars with direct ties.*
Table 10. (continued)

<table>
<thead>
<tr>
<th>Number of ties</th>
<th>Number of pens</th>
<th>Accuracy</th>
<th>Average daily gain</th>
<th>Backfat probe</th>
</tr>
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<td></td>
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</table>

through ties more than offset the nonzero off-diagonals, resulting in a higher accuracy throughout (Table 10).

As number of ties increased, the rate of change in accuracy of directly and indirectly tied boars in small tests decreased; conversely, the rate of change accelerated in the negative direction for the directly tied boars in the larger tests, while the positive rate of change decreased for the indirectly tied animals (Table 11). Based on these observations, and similar patterns in other designs, it appears that the effect is of a quadratic nature.

**Paternal half-cousin ties**

Paternal half-cousin ties are ties generated as a result of using half-sib sires to produce litters which are tested in different stations,
Table 11. Percent change in accuracy relative to untied stations for full-sibs tied across stations by sires (half-sib ties)\textsuperscript{a}

<table>
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<th>4</th>
<th>5</th>
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<td>IND</td>
<td>DIR</td>
<td>IND</td>
<td>DIR</td>
</tr>
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<td>2.1517</td>
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<td>0.0031</td>
<td>2.0258</td>
<td>0.0046</td>
<td>2.0066</td>
</tr>
</tbody>
</table>

\textsuperscript{a}Average daily gain measured on full-sibs.

\textsuperscript{b}DIR = directly tied boars; IND = test mates of directly tied boars.
The sires themselves may not be in the same location. The paternal grandsire is the least related common relative. This situation is common in the purebred swine industry: a popular boar sires sons which are sold to a number of breeders. They in turn enter litters out of these sons in performance tests. If these ties are common enough, it might be possible to dispense with some of the restrictions and cooperation necessary to generate artificial ties.

Unfortunately, relative to half-sib ties, these are quite weak in so far as improvements in accuracy are concerned. Table 12 contains average PEV carried to three significant digits. No change is apparent as half-cousin ties are added. Intuitively, one may feel better about comparing animals across stations after adding these ties, but other methods must be employed to improve accuracy. Figures 6 and 7 bear this out and demonstrate the role larger numbers can play in obtaining accuracies above those obtained from single records on the individual.

On the other hand, possible genetic change per year is expressed as

\[ \Delta G = \frac{\sigma_G^* r_{uu}}{I} \]

Genetic change is maximized by maximizing the numerator and minimizing the denominator. Additive genetic variance \( (\sigma_G^2) \) is essentially a constant within any one person's lifetime. The correlation between true and estimated breeding values \( (r_{u}) \) is maximized by using BLUP
Figure 6. Average accuracy of evaluation of average daily gain measured on full-sib boars with or without half-cousin ties across stations.
Figure 7. Influence of family size on average accuracy of evaluation of average daily gain measured on full-sib boars tied by half-cousins across stations.
Table 12. Average prediction error variances of average daily gain and backfat probe for boars in tests tied by half-cousins

<table>
<thead>
<tr>
<th>Number per family</th>
<th>Total number</th>
<th>Number of sires</th>
<th>Number of ties</th>
<th>Average prediction error variance</th>
</tr>
</thead>
<tbody>
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<td></td>
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<td></td>
<td>Average daily gain</td>
</tr>
<tr>
<td>2</td>
<td>92</td>
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<td>46</td>
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</tbody>
</table>

*Three stations with 5, 16 and 25 pens.

except under very limiting conditions and the generation interval (I) may be minimized by using the animal model and the animal's own performance record, rather than progeny test. Finally, the selection differential (i) may be increased by fairly comparing more animals and choosing a smaller proportion of the total, and this is what the half-cousin ties influence.

A closer look at the individual accuracies reveals the same general pattern discussed earlier (Table 13): the inflection occurs sooner than in the case of half-sib ties, and the order of magnitude is about 1/16 that of half-sib ties. This is the reason the average PEV changes so little.
Table 13. Comparison of accuracy of evaluation of full-sib boars tied across stations by half-cousin ties

<table>
<thead>
<tr>
<th>Number of ties</th>
<th>Number of pens</th>
<th>Average daily gain</th>
<th>Accuracy&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Backfat probe</th>
</tr>
</thead>
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<td>Indirect</td>
<td>Direct</td>
</tr>
<tr>
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<sup>a</sup>Direct = directly tied boars; Indirect = test mates of directly tied boars.
Full-sib ties

Full-sib ties are generated by sending one or more littermates to different test stations. This is the most artificial of the ties considered, but locations of stations (Appendix A) would lend themselves to a regional network consisting of tightly linked groups of stations tied on a national basis by designed ties such as those provided by AI sires.

Average PEV are found in Table 14. In contrast to the other ties, these are quite strong if numbers are comparable. Even if individuals are sent to different stations, that one tie is strong enough to increase accuracy from less than .60 to .63 for small tests (5 families), as shown

Table 14. Average prediction error variances of average daily gain and backfat probe for boars in tests tied by full-sibs

<table>
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<tr>
<th>Number per family</th>
<th>Total number</th>
<th>Number of sires</th>
<th>Number of ties</th>
<th>Average prediction error variance</th>
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a Three stations with 5, 16 and 25 pens.
in Figure 8. However, some caution must be exercised, since $c^2$ is not in the model. The other major drawback is that there is at present a biological limit to the number of ties possible, relative to half-sib and half-cousin ties. From Figure 9, it also appears that the beneficial effect of additional families is masked somewhat by the presence of a full-sib tie; the slope of the tie line is much flatter than the untied line. However, it is well above .6325, whereas more than ten families are required to match that accuracy if no tie exists.

Table 15 shows the changes in individual accuracies. The pattern is the same as that for half-sib ties, just four times as large. In general, the differences in order of magnitude among the three kinds of ties are functions of the square of the degree of relationship, relative to one of the relationships involved. For example, full-sibs have 1/2 of their genes in common. Comparing half-cousin ties relative to full-sib ties, the degree of relationship is weighted by the inverse of 1/2, then the result is squared. Half-cousin ties are approximately

$$[1/16*2]^2 = [1/8]^2 = 1/64$$

as strong as full-sib ties. Table 16 summarizes differences in average accuracy for the three types of ties across stations. The numbers must be taken to five significant digits for paternal half-cousin ties to show any changes in percent increase in accuracy relative to no ties at all.
Figure 8. Influence of family size on average accuracy of evaluation of average daily gain measured on boars with full-sib ties across stations.
Figure 9. Average accuracy of evaluation of average daily gain for boars with or without full-sib ties across stations
Table 15. Accuracy of evaluation for full-sibs tied across stations by littermates (full-sib ties)

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<th>Backfat probe</th>
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Individual boars tied by littermates across stations

|                |                |                    |               |              |               |
|                |                |                    |               |              |               |
| 1              | 5              | 0.63065            | 0.56664       | 0.68902      | 0.63410       |
| 1              | 16             | 0.66109            | 0.61246       | 0.72420      | 0.68480       |
| 1              | 25             | 0.66605            | 0.61971       | 0.72997      | 0.69288       |
| 2              | 5              | 0.63069            | 0.56747       | 0.68942      | 0.63552       |
| 2              | 16             | 0.66074            | 0.61252       | 0.72384      | 0.68490       |
| 2              | 25             | 0.66576            | 0.61974       | 0.72966      | 0.69292       |
| 3              | 5              | 0.63069            | 0.56747       | 0.68942      | 0.63552       |
| 3              | 16             | 0.66037            | 0.61256       | 0.72345      | 0.68498       |
| 3              | 25             | 0.66545            | 0.61975       | 0.72933      | 0.69295       |

aDirect = directly tied boars; Indirect = test mates of directly tied boars.
Table 15. (continued)

<table>
<thead>
<tr>
<th>Number of ties</th>
<th>Number of pens</th>
<th>Accuracy (^a)</th>
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<th>Backfat probe</th>
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Table 16. Percent increase in average accuracy of evaluation when full-sib, half-sib or half-cousin ties are added across stations

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<th>Type of tie</th>
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\(^a\)Percent reduction is relative to accuracy of evaluation for average daily gain when there are no ties across stations.
Accuracy of sire evaluations

One advantage to using the animal model is that related animals with no records of their own can also be evaluated, simultaneously. A measure of accuracy for those animals is also obtained. Sire average PEV are summarized in Table 17. Because the portion of the relationship matrix directly concerned with sires was relatively sparse (they were assumed to be unrelated except in the case of half-cousin ties), the average PEV decreased as more information about greater numbers of progeny was assumed, up to a point represented by the evaluation of two sires based on a total of 15 or 20 progeny. The limit to prediction error variance is the additive genetic variance of the trait; either known without error, or with no information at all. In the case of related sires, average prediction error variance decreased very little. These results are in agreement with work on sire models by Henderson (1975c,d); Wilson (1982); Ojala et al. (1985); and Wilmink and Dommerholt (1985).

On the other hand, classical experiments have shown the danger of using full-sibs to evaluate parents (Lush, 1935, 1945; Falconer, 1981; and Pirchner, 1983) and that knowledge should be accounted for when deciding what to emphasize, young boars or sires. Also, in contrast to most traits evaluated under a sire model, ADG and BF are fairly highly heritable. As might be expected, in this study the best sire evaluation occurred when eight half-sibs were used to progeny test their sire. One possibility is use of market pig progeny to evaluate...
Table 17. Average prediction error variances of evaluations for sires of boars\(^{a,b}\)

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\(^{a}\)NO = Number of boars per family; N = Total number of boars; NS = Number of sires; ADG = Average daily gain; BF = Backfat probe.

\(^{b}\)Common environmental effects are not included in the model.
Table 17. (continued)

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sires and/or young boars. This may be the most efficient utilization of on-farm information, and would also help in cases where selection for marketability through traits of boars is less than perfect (Standal, 1977; Roberts and Curran, 1981).

Sources of Error

Consequences of using the wrong model

There are several consequences associated with use of the wrong model (Henderson, 1975a). If fixed effects are ignored, solutions will be biased. However, inclusion of trivial fixed effects will cause a needless increase in PEV and cost of computing. If too many are included relative to the number of animals, PEV may increase instead of decreasing. As shown earlier, with very limited numbers of animals, a single fixed effect can be enough to cause damage. However, if and only if the magnitude of a particular fixed effect can be estimated can the actual bias be estimated and an evaluation of its removal from the model be performed. Otherwise, it is up to the investigator to decide exactly where to draw the line. Possible candidates for removal include fixed effects with no statistical or biological significance. If the effect can be estimated well enough to calculate the bias, it probably can be estimated well enough to adjust the data before analysis, eliminating the need for its inclusion in the first place.

Ignoring random effects causes an increase in sampling variance, but solutions still are unbiased. If random effects are treated as
though they were fixed, to account for selection, the prediction error variance will be larger (Henderson, 1975a). The consequences of using the wrong variance-covariance matrix is harder to discern, but Henderson (1975a) showed that using a simplified relationship matrix relative to the actual one will result in larger PEV.

All of the results reported and discussed so far are predicated on the assumption that the model was specified correctly. Obviously, the animal model used in this study was a simplification of the true data structure. Many studies have been conducted to determine the magnitude and/or adjustment factors of effects which may influence the estimation of an animal's true breeding value. These encompass physiological effects such as sex or age, environmental effects like season and housing and genetic factors like breed or level of inbreeding. In swine, one factor of great concern is common environmental effects.

**Fixed effects**

The first decision is whether a particular effect should be treated as fixed or random. Kennedy (1982) listed several fixed effects considered to be important: herd-year-season, weight of the pig at testing, sex of the pig, genetic groups and breed composition. Several of these were necessary to account for some of the preselection occurring before pigs were put on test. Inclusion of litter effects as fixed was discussed, but the conclusion was that it was more important to treat them as random. In the actual analysis of Canadian field data (Hudson and Kennedy, 1985a), breeds were analyzed separately, because the variance-
covariance matrix was not the same across breeds (Kennedy et al., 1985).

Carlson (1980) found that pen effects were significant in the station-seasons analyzed. However, because several factors probably were confounded in the effect, he chose to ignore it. Other factors discussed by Carlson (1980) included preweaning environment, farm effect (pretest environment, management and selection), within litter selection, season and weight of the pig.

**Breed**

There are two methods for taking into account differences in subpopulations due to factors such as sex or breed. The first is to analyze each factor separately. The second is similar to multiple trait analysis in that animals within a sex or breed are given separate variance-covariance structures (Kennedy, 1982). In this study, the model was written on the assumption of within-breeding analysis of one sex (boars). Even if breed effect is taken out by treating it as fixed (which assumes homogeneity of variance across breeds) comparing boars of different breeds directly may be detrimental to the industry because the commercial pig is a crossbred, and the wider the cross, the more heterosis that is generated. Keeping the analysis within breed hopefully will encourage the use of superior boars in planned programs of genetic improvement in the seedstock industry (Willham, 1982).

**Pen effects**

In central swine testing stations, pen effects are a major source of possible bias and confusion. The practice has been to pen together animals sired by the same boar, for several reasons.
Measurement of FE is an obvious one. Other reasons include fear of disease, ease of locating boars from particular breeders and logistics (multiple entry dates). However, this practice makes it very difficult to obtain good estimates of breeding values for ADG and BF, because pen effects tend to contribute a nongenetic cause to the likeness among relatives (Lush, 1935; Falconer, 1981), especially for littermates, which have been together since conception. Coupled with the fact that there usually are few animals per pen, the end result has been to ignore the effect and accept the bias (Carlson, 1980).

To gain a better understanding of pen effects, a designed experiment should be conducted. Features which should be considered are use of a sire model (an interaction model was proposed by Henderson, 1973), with progeny of sires distributed over a wide range of pen locations; use of paternal half-sibs, to lessen the effect of preweaning common environment; and commingling of animals at the test site, to minimize confounding of pen effects with other fixed effects. The purpose is to estimate the true fixed effect of pens, not the combined effects of common environment and pen. These estimates should provide insight into the problem of common environmental effects.

Common environment Hudson and Kennedy (1985a) attempted to account for at least some of the possible common environmental effects in their data by treating litters as random and fitting a litter effect. In this study, it was ignored, because very few estimates of the variance are available, and because it was one more factor to consider.
If \( c^2 \) is ignored, the variance is added to the estimate of genetic variance: \( \sigma^2_G + \sigma^2_G \). This tends to inflate heritability, since

\[
E(h^2) = \sigma^2_G / (\sigma^2_G + \sigma^2_G + \sigma^2_e);
\]

but \( h^2 = (\sigma^2_G + \sigma^2_G) / (\sigma^2_G + \sigma^2_G + \sigma^2_e) \).

In the case of mixed model equations, the ratio added to the diagonals of the animal equations is \( k = \sigma^2_e / \sigma^2_G = 1 - h^2 / h^2 \) if \( h^2 = \sigma^2_G / (\sigma^2_G + \sigma^2_G + \sigma^2_G) \)

but \( k = \sigma^2_e / (\sigma^2_G + \sigma^2_G) \) if \( c^2 \) is ignored. This results in accuracies that are too high. The exact amount overestimated is dependent on the variance of the common effect. If tests are designed to minimize \( c^2 \), resulting PEV estimates should be close to the actual PEV.

If \( c^2 \) is added to the model,

\[
y = X\beta + Z_1c + Z_2u + e,
\]

where \( Z_1 \) is a \( n\times d \) incidence matrix relating observations to litter effects; \( c \) is a \( d \times 1 \) vector of unknown nongenetic and epistatic random litter effects; and all other terms are defined as in (2).

The mixed model equations are

\[
\begin{bmatrix}
X'X & X'Z_1 \\
Z_1'X & Z_1'Z_1 + k_1 Z_1Z_2
\end{bmatrix}
\begin{bmatrix}
\hat{\beta} \\
\hat{u}
\end{bmatrix}
= 
\begin{bmatrix}
X'y \\
Z_1'y
\end{bmatrix}
\]

where \( k_1 = \sigma^2_e / \sigma^2_G \) and \( k_2 = \sigma^2_e / \sigma^2_G \).
In that case, prior knowledge of $\sigma^2_c$ is required, or it can be estimated from the data (Henderson, 1984), with the proper specifications. Kennedy et al. (1985) obtained an estimate of litter variance, which was used to approximate $\sigma^2_c$. Another possibility would be to account for true pen effects using previously estimated adjustment factors, or by simultaneously obtaining the appropriate adjustments and variances during the analysis. The effect of full- or half-sibs penned together then could be used as an estimate. Detailed studies of possibilities need to be conducted.

Recommended Designs

Central test stations

Based on the literature survey and results from this study, the following recommendations for efficient evaluation of potential herd sires are suggested.

1) Tests should be within breed, but as large as possible. Given the current locations of central test stations (Appendix A), regional tests drawing from several states could be organized, similar to the state and national breed tests now conducted. Genetic ties among tested boars would be very useful in tying such tests over time, so young boars could be compared with older sires, within the same breed.

2) Entries should be composed of four boars from a maximum of two litters, or three littermate boars. This is based on the assumption that common environmental effects are minimized or estimated in the
If sire evaluation is an important (though secondary) concern, consideration of a concurrent progeny test based on market pigs might be worthwhile. A minimum of eight half-sib pigs would be required if the information is going to be helpful in evaluating the young boars. Realistically, however, outstanding performance tested boars should soon be siring test station candidates and those progeny will simply contribute information to increase the accuracy of the older sires' estimates and vice versa.

3) For breeds which are not as concentrated in any one area of the country, small tests are a distinct possibility. Under such circumstances, restrictions on number of ties should be made. If fewer than five families are tested, every effort to tie in with other tests should be made. Otherwise, entries should be restricted to full-sibs, so that only one litter per sire is entered. If fewer than 15 families are tested and cannot be tied to other station-seasons, the usual entry requirements hold, but are limited to one per sire. Again, however, it will not take long before there are enough data to tie tests together over time, if not space, and the problem should become academic.

4) In order to lessen the probability of correlated samples causing increased PEV, as many tests as possible should be directly comparable. Until a thorough analysis of several years worth of data can be conducted, the safest course is to tie stations and tests over time by designing either half-sib ties, full-sib ties, or a combination of both, much as the beef industry did when the national sire evaluations
were begun (Winrock International, 1983). Once the program is well under way, the possibility of discontinuing the designed ties should be considered.

On-farm performance programs

A goal of geneticists and breeders is the inclusion of all available information when evaluating breeding values of animals. On-farm tests offer the opportunity to gain more information, and better represent the true conditions under which progeny of selected boars must perform. On the other hand, field data tends to be messier to analyze, and there is greater room for error and misuse. The amount of information gathered may also be overwhelming.

In on-farm tests, the problems associated with small numbers of closely tied animals are more likely to appear. One solution to many would be the best of both: combining on-farm and central test information. Until then, geneticists analyzing on-farm data should be aware of problems that can occur and realize there is little that can be done beyond specifying as complete a model as possible. This may mean accepting higher PEV in order to minimize bias, or accept a higher cost to account for more effects, random and fixed.

Sire evaluation

The dairy industry was forced to use progeny tests; the beef industry made it work as well. Whether sire evaluation will become the mainstay of swine breeding programs remains to be seen, although most
work has been headed that way (Mabry and Beneshek, 1984; Hudson and Kennedy, 1985a,b; Schinckel et al., 1985). Through AI, a sire can have a large number of half-sib progeny, which leads to the working definition of breeding value: twice the deviation of the mean of the progeny of selected parents from the population mean. It also side-steps the questions surrounding common environment and confounding of effects if half-sibs are not penned together. On the other hand, such progeny tests extend the generation interval, and the swine AI industry is not yet large enough to remodel the swine industry in the beef or dairy mold.
CONCLUSIONS

Summary of Findings

Design parameters

Based on an extensive review of the literature, the average genetic correlation between ADG and BF was determined to be close to zero. This allowed the use of single trait mixed model equations for this simulation. An additional simplification—selecting for FE indirectly—was possible because the genetic correlations between ADG and FE and BF and FE appeared to be favorable and relatively large. However, individual data sets will require evaluation on a case-by-case basis before these assumptions can be used to predict breeding values of specific animals.

Influence of heritability

Accuracy of evaluation for ADG \( (h^2 = .40) \) was lower than that of BF \( (h^2 = .50) \), when all else was held constant. Addition of genetic relationships resulted in greater rate of improvement in accuracy for ADG than for BF, although neither trait showed a large absolute increase in accuracy. Conversely, increasing the number of boars within station-seasons was more helpful in the evaluation of BF, since fixed (nongenetic) effects were more accurately estimated.

Number of boars

To obtain the same level of accuracy when fitting one fixed effect as was obtained when individual performance was used, close to 48 boars had to be evaluated for ADG and 64 boars were required for BF. As number
of boars per station-season increased, accuracy of evaluation increased. Rate of increase was greatest as number of independent families increased from 5 to 15. Beyond 15 families, accuracy could best be improved by increasing family size within station-season, and by tying station-seasons using the genetic relationships among boars. To minimize the impact of small tests, serious consideration should be given to entry requirements which will limit the genetic covariances among families of boars.

**Genetic relationships**

Increasing family size when families were not related to each other resulted in increased accuracy of evaluation. The impact of increasing full-sib family size by one was more than double that of adding a half-sib, and the advantage was greater as test size (numbers of families) increased.

Pedigree information linking half-sib or full-sib families within station-season was useful when the diagonal elements of the animal equations were large relative to the magnitude of the off-diagonal elements. Factors which influenced the degree of diagonal dominance were total number of boars, number of fixed effects, distribution of boars within fixed effects, heritability and degree of relationship among boars. More closely related animals had larger PEV than less closely related animals when small numbers of closely related families were evaluated and if fixed effects were fitted. Adjusting for one effect (station-season) caused decreases in accuracy for boars in closely related families if numbers were small. Fitting more effects
worsened the situation if total numbers did not increase. Accuracy of evaluation of BF was more robust to decreases in diagonal dominance than that of ADG. Tying station-seasons using genetic relationships resulted in the same pattern, but total increase in accuracy over untied levels of fixed effects far outweighed the slight decrease in accuracy for closely related boars, resulting in an increase in average accuracy. Small tests tied with larger ones had accuracies higher than those obtained by using individual performance and even closely related boars in small tests were evaluated with increased accuracy.

Full-sib ties across three stations representing small, medium and large test sizes were four times as strong as half-sib ties and half-cousin ties increased accuracy only 1/16 as much as half-sib ties, when number of boars was equal.

**Designing relationship ties**

Relationship matrices may be used to tie stations together to compare more boars (thus increasing the selected differential) and to provide matrices which may be sparse enough to yield more accurate predictions of breeding values. It also is possible in the context of a central test situation to specify covariances among animals through imposition of entry requirements. By limiting genetic relationships among families, small numbers of boars can still be accurately evaluated. Likewise, specific ties could prove especially valuable if on-farm performance tests are linked with the central tests.
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ACKNOWLEDGMENTS

A brief section at the end of a dissertation is not enough to delineate all the emotions wrapped into the ending of one aspect of a life and the beginning of a new, but some of the many people who made our stay in Ames a time to remember should get special mention.

I would like to recognize the contributions of all the swine test station managers and personnel who took the time out of their busy schedules to answer my questions, and who were more than willing to share their knowledge. Their replies helped shape the study reported in this dissertation.

For their willingness to serve on my committee, with the responsibility and extra work that entails, I would like to thank Dr. Freeman, Dr. Harville, Dr. Rothschild and Dr. Speer. A special thank you goes to Dr. Willham for serving as a substitute on my committee, and for his encouragement and advice.

Kudos to Paul Van Raden for refreshing my memory on FORTRAN and for the ensuing discussions about the contents of this dissertation. Good luck, Paul.

One paragraph can't adequately cover three and a half years shared with all the breeding graduate students, but thanks, guys. It's been real. Special recognition goes to Becky Hagenow, Lois Lawrisuk and Susan Durham. Camaraderie does wonders when the going gets rough.

Decide on who you want to study under and count the school as a bonus. That piece of advice has proven 100% right. Dr. Howard Miller
was an excellent major professor in Mississippi and the choice of
Dr. Christian here makes it two for two. Working as a TA, I have had the
opportunity to learn by observing while receiving a formal education.
I am proud to be counted as one of his students and I only hope I do
as well; I certainly have a good example to follow. Thanks, LC!

I've said it before, but it deserves repeating: Mom and Dad Maxson
and Mom and Dad Green—you all did a better job than we used to think.
Hopefully, the next generation will also navigate safely the process of
growing up, with our help. Thanks. I understand more the older I get.

I am blessed with a most understanding husband, Keith and a very
precious daughter, Mary. To them is dedicated this work: without their
love and support, it would not have happened. But along with the joys,
each is allotted sorrow. My brother, dedicated to serving the Lord,
lost his fight against lymphoma on February 19, 1985. So this is also a
memorial to Michael Russell Maxson, born January 13, 1961. He rests in
peace, and we remember.
APPENDIX A.

TEST STATION SURVEY RESULTS
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<td>355</td>
<td>24</td>
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<td>1</td>
<td>3</td>
<td>0</td>
<td>14</td>
<td>1</td>
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Table A2. Entry requirements

<table>
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<th>Test station</th>
<th>Number per pen</th>
<th>Relationship</th>
<th>Remarks</th>
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</thead>
<tbody>
<tr>
<td>Florence, AL</td>
<td>3</td>
<td>half-sibs</td>
<td></td>
</tr>
<tr>
<td>Sand Mtn, AL</td>
<td>2</td>
<td>full-sibs</td>
<td></td>
</tr>
<tr>
<td>Arkansas</td>
<td>2</td>
<td>half-sibs</td>
<td></td>
</tr>
<tr>
<td>California</td>
<td>3</td>
<td>half-sibs</td>
<td>no barrows</td>
</tr>
<tr>
<td>Florida</td>
<td>2</td>
<td>half-sibs</td>
<td></td>
</tr>
<tr>
<td>Georgia</td>
<td>single</td>
<td></td>
<td>plan to change to groups in fall</td>
</tr>
<tr>
<td>Western IL</td>
<td>2</td>
<td>half- or full-sib</td>
<td></td>
</tr>
<tr>
<td>Indiana</td>
<td>2</td>
<td>half-sibs</td>
<td>plan to change to 4 or 8/pen with feeding stalls</td>
</tr>
<tr>
<td>Ames, IA</td>
<td>3; 1</td>
<td>full- or half-sibs</td>
<td>barrows littermate to at least 1 boar</td>
</tr>
<tr>
<td>Farmland (IA)</td>
<td>3 or 4</td>
<td>full- or half-sibs</td>
<td></td>
</tr>
<tr>
<td>Lisbon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ida Grove</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northeast IA</td>
<td>3 or 4; 1</td>
<td>full- or half-sibs</td>
<td>1 barrow/pen</td>
</tr>
<tr>
<td>Louisiana</td>
<td>4</td>
<td>half-sib</td>
<td>open, but not testing now</td>
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<tr>
<td>Michigan</td>
<td>3</td>
<td>half- or full-sib</td>
<td></td>
</tr>
<tr>
<td>Minnesota</td>
<td>2 (4)</td>
<td>half-sib (full)</td>
<td>barrows only; 4/pen are 2 pairs of full-sibs</td>
</tr>
<tr>
<td>Northeast MO</td>
<td>3</td>
<td>full- or half-sibs</td>
<td>maximum of 2 litters</td>
</tr>
<tr>
<td>Northwest MO</td>
<td>3</td>
<td>full- or half-sibs</td>
<td>no barrow maximum of 2 litters</td>
</tr>
<tr>
<td>Southeast MO</td>
<td>3</td>
<td>full- or half-sibs</td>
<td>maximum of 2 litters</td>
</tr>
<tr>
<td>Test station</td>
<td>Number per pen</td>
<td>Relationship</td>
<td>Remarks</td>
</tr>
<tr>
<td>-------------------</td>
<td>---------------</td>
<td>---------------------</td>
<td>------------------------------</td>
</tr>
<tr>
<td>U of MO-Col</td>
<td>3</td>
<td>full- or half-sibs</td>
<td>maximum of 2 litters no barrows</td>
</tr>
<tr>
<td>Montana</td>
<td>2</td>
<td>full- or half-sibs</td>
<td></td>
</tr>
<tr>
<td>N. Carolina</td>
<td>2</td>
<td>full-sib</td>
<td></td>
</tr>
<tr>
<td>Ohio</td>
<td>3</td>
<td>full- or half-sibs</td>
<td>maximum of 2 litters</td>
</tr>
<tr>
<td>Oklahoma</td>
<td>4</td>
<td>pooled by wt, then</td>
<td>market gilts and barrows</td>
</tr>
<tr>
<td></td>
<td></td>
<td>breed then sire</td>
<td></td>
</tr>
<tr>
<td>S. Carolina</td>
<td></td>
<td>full- or half-sib</td>
<td></td>
</tr>
<tr>
<td>S. Dakota</td>
<td>3 or 4</td>
<td>half-sib</td>
<td>trying to get organized</td>
</tr>
<tr>
<td>Tennessee</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Texas</td>
<td>3 or 4</td>
<td>none, specifically</td>
<td>pens comingled</td>
</tr>
<tr>
<td>Virginia</td>
<td>2</td>
<td>full-sibs</td>
<td></td>
</tr>
<tr>
<td>Wisconsin</td>
<td>4</td>
<td>full- or half-sibs</td>
<td>maximum of 2 litters</td>
</tr>
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</table>
Figure A1. Locations of central swine testing stations in the United States, 1985
APPENDIX B.

SUMMARY OF LITERATURE ESTIMATES OF

PHENOTYPIC AND GENETIC PARAMETERS FOR

AVERAGE DAILY GAIN, BACKFAT PROBE AND FEED EFFICIENCY
Table B1. Estimates of heritability for average daily gain

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Number of records</th>
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<th>Source</th>
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<tbody>
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<td>.40</td>
<td>59 estimates</td>
<td>LIT</td>
<td>Hutchens and Hintz (1981)</td>
</tr>
<tr>
<td>.38</td>
<td>51 estimates</td>
<td>LIT</td>
<td>Hutchens and Hintz (1981)</td>
</tr>
<tr>
<td>.665±.112</td>
<td>1872 progeny (males)</td>
<td>PHS</td>
<td>Fredeen and Jonsson (1957)</td>
</tr>
<tr>
<td>.351±.107</td>
<td>1872 progeny (females)</td>
<td>PHS</td>
<td>Fredeen and Jonsson (1957)</td>
</tr>
<tr>
<td>.627</td>
<td>5996 progeny</td>
<td>PHS</td>
<td>Jonsson (1959)</td>
</tr>
<tr>
<td>.236</td>
<td>2591 progeny</td>
<td>PHS</td>
<td>Jonsson (1959)</td>
</tr>
<tr>
<td>.41</td>
<td>6871 boars and gilts</td>
<td>RH</td>
<td>Vangen (1979)</td>
</tr>
<tr>
<td>.37±.164</td>
<td>253 sires</td>
<td>PHS</td>
<td>Sang et al. (1985)</td>
</tr>
<tr>
<td>.20</td>
<td>3360 litters</td>
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<td>Barbosa et al. (1985)</td>
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<tr>
<td>.38±.07</td>
<td>4636 individuals</td>
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<td>Sonnichsen et al. (1985)</td>
</tr>
<tr>
<td>.17±.08</td>
<td>1505 progeny</td>
<td>PHS</td>
<td>Luxford and Beilharz (1983)</td>
</tr>
<tr>
<td>.26±.06</td>
<td>5841 progeny</td>
<td></td>
<td>Gogue and Gueblez (1983)</td>
</tr>
<tr>
<td>.34±.07</td>
<td>495 progeny</td>
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<td>Gogue and Gueblez (1983)</td>
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<tr>
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<td>82 progeny</td>
<td></td>
<td>Leshchenya (1981)</td>
</tr>
<tr>
<td>.26</td>
<td>112 progeny</td>
<td></td>
<td>Leshchenya (1981)</td>
</tr>
<tr>
<td>.40</td>
<td>259 progeny</td>
<td></td>
<td>Leshchenya (1981)</td>
</tr>
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</table>

*LIT = Literature review; DDR = Daughter-dam regression; PHS = Paternal half-sib; RH = Realized heritability; SSR = Sire-son regression; MHS = Maternal half-sib.*
<table>
<thead>
<tr>
<th>Estimate</th>
<th>Number of records</th>
<th>Method of estimation</th>
<th>Source</th>
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<td>.22±.09</td>
<td>2403 progeny</td>
<td>PHS</td>
<td>Jeffries and Peterson (1982)</td>
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<tr>
<td>.38±.12</td>
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<td></td>
<td>Jonsson and Andresen (1981)</td>
</tr>
<tr>
<td>.22±.40</td>
<td>7530</td>
<td></td>
<td>Cuc et al. (1981)</td>
</tr>
<tr>
<td>.27</td>
<td>Farmer's hybrid</td>
<td></td>
<td>Sellers (1981)</td>
</tr>
<tr>
<td>.70±.21</td>
<td>564 progeny</td>
<td>PHS</td>
<td>Jungst et al. (1981)</td>
</tr>
<tr>
<td>.06±.08</td>
<td>532 pairs</td>
<td>SSR</td>
<td>Jungst et al. (1981)</td>
</tr>
<tr>
<td>.92±.23</td>
<td>564 progeny</td>
<td>MHS</td>
<td>Jungst et al. (1981)</td>
</tr>
<tr>
<td>.53</td>
<td>review</td>
<td>PHS</td>
<td>Jungst et al. (1981)</td>
</tr>
<tr>
<td>.83</td>
<td>656 progeny</td>
<td>MHS</td>
<td>Duckworth et al. (1961)</td>
</tr>
<tr>
<td>.42</td>
<td>656 progeny</td>
<td>PHS</td>
<td>Duckworth et al. (1961)</td>
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### Table B2. Estimates of heritability for backfat

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<td>LIT</td>
<td>Hutchens and Hintz (1981)</td>
</tr>
<tr>
<td>.39</td>
<td>39</td>
<td>LIT</td>
<td>Hutchens and Hintz (1981)</td>
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<tr>
<td>.44</td>
<td>74,661</td>
<td>PHS (HIV)</td>
<td>Kennedy et al. (1985)</td>
</tr>
<tr>
<td>.61</td>
<td>46,347</td>
<td>PHS (HIV)</td>
<td>Kennedy et al. (1985)</td>
</tr>
<tr>
<td>.44</td>
<td>16,860</td>
<td>PHS (HIV)</td>
<td>Kennedy et al. (1985)</td>
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<tr>
<td>.40</td>
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<td>PHS (HIV)</td>
<td>Kennedy et al. (1985)</td>
</tr>
<tr>
<td>.503</td>
<td>5,996</td>
<td>PHS</td>
<td>Jonsson (1957)</td>
</tr>
<tr>
<td>.727</td>
<td>5,996</td>
<td>POR</td>
<td>Jonsson (1957)</td>
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<tr>
<td>.47</td>
<td>732 pairs</td>
<td>DDR</td>
<td>Bereskin (1984)</td>
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<tr>
<td>.34+.10</td>
<td>1,245 pairs</td>
<td></td>
<td>Toelle et al. (1984)</td>
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<td>.16+.025</td>
<td>75,661</td>
<td>PHS</td>
<td>David et al. (1983)</td>
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<td>.79+.07</td>
<td>522 progeny</td>
<td>MOR</td>
<td>Kuhlers and Jungst (1983)</td>
</tr>
<tr>
<td>.78+.09</td>
<td>522 progeny</td>
<td>RH</td>
<td>Kuhlers and Jungst (1983)</td>
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<tr>
<td>.12</td>
<td>5,516 litters</td>
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<td></td>
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<td>2,824 litters</td>
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<td>Johansson and Kennedy (1983)</td>
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<tr>
<td>.555</td>
<td>2,591 progeny</td>
<td>PHS</td>
<td>Jonsson (1959)</td>
</tr>
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<sup>a</sup>LIT = Literature review; PHS = Paternal half-sib; HIV = Henderson's method IV; POR = Parent-offspring regression; DDR = Daughter-dam regression; MOR = Midparent-offspring regression; RH = Realized heritability; SOR = Sire-offspring regression; MHS = Maternal half-sib.
Table B2. (continued)

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<td>.711±.05</td>
<td>576 progeny</td>
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<td>Jonsson (1958)</td>
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<td>6,871 boars and gilts</td>
<td>RH</td>
<td>Vangen (1979)</td>
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<td>526 df (sire)</td>
<td>PHS (LIT)</td>
<td>Jonsson (1971)</td>
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<td>.272±.165</td>
<td>253 sires</td>
<td>PHS</td>
<td>Sang et al. (1985)</td>
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<tr>
<td>.29±.03</td>
<td>15,911</td>
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<td>Sonnichsen et al. (1985)</td>
</tr>
<tr>
<td>.52±.19</td>
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<td>Sonnichsen et al. (1985)</td>
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<td>4,636</td>
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<td>Sonnichsen et al. (1985)</td>
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<td>.57±.15</td>
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<td>SOR</td>
<td>Morris et al. (1983)</td>
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<td>1,505 progeny</td>
<td>PHS</td>
<td>Luxford and Beilharz (1983)</td>
</tr>
<tr>
<td>.44±.07</td>
<td>5,841 progeny</td>
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<td>Gogue and Gueblez (1983)</td>
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<td>.35</td>
<td>82 progeny</td>
<td></td>
<td>Leshchenya (1981)</td>
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<td>.86</td>
<td>112 progeny</td>
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<td>0</td>
<td>259 progeny</td>
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<td>Leshchenya (1981)</td>
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<td>.26±.10</td>
<td>2,403 progeny</td>
<td>PHS</td>
<td>Jeffries and Peterson (1982)</td>
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<td>.40 to .68</td>
<td>7,530</td>
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<td>Cuc et al. (1981)</td>
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<td>.35</td>
<td>Farmer's hybrid</td>
<td></td>
<td>Sellers (1981)</td>
</tr>
<tr>
<td>.04±.16</td>
<td>564</td>
<td>PHS</td>
<td>Jungst et al. (1981)</td>
</tr>
<tr>
<td>.49±.24</td>
<td>645</td>
<td>MHS</td>
<td>Jungst et al. (1981)</td>
</tr>
<tr>
<td>.09</td>
<td>review</td>
<td>PHS</td>
<td>Jungst et al. (1981)</td>
</tr>
<tr>
<td>.78</td>
<td>656 progeny</td>
<td>MHS</td>
<td>Duckworth et al. (1961)</td>
</tr>
<tr>
<td>Estimate</td>
<td>Number of records</td>
<td>Method of estimation</td>
<td>Source</td>
</tr>
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<td>-------------------</td>
<td>----------------------</td>
<td>-----------------------------</td>
</tr>
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<td>.76</td>
<td>656 progeny</td>
<td>MHS</td>
<td>Duckworth et al. (1961)</td>
</tr>
<tr>
<td>.72</td>
<td>656 progeny</td>
<td>MHS</td>
<td>Duckworth et al. (1961)</td>
</tr>
<tr>
<td>.32</td>
<td>656 progeny</td>
<td>PHS</td>
<td>Duckworth et al. (1961)</td>
</tr>
<tr>
<td>.80</td>
<td>656 progeny</td>
<td>PHS</td>
<td>Duckworth et al. (1961)</td>
</tr>
<tr>
<td>.67</td>
<td>656 progeny</td>
<td>PHS</td>
<td>Duckworth et al. (1961)</td>
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Table B3. Estimates of heritability for feed to gain ratio

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</tr>
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<td>122 df</td>
<td>PHS</td>
<td>Jungst (1978)</td>
</tr>
<tr>
<td>.12</td>
<td>320 df</td>
<td>MHS</td>
<td>Jungst (1978)</td>
</tr>
<tr>
<td>.08</td>
<td>122,320 df</td>
<td>MHS/PHS,SSR</td>
<td>Jungst (1978)</td>
</tr>
<tr>
<td>.57</td>
<td>62 df</td>
<td>PHS</td>
<td>Jungst (1978)</td>
</tr>
<tr>
<td>.24</td>
<td>493 progeny</td>
<td>RH</td>
<td>Dickerson and Grimes (1947)</td>
</tr>
<tr>
<td>.26</td>
<td>62 df</td>
<td>MOR</td>
<td>Dickerson and Grimes (1947)</td>
</tr>
<tr>
<td>.46</td>
<td>62 df</td>
<td>SOR</td>
<td>Dickerson and Grimes (1947)</td>
</tr>
<tr>
<td>.02</td>
<td>62 df</td>
<td>SOR</td>
<td>Dickerson and Grimes (1947)</td>
</tr>
<tr>
<td>.23</td>
<td>391 df</td>
<td>PHS</td>
<td>Jungst (1978)</td>
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<td>.12</td>
<td>321 df</td>
<td>PHS</td>
<td>Jungst (1978)</td>
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<tr>
<td>.30</td>
<td>647 df</td>
<td>PHS</td>
<td>Jungst (1978)</td>
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<tr>
<td>.26</td>
<td>67 df</td>
<td>PHS</td>
<td>Jungst (1978)</td>
</tr>
<tr>
<td>.78</td>
<td>1,125 litters</td>
<td>PHS</td>
<td>Jonsson (1957)</td>
</tr>
<tr>
<td>.70</td>
<td>1,125 litters</td>
<td>FS</td>
<td>Jonsson (1957)</td>
</tr>
<tr>
<td>.72+.114</td>
<td>432 df</td>
<td>PHS</td>
<td>Fredeen and Jonsson (1957)</td>
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<tr>
<td>.45+.112</td>
<td>432 df</td>
<td>PHS</td>
<td>Fredeen and Jonsson (1957)</td>
</tr>
<tr>
<td>.24</td>
<td>688 progeny</td>
<td>(MHS+PHS)/2</td>
<td>Jungst (1978)</td>
</tr>
<tr>
<td>.27</td>
<td>999 litters</td>
<td>PHS</td>
<td>Jungst (1978)</td>
</tr>
</tbody>
</table>

\(^{a}\) PHS = Paternal half-sib; MHS = Maternal half-sib; SSR = Sire-son regression; RH = Realized heritability; MOR = Midparent-offspring regression; SOR = Sire-offspring regression; FS = Full-sib.
Table B3. (continued)

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Number of records</th>
<th>Method of estimation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>.48</td>
<td>2,296 progeny</td>
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</tr>
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<td>Bereskin and Steele (1985)</td>
</tr>
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</tr>
<tr>
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<tr>
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<td>321 progeny</td>
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</tr>
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</tr>
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<td>Leshchenya (1981)</td>
</tr>
<tr>
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<td></td>
<td>Sellers (1981)</td>
</tr>
<tr>
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<td>Jungst (1981)</td>
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<td>532 pairs</td>
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<td>Jungst (1981)</td>
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<td>564 progeny</td>
<td>MHS</td>
<td>Jungst (1981)</td>
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<tr>
<td>.09 ± .08</td>
<td>564 progeny</td>
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<td>10 gen.</td>
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<tr>
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<td>10 gen.</td>
<td>RH</td>
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<td>Bereskin and Steele (1985)</td>
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Table B4. Estimates of phenotypic variance for average daily gain

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<td>Hutchens and Hintz (1981)</td>
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<td>Vogt et al. (1963)</td>
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<tr>
<td>.0038</td>
<td>732 pairs</td>
<td></td>
<td>Bereskin (1984)</td>
</tr>
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<td>.0018</td>
<td>707 litters</td>
<td>barrows and gilts</td>
<td>Morris (1975)</td>
</tr>
<tr>
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<td>barrows and gilts</td>
<td>Morris (1975)</td>
</tr>
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<td>boars</td>
<td>Morris (1975)</td>
</tr>
<tr>
<td>.0021</td>
<td>1454 pairs</td>
<td>boars</td>
<td>Morris (1975)</td>
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<td>1087 progeny</td>
<td>controls</td>
<td>Newton et al. (1977)</td>
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<td>gilts</td>
<td>Fredeen and Jonsson (1957)</td>
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<td>1872 progeny</td>
<td>boars</td>
<td>Fredeen and Jonsson (1957)</td>
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LIT = Literature review.
Table B5. Estimates of phenotypic variance for backfat

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<td>David et al. (1983)</td>
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<td>.174</td>
<td>3,797 progeny</td>
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<td>Johansson and Kennedy (1983)</td>
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^LIT = Literature review.

Table B6. Estimates of phenotypic variance for feed to gain ratio

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<td>gilt/barrow pair</td>
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<td>1454 litters</td>
<td>fed to appetite</td>
<td></td>
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<tr>
<td>.0441</td>
<td>707 litters</td>
<td>individually</td>
<td>Morris (1975)</td>
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<td>.0361</td>
<td>1454 litters</td>
<td>fed boars</td>
<td></td>
</tr>
<tr>
<td>.11</td>
<td>1872 progeny</td>
<td>boars and gilts</td>
<td>Predeen and Jonsson (1957)</td>
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Table B7. Estimates of phenotypic correlation between average daily gain and backfat

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<td>LIT</td>
<td>Hutchens and Hintz (1981)</td>
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<td>Jonsson (1957)</td>
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<tr>
<td>-0.218</td>
<td>2996 df</td>
<td>male</td>
<td>Jonsson (1957)</td>
</tr>
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<td>-0.01+.02</td>
<td>2403 progeny</td>
<td></td>
<td>Jeffries and Peterson (1982)</td>
</tr>
<tr>
<td>.04</td>
<td>Farmer's hybrid</td>
<td></td>
<td>Sellers (1981)</td>
</tr>
<tr>
<td>.32</td>
<td>732 pairs</td>
<td></td>
<td>Bereskin (1984)</td>
</tr>
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</table>

*LIT = Literature review.*

Table B8. Estimates of genetic correlation between average daily gain and backfat

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<td>LIT</td>
<td>Hutchens and Hintz (1981)</td>
</tr>
<tr>
<td>-0.05</td>
<td>17 estimates</td>
<td>LIT</td>
<td>Hutchens and Hintz (1981)</td>
</tr>
<tr>
<td>0.094</td>
<td>1125 df</td>
<td>gilts</td>
<td>Jonsson (1957)</td>
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<td>-0.166</td>
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<td>boars</td>
<td>Jonsson (1957)</td>
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<td>0.002</td>
<td>732 pairs</td>
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<td>Bereskin (1984)</td>
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<tr>
<td>-0.02</td>
<td>6871 pigs</td>
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<td>Vangen (1979)</td>
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*LIT = Literature review.*
Table B8. (continued)

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<td>4636</td>
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<td>1505 progeny</td>
<td>会計</td>
<td>Luxford and Beilharz (1983)</td>
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<td>0.05±0.29</td>
<td>2403 progeny</td>
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<td>Jeffries and Peterson (1982)</td>
</tr>
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<td>0.19</td>
<td>Farmer's hybrid</td>
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<td>Sellers (1981)</td>
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Table B9. Estimates of phenotypic correlation between average daily gain and feed to gain ratio

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<td>494 litters</td>
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<td>Smith et al. (1962)</td>
</tr>
<tr>
<td>-0.834</td>
<td>5996 progeny</td>
<td>female</td>
<td>Jonsson (1957)</td>
</tr>
<tr>
<td>-0.836</td>
<td>5996 progeny</td>
<td>male</td>
<td>Jonsson (1957)</td>
</tr>
<tr>
<td>-0.67±0.02</td>
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<td></td>
<td>Smith and Ross (1965)</td>
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<tr>
<td>-0.844</td>
<td>1833 df</td>
<td></td>
<td>Fredeen and Jonsson (1957)</td>
</tr>
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<td>-0.84</td>
<td>5996 progeny</td>
<td></td>
<td>Jonsson and King (1962)</td>
</tr>
<tr>
<td>-0.66</td>
<td>495 sires</td>
<td></td>
<td>Gogue and Gueblez (1983)</td>
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<tr>
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<td>495 progeny</td>
<td></td>
<td>Gogue and Gueblez (1983)</td>
</tr>
<tr>
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<td>Farmer's hybrid</td>
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<td>-0.43</td>
<td>LIT</td>
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<td>Bereskin and Steele (1985)</td>
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\(^a\)LIT = Literature review.
Table B9. (continued)

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<td>LIT</td>
<td>Bereskin and Steele (1985)</td>
</tr>
<tr>
<td>-0.32</td>
<td>LIT</td>
<td>Bereskin and Steele (1985)</td>
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<td>-0.24</td>
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Table B10. Estimates of genetic correlation between average daily gain and feed to gain ratio

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<td>Jungst (1978)</td>
</tr>
<tr>
<td>-0.32</td>
<td>LIT</td>
<td>Jungst (1978)</td>
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<tr>
<td>-0.35</td>
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\(^a\)LIT = Literature review.
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<td>Jungst (1978)</td>
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<td>Jungst (1978)</td>
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### Table B10. (continued)

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### Table B11. Estimates of phenotypic correlation between backfat and feed to gain ratio

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<td>Jonsson (1957)</td>
</tr>
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<td>.22±0.02</td>
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<td>Smith and Ross (1965)</td>
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<td>5996 progeny</td>
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<td>Jonsson and King (1962)</td>
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\(^a\)LIT = Literature review.
Table B12. Estimates of genetic correlation between backfat and feed to gain ratio

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<td>5996 progeny</td>
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<td>Jonsson and King (1962)</td>
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^LIT = Literature review.

Table B13. Summary of literature estimates of heritabilities, standard deviations and correlations

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<td>Weighted</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>42</td>
<td>.04 to .86</td>
<td>.50</td>
<td>.44</td>
<td>.48±.03</td>
<td>.41±.02</td>
</tr>
<tr>
<td>F</td>
<td>38</td>
<td>.007 to .78</td>
<td>.295</td>
<td>.30, .38</td>
<td>.33±.03</td>
<td>.31±.01</td>
</tr>
<tr>
<td>G</td>
<td>21</td>
<td>.17 to .782</td>
<td>.38</td>
<td>.40</td>
<td>.38±.03</td>
<td>.39±.01</td>
</tr>
</tbody>
</table>

^B = Backfat probe; F = Feed to gain ratio (feed efficiency); G = Average daily gain.
Table B13. (continued)

<table>
<thead>
<tr>
<th>Trait</th>
<th>N</th>
<th>Range</th>
<th>Mean</th>
<th>Estimate</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>10</td>
<td>.162 to .5</td>
<td>.37+.04</td>
<td>.10</td>
<td>inch</td>
</tr>
<tr>
<td>F</td>
<td>6</td>
<td>.11 to .21</td>
<td>.16+.02</td>
<td>.25</td>
<td>---</td>
</tr>
<tr>
<td>G</td>
<td>12</td>
<td>.024 to .131</td>
<td>.05+.01</td>
<td>.12</td>
<td>pound/day</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Correlation</th>
<th>N</th>
<th>Mean</th>
<th>Range</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>G B</td>
<td>14</td>
<td>.01+.07</td>
<td>-.218 to .32</td>
<td>.15</td>
</tr>
<tr>
<td>G F</td>
<td>14</td>
<td>-.59+.06</td>
<td>-.844 to -.24</td>
<td>-.60</td>
</tr>
<tr>
<td>B F</td>
<td>7</td>
<td>.22+.02</td>
<td>.12 to .32</td>
<td>.20</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Correlation</th>
<th>N</th>
<th>Mean</th>
<th>Range</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>B F</td>
<td>7</td>
<td>.28+.05</td>
<td>.024 to .44</td>
<td>.30</td>
</tr>
<tr>
<td>G B</td>
<td>9</td>
<td>0+.03</td>
<td>-.186 to .19</td>
<td>0</td>
</tr>
<tr>
<td>G F</td>
<td>34</td>
<td>-.60+.04</td>
<td>-.962 to .086</td>
<td>-.60</td>
</tr>
</tbody>
</table>

\[\text{cm.}\]

\[\text{kg/day.}\]
APPENDIX C.

GENERATION OF RELATIONSHIP MATRIX

INVERSES REQUIRED FOR DESIGNS
I. Relationships unknown or known to be unrelated

\[ A^{-1} = I_n \]

\( n = \) number of boars in test plus relatives included in mixed model equations

\[
\begin{bmatrix}
1 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 \\
0 & 0 & 1 & 0 \\
0 & 0 & 0 & 1
\end{bmatrix}
\]

II. Half-sibs

-Dams unknown

-Paternal grandsires unknown

\[
\begin{bmatrix}
B_1 & B_2 & B_3 & B_4 & S_1 & S_2 \\
4/3 & 0 & 0 & 0 & -2/3 & 0 \\
0 & 4/3 & 0 & 0 & -2/3 & 0 \\
0 & 0 & 4/3 & 0 & -2/3 & 0 \\
0 & 0 & 0 & 4/3 & 0 & -2/3 \\
-2/3 & -2/3 & -2/3 & 0 & 2 & 0 \\
0 & 0 & 0 & -2/3 & 0 & 4/3
\end{bmatrix}
\]

Boar diagonal = 4/3

Sire diagonal = 1 + (1/3 for each son)

Boar/sire element = \(-2/3\)
III. **Half-sibs**

- Dams known to be unrelated
- Paternal grandsires unknown or known to be unrelated

\[
\begin{pmatrix}
B_1 & B_2 & B_3 & B_4 & S_1 & S_2 & D_1 & D_2 & D_3 & D_4 \\
2 & 0 & 0 & 0 & -1 & 0 & -1 & 0 & 0 & 0 \\
0 & 2 & 0 & 0 & -1 & 0 & 0 & -1 & 0 & 0 \\
0 & 0 & 2 & 0 & -1 & 0 & 0 & 0 & -1 & 0 \\
0 & 0 & 0 & 2 & -1 & 0 & 0 & 0 & 0 & -1 \\
-1 & -1 & -1 & 0 & 2.5 & 0 & .5 & .5 & .5 & 0 \\
0 & 0 & 0 & -1 & 0 & 1.5 & 0 & 0 & 0 & .5 \\
-1 & 0 & 0 & 0 & .5 & 0 & 1.5 & 0 & 0 & 0 \\
0 & -1 & 0 & 0 & .5 & 0 & 0 & 1.5 & 0 & 0 \\
0 & 0 & -1 & 0 & .5 & 0 & 0 & 0 & 1.5 & 0 \\
0 & 0 & 0 & -1 & 0 & .5 & 0 & 0 & 0 & 1.5 \\
\end{pmatrix}
\]

Boar diagonal = 2
Sire diagonal = \(1 + (1/2 \text{ for each son})\)
Dam diagonal = \(1 + (1/2 \text{ for each son})\)
Boar/parent element = -1
Sire/dam element = .5 for each son

IV. For **full-sib** families and families related through sires, sire and dam equations are augmented in the same way as half-sibs with both parents known.
V. Full-sib families related by paternal grandsires (sires are half-sibs)

\[
\begin{pmatrix}
2 & 0 & 0 & 0 & -1 & 0 & -1 & 0 & 0 & 0 \\
0 & 2 & 0 & 0 & -1 & 0 & -1 & 0 & 0 & 0 \\
0 & 0 & 2 & 0 & -1 & 0 & 0 & -1 & 0 & 0 \\
0 & 0 & 0 & 2 & 0 & -1 & 0 & 0 & -1 & 0 \\
-1 & -1 & -1 & 0 & 2.833 & 0 & 1 & .5 & 0 & -2/3 \\
0 & 0 & 0 & -1 & 0 & 1.833 & 0 & 0 & .5 & -2/3 \\
-1 & -1 & 0 & 0 & 1 & 0 & 2 & 0 & 0 & 0 \\
0 & 0 & -1 & 0 & .5 & 0 & 0 & 1.5 & 0 & 0 \\
0 & 0 & 0 & -1 & 0 & .5 & 0 & 0 & 1.5 & 0 \\
0 & 0 & 0 & 0 & -2/3 & -2/3 & 0 & 0 & 0 & 1.667
\end{pmatrix}
\]

Boar diagonal = 2

Sire diagonal = \(4/3 + (.5 \text{ for each son})\)

Dam diagonal = 1 + (.5 for each son)

Paternal grandsires = 1 + (1/3 for each son)

Boar/parent elements = -1

Sire/dam element = .5 for each son

Sire/paternal grandsire element = -2/3