Genetic improvement of lean growth rate and reproductive traits in pigs

Peiqi Chen
Iowa State University
INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®
Genetic improvement of lean growth rate and reproductive traits in pigs

by

Peiqi Chen

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Co-majors: Animal Breeding and Genetics (Quantitative Genetics); Statistics

Program of Study Committee:
Tom J. Baas, Co-major Professor
Kenneth J. Koehler, Co-major Professor
Jack C. M. Dekkers
Michael J. Daniels
John W. Mabry
David G. Topel

Iowa State University

Ames, Iowa

2002

Copyright © Peiqi Chen, 2002. All rights reserved.
Graduate College
Iowa State University

This is to certify that the doctoral dissertation of

Peiqi Chen

has met the dissertation requirements of Iowa State University

Signature was redacted for privacy.

Co-major Professor

Signature was redacted for privacy.

Co-major Professor

Signature was redacted for privacy.

For the Co-major Program

Signature was redacted for privacy.

For the Co-major Program
# TABLE OF CONTENTS

## CHAPTER 1. GENERAL INTRODUCTION  
1
  Introduction  
1
  Organization of Dissertation  
3
  Literature Review  
4
  Literature Cited  
26

## CHAPTER 2. GENETIC PARAMETERS AND TRENDS FOR LEAN GROWTH RATE AND ITS COMPONENTS IN U.S. YORKSHIRE, DUROC, HAMPSHIRE, AND LANDRACE PIGS  
37
  Introduction  
38
  Materials and Methods  
39
  Results and Discussion  
41
  Implications  
49
  Literature Cited  
50

## CHAPTER 3. GENETIC PARAMETERS AND TRENDS FOR LITTER TRAITS IN U.S. YORKSHIRE, DUROC, HAMPSHIRE, AND LANDRACE PIGS  
67
  Introduction  
68
  Materials and Methods  
68
  Results and Discussion  
71
  Implications  
77
  Literature Cited  
77

## CHAPTER 4. GENETIC CORRELATIONS BETWEEN LEAN GROWTH AND LITTER TRAITS IN U.S. YORKSHIRE, DUROC, HAMPSHIRE, AND LANDRACE PIGS  
91
  Introduction  
92
  Materials and Methods  
93
  Results and Discussion  
95
  Implications  
99
  Literature Cited  
100
CHAPTER 1. GENERAL INTRODUCTION

Introduction

Lean growth rate is an important trait for genetic improvement programs in pigs because lean tissue can be deposited more efficiently than fat tissue and consumer demands are for lean products. The future competitiveness of pork producers, therefore, depends in part on genetic improvement of efficiency of quality lean production. Simultaneous improvement in leanness and growth rate is important, but difficult to achieve, because the genetic correlation between the two traits is generally unfavorable, as demonstrated by several studies (McPhee et al., 1988; Cameron and Curren, 1994a). Fowler et al. (1976) proposed that selection for lean tissue growth could be accomplished by using lean growth rate (LGR) as a biological index that combines lean percentage and growth rate into one single trait.

A successful genetic improvement program requires accurate genetic parameter estimates. Knowledge of breed-specific genetic parameters of LGR is necessary to accurately estimate breeding values to optimize breeding schemes and to predict genetic responses. Several studies (Stern et al., 1993; Cameron, 1994; Chen et al., 2001) have reported estimates of genetic parameters for LGR based on different selection experiments; however, the data have generally been limited to small sample sizes and specific populations. Breed-specific estimates of genetic parameters for LGR, which could be applied in genetic evaluation programs, have not been reported. Therefore, the first objective of this study was to estimate breed-specific genetic parameters for LGR and its components for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations.
Selection for litter traits is attractive to breeders when lean growth traits have been the selection objective for many years (Webb, 1999). Several studies (Southwood and Kennedy, 1990; Crump et al., 1997a; Kaufmann et al., 2000) have reported estimates of genetic parameters for litter traits based on different commercial populations and limited field data. Parameter estimates in the literature for litter traits vary substantially among studies or breeds (Southwood and Kennedy, 1990; Ferraz and Johnson, 1993; Kaufmann et al., 2000). Genetic parameters currently recommended by the National Swine Improvement Federation (NSIF, 1997) for genetic evaluation programs are based on the literature and are not breed-specific. Therefore, the second objective of this study was to estimate breed-specific genetic parameters for litter traits for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations.

The genetic improvement of both LGR and litter traits is important for increasing the efficiency of pork production. Multiple-trait BLUP estimations of breeding values have been widely used in swine genetic evaluations for lean growth and litter traits (Hofer et al., 1992; Kennedy et al., 1996). The use of multiple-trait BLUP procedures assumes that correlations among the traits evaluated are known without error. Currently, the genetic correlation between lean growth and litter traits has not been taken into account in most genetic evaluation programs because of the lack of understanding of the relationships between lean growth and litter traits. In order to increase the accuracy of the evaluations, especially for traits with low heritability (e.g., litter traits), it is necessary to evaluate lean growth and litter traits jointly using multiple trait analyses. Therefore, the third objective of this study was to estimate genetic correlations between lean growth and litter traits for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations.
To study the potential implications and effectiveness of selection for LGR, a selection experiment was designed where pigs were tested for LGR in a synthetic line of pigs based on a Meishan-Yorkshire cross. To evaluate the possibilities to improve both LGR and litter traits simultaneously, the direct responses in LGR and correlated responses in litter traits have to be evaluated. Therefore, the fourth objective of this study was to investigate the effectiveness of selection for LGR and evaluate the correlated responses in litter traits in a synthetic line of pigs based on a Meishan-Yorkshire cross.

Since LGR is a non-linear biological function of leanness and growth rate, several strategies exist for selection for LGR. Although several selection experiments have demonstrated that selection for LGR is effective (Stem et al., 1993; Cameron, 1994; Chen et al., 2001), little attention has been paid to the comparison of selection strategies for LGR. Therefore, the fifth objective of this study was to evaluate different strategies for selection on LGR.

Organization of Dissertation

This dissertation presents a general introduction, a general review of literature, five individual papers, and general conclusions. A list of references cited in the general introduction chapter is given at the end of that chapter. The papers are written following the guidelines for publication in either the Journal of Animal Science or the Canadian Journal of Animal Science. Each paper consists of an abstract, introduction, materials and methods, results and discussion, and an implications section. References cited within each individual paper follow the implications section.
LITERATURE REVIEW

Selection experiments for lean growth rate

Many experiments have been conducted to study the effects of selection for lean growth rate (LGR) or its components (lean percentage and growth rate) in pigs during the past several decades. A comprehensive review of selection experiments in pigs based on single component traits can be found in Clutter and Brascamp (1998). However, modern demands for the efficient production of lean pork and unfavorable relationships between some component traits have led to the evaluation of alternative selection criteria, including classical and biological indexes. In this review, selection results based on index selection from the past thirty years have been summarized.

Classical index selection

Several experiments used a classical selection index which combines backfat thickness (BF) and average daily gain (ADG) to select for LGR (Vangen, 1979; Cleveland et al., 1982; Fredeen and Mikami, 1986; McKay, 1990, 1992; Cameron, 1994; Cameron and Curran, 1994). In general, index selection resulted in significant improvement in the component traits of ADG and BF. Fredeen and Mikami (1986) demonstrated that index selection improved ADG and BF as much as each component was improved by single-trait selection in two contemporary lines, and selection in neither single-trait line was as effective as the index in improving LGR. Cameron (1994) and Cameron and Curran (1994) reported significant improvement in LGR over four generations of selection for LGR in Large White pigs.

Biological index selection
There have been a limited number of reports of selection experiments based on a biological index. Leymaster et al. (1979) reported significant improvements in ADG and BF simultaneously when selection was based on ultrasonic estimates of weight of lean cuts at 160 days of age. Stern et al. (1993) estimated LGR from ultrasonic measurements of fat and muscle depth, and reported significant direct responses in LGR to selection in halothane gene-free Swedish Yorkshire pigs. Recently, Chen et al. (2001) reported a significant direct response in LGR with selection for LGR based on the prediction equation developed by the National Pork Producers Council (NPPC, 1995) in a synthetic line of Yorkshire-Meishan pigs.

Direct response and feeding regime

Several researchers have reported that LGR as a selection criterion is sensitive to both feeding regime and dietary protein. Simultaneous selection for leanness and growth rate is difficult to carry out on an ad libitum feeding regime since the genetic correlation is generally unfavorable (McPhee et al., 1988). Thus, selection for LGR on ad libitum feeding will only positively change one of the two traits. McKay (1990) used an index including BF and ADG, and reported that it was only BF that changed. On the other hand, several researchers (McPhee et al., 1988; Gu et al., 1989; Cameron et al., 1994) reported a favorable genetic correlation between the two traits exists when restrictive feeding regimes are used. This indicates that selection for LGR will improve both leanness and growth rate simultaneously, as suggested by several studies (McPhee et al., 1991; Cameron et al., 1994). Stern et al. (1993) also reported that selection for LGR will improve both leanness and growth rate simultaneously at a high protein level, however, it will decrease leanness and increase growth rate at a low protein level on restrictive feeding regimes. Further, Cameron
and Curran (1994) reported that selection for LGR on ad libitum feeding increased LGR, but did not change rate of fat growth, and selection for LGR on restricted feeding significantly increased LGR and decreased rate of fat growth.

Parameter estimates of lean growth rate and its component traits

Knowledge of genetic parameters of LGR and its components is necessary to accurately estimate breeding values to optimize breeding schemes and to predict genetic responses.

Heritability

*LGR*. There have been a limited number of heritability estimates for LGR in the literature. Stern et al. (1993) reported an estimate of heritability of 0.37 for LGR in a selection experiment that was conducted in halothane gene-free Swedish Yorkshire pigs. Mrode and Kennedy (1993) used Yorkshire, Landrace, and Duroc records from Canadian test stations, and reported a heritability estimate of 0.39 for LGR. Cameron (1994) reported an estimate of heritability of 0.38 from a selection experiment in Large White pigs. Cameron and Curran (1994) also found an estimate of heritability of 0.25 from a selection experiment in Landrace pigs. In the NPPC National Genetic Evaluation Program (NGEP), an estimate of heritability of 0.48 for LGR was reported by combining data from nine sire breeds (NPPC, 1995). Recently, Chen et al. (2001) reported a heritability estimate of 0.37 for LGR from a selection experiment in a synthetic line of Yorkshire-Meishan pigs. Differences in estimates may be due to differences in population structures, selection criteria, breed differences, and sampling error.

Component traits of LGR. Hutchens and Hintz (1981) reported an average literature estimate of 0.47 for heritability of days to 90 kg. Ducos et al. (1993) reported an estimate of
0.32 for days to 100 kg. Li and Kennedy (1994) also reported estimates of heritability for
days to 100 kg ranging from 0.26 to 0.32 based on Yorkshire, Landrace, Duroc, and
Hampshire data from the Canadian Swine Improvement Program. The estimate of
heritability for days to 113.5 kg (DAYS) was 0.57 in the NGEP (NPPC, 1995).

Clutter and Brascamp (1998) reported average literature estimates of heritability for
BF of 0.49. Kennedy et al. (1985) reported heritabilities for BF at 90 kg ranging from 0.40 to
0.44 for Canadian Yorkshire, Landrace, Duroc, and Hampshire pigs. Lo et al. (1992) found
an estimate of 0.54 for ultrasonic measure of BF from 5,649 Landrace- and Duroc-sired pigs.
Bryner et al. (1992) used Yorkshire records from U.S. Central test stations and reported a
heritability estimate for BF of 0.56. Ferraz and Johnson (1993), using four animal models for
herds of Landrace and Large White pigs, reported estimates of heritability that ranged from
0.39 to 0.50 for BF. Mrode and Kennedy (1993) reported an average heritability for
Yorkshire, Landrace, and Duroc breeds of 0.59 for BF adjusted to 100 kg. Crump et al.
(1997a) reported an average estimate of 0.38 for BF in British Landrace pigs. Johnson et al.
(1999) reported a heritability estimate of 0.36 for BF in Large White boars.

Lo et al. (1992) found an estimate of 0.46 for ultrasonic measure of LEA from 5,649
Landrace- and Duroc-sired pigs. The estimate of heritability for LEA at 113.5 kg was 0.48 in
the NGEP (NPPC, 1995). Johnson et al. (1999) reported an estimate of heritability of 0.24
for LEA with a common litter effect of 0.18 using data from purebred Large White boars
born from 1990 to 1997.

**Genetic correlations**

Lean growth rate was estimated to have high genetic correlations with DAYS, BF,
and LEA of −0.62, −0.53, and 0.62, respectively, in the NGEP (NPPC, 1995). Genetic
correlation estimates of DAYS with BF and LEA were near zero (−0.07 and 0.05, respectively). Kennedy et al. (1985) also reported genetic correlations between days to 100 kg and BF to be −0.11 for Durocs and −0.17 for Yorkshires. Moderate, unfavorable genetic correlation estimates between BF and LEA were found in several studies (NPPC, 1995; Johnson et al., 1999). The estimated genetic correlations between LGR and its components in the literature suggest that selection in pigs based on LGR can be accomplished without adverse effects on DAYS, BF, and LEA.

Genetic parameter estimates of litter traits

Genetic parameters of litter traits have been estimated by a number of researchers. This section only reviews the estimates by the restricted maximum likelihood (REML) method. A comprehensive review of the estimates by other methods can be found in Lamberson (1990).

Southwood and Kennedy (1990) reported estimates of $h^2$ of 0.131 and 0.086 for number born alive (NBA) based on Canadian Yorkshire and Landrace gilts. Ferraz and Johnson (1993) estimated $h^2$ for NBA based on 2,495 litters and 14,605 Landrace and Large White pigs, and found values ranged from 0.01 to 0.14. See et al. (1993) reported estimates of 0.12 to 0.13 for NBA from field data for the Hampshire, Landrace, and Spotted breeds. Roehe and Kennedy (1995) produced $h^2$ estimates ranging from 0.09 to 0.14 for NBA. Crump et al. (1997b) reported an estimate of 0.11 for NBA based on 1,891 British Landrace sows with 5,291 records across different parities. Kaufmann et al. (2000) reported an estimate of 0.22 for NBA based on 1,928 litters in French Large White sows. Ferraz and Johnson (1993) reported average heritability of 0.19 for litter weight at 21-day (L21WT) over four models for this trait in Landrace and Large White sows. Chen et al. (2001) reported an
estimate of 0.06 for this trait from a selection experiment in a synthetic line of Yorkshire-Meishan pigs. Southwood and Kennedy (1990) reported estimates of heritability of 0.10 and 0.068 for number weaned (NW) based on Canadian Yorkshire and Landrace gilts. Roehe and Kennedy (1995) produced heritability estimates for NW ranging from 0.057 to 0.107 and from 0.053 to 0.083 in Canadian Yorkshire and Landrace sows, respectively. Chen et al. (2001) reported a heritability estimate of 0.10 for NW from a selection experiment in a synthetic line of Yorkshire-Meishan pigs.

**Genetic correlations among lean growth rate and reproductive traits**

To determine the optimum emphasis on LGR in selection objectives in pigs, the genetic relationships of LGR and its components with reproductive traits must be known. From a selection experiment in a synthetic line of Yorkshire-Meishan pigs, Chen et al. (2001) reported negative genetic correlations of -0.18 and -0.05 for LGR with NBA and NW, respectively, but a positive correlation of 0.13 for LGR with L21WT.

Crump et al. (1997c) reported an estimate of -0.084 for the genetic correlation of ADG with NBA. However, Short et al. (1994) reported that three of the four estimates of the genetic correlation between ADG and total number born in Landrace and Large White dam lines from two farms were positive, 0.04, 0.05, 0.23, and -0.15.

An estimate of the genetic correlation of BF with NBA was 0.205 reported by Crump et al. (1997) in British Landrace pigs. Johannson and Kennedy (1983) also reported positive estimates of 0.13 to 0.22 for BF with NBA in Swedish Landrace and Yorkshire pigs. Löbke et al. (1986) reported positive correlations of 0.03 and 0.28 for BF with NBA for the first litter and the first three litters in Landrace pigs, respectively. However, Morris (1975) and Bereskin (1984) each reported negative genetic correlations between BF and litter size, not
significantly different from zero, in British and U. S. Landrace pigs, respectively. Bereskin (1984) reported that genetic correlations of a performance index of ADG and BF with two indexes of sow productivity were not different from zero (average estimate = 0.07). Short et al. (1994) also reported three of the four estimates of the genetic correlation between BF and total number born were negative, −0.12, −0.03, −0.08, and 0.06.

In general, reported estimates of genetic correlations between reproduction traits and LGR and its component traits have been inconsistent and imprecise (Clutter and Brascamp, 1998). Also, most studies have not detected significant genetic relationships between LGR and its component traits with reproductive traits. However, Rydhmer et al. (1994) reported a genetic correlation of 0.40 between lean percentage and age of puberty. This result suggests that selection for a greater percentage of lean may delay sexual maturity.

**Correlated responses in reproductive traits to selection for lean growth rate**

**Litter size**

Correlated responses in litter size to selection for LGR were variable among other experiments reported in the literature. Berruecos et al. (1970) reported selection for decreased backfat resulted in a significant decline in litter size at birth and weaning. Cleveland et al. (1988) reported that index selection for ADG and BF resulted in negative, but non-significant, correlated responses for total number born (TNB), NBA, and number of piglets weaned at 42 days (N42). Vangen (1980) found positive responses for TNB and NBA, but negative correlated responses for N42 to index selection for lean growth in a Norwegian Landrace line. However, none of the correlated responses in their study was significant. Fredeen and Mikami (1986) noted significant negative phenotypic trends for NBA over years in a Lacombe line selected for rate of lean growth. Selection for weight of
lean cuts at a constant age in a Yorkshire line (DeNise et al., 1983) resulted in negative ($P > 0.05$) correlated responses for litter size at 1 and 7 days in first parity gilts. Correlated responses were negative ($P < 0.05$) in second parity sows for litter size at 1, 7, and 21 days. McKay (1990), who used a selection index based on BF and ADG, did not find any change in litter size. Kuhlers and Jungst (1992b) reported a positive effect of selection for weight at 70 days of age on 21-day litter size. However, Kuhlers and Jungst (1992a) found that selection for weight at 200 days of age in Durocs decreased total litter size at birth. Stern et al. (1994) reported that litter size at birth did not differ between high and low protein lines when selection was on LGR. Kerr and Cameron (1996) also did not observe significant differences in litter size at birth and at 21 days between a selection line and control line after seven generations of selection for lean growth with ad libitum feeding or restricted feeding in a population of Large White pigs. Clutter and Buchanan (1997) reported that litter traits did not change significantly after eight generations of divergent selection for ADG.

**Litter weight**

Vangen (1974) reported that correlated responses to index selection for rate of lean growth were positive ($P > 0.05$) for litter weight at birth but negative for litter weight at 42 days. DeNise et al. (1983) found that selection for weight of lean cuts resulted in negative correlated responses for litter weight at birth and at 21 days in first and second parity litters, but responses were significant only for the second parity. Fredeen and Mikami (1986) observed a significant negative phenotypic trend over years for litter weight at birth in a Lacombe selection line. Cleveland et al. (1988) noted consistently heavier litter birth weight (LBWT) and L42WT in a line selected for rate of lean growth compared with a control line, but the regressions on cumulative selective differential were not significant. Kerr and
Cameron (1996) also found that there were no significant differences in LBWT, L21WT, and L42WT between selection and control lines after seven generations of selection for lean growth rate with ad libitum feeding or restricted feeding. The results of experiments reported above indicate that selection for LGR in pigs will have very little effect on litter weights.

*Individual piglet traits*

Vangen (1980) reported positive correlated responses to index selection for rate of lean growth in piglet birth weight (PBWT) \(P < 0.05\) and piglet weight at 42 days (P42WT) \(P > 0.05\). Cleveland et al. (1988) observed positive but non-significant correlated responses for PBWT and P42WT. Kerr and Cameron (1996) also reported no differences in PBWT and piglet weight at 21-day (P21WT) between selection and control lines after seven generations of selection for LGR.

*Selection for non-linear profit function*

Profit or efficiency is often a non-linear function of the biological traits that are the focus of a selection program. Hazel (1943) developed a linear selection index that maximizes genetic progress in profit for a non-linear profit function. Wilton et al. (1968) applied the same theory to non-linear profit function by first deriving a breeding goal, which is a linear function of genotypes of biological traits that affect profitability, with first derivatives of the profit function at current population means as economic values. Goddard (1983) has shown that a linear selection index is optimal with a non-linear profit function provided that the traits are linearly related and there is no non-additive variance. Moav and Hill (1966) used graphical methods to illustrate the problem of deriving optimum linear selection indexes for non-linear profit function in a given future generation. To find the optimal linear selection index to maximize the profit at the last generation, the breeding goal
has to be linearized at the mean of the last generation in a planning horizon. Itoh and
Yamada (1988) developed a general formulation for the graphical method of Moav and Hill
(1966), which allows for a numerical solution and consideration of more than two traits.
Pasternak and Weller (1993) developed an iterative algorithm to find optimal weights for
linear selection indexes. Groen et al. (1994) used a general derivative-free search algorithm
to derive linear selection indexes that maximize average profit in the last generation of a
planning horizon. Dekkers et al. (1995) developed a method to obtain linear selection
indexes that maximizes objectives that involve average profit in one or more generations
within a planning horizon through application of optimum control theory. They showed that
optimum linear indexes for non-linear profit functions can be derived using selection index
theory based on a linear breeding goal with economic values that are derived at population
means in the future rather than in the current generation. Meuwissen and Goddard (1997)
compared 10 selection strategies for selection for non-linear profit functions and concluded
that the non-linear indexes yield almost the same response in profit as the optimal linear
indexes suggested by Moav and Hill (1966). The non-linear indexes do not require any
updating of economic weights and prediction of future selection responses. Meuwissen and
Goddard (1997) also found that if profit was recorded, direct selection for profit by including
it as a trait in estimated breeding value calculations was quite robust against infrequent
updating of genetic parameters.

Optimality of linear indexes for non-linear profit functions holds for selection indexes
that maximize profit evaluated at population means for the traits involved. Elsen et al.
(1986) argued, however, that the objective should be to maximize the average profit in the
population, which is not necessarily equal to maximizing profit evaluated at the mean of
component traits. However, Itoh and Yamada (1988) showed that for quadratic profit functions, linear indexes that maximize profit evaluated at population means also maximize average profit in the population. Chen et al. (1998) showed that there were only small differences in economic values for meat quality traits that were based on individual and average profit functions.

**Statistical methods for variance component estimation**

*Evolution*

Statistical methods for variance component estimation have been extensively used in animal breeding. Variance component estimation methods were proposed by Henderson (1953) for unbalanced data that often occur in animal breeding. These methods were frequently used by animal breeders into the 1970s. Lowry (1955) discussed Henderson’s methods related to genetic parameters. Hartly and Rao (1967) proposed the maximum likelihood (ML) method. Patterson and Thompson (1971) proposed a ML transformation to divide the likelihood into a portion that was free of fixed effects, which was called restricted maximum likelihood (REML) method. Corbeil and Searle (1976) revised the transformation to produce REML estimators that are invariant to fixed effects, and for equal numbers of observations in the subclasses, are identical to ANOVA estimators of variance components. Harville (1977) reviewed ML and REML approaches to variance component estimation, and concluded that REML estimates derived with the assumption that the data follow a multivariate distribution are reasonable estimates even if the distribution is unknown. Ouweltjes et al. (1988) reported that REML estimators are robust with selected data. Foulley (1993) compared the derivation of REML estimators with ML estimators. Gianola and Foulley (1990) proposed a Bayesian method to estimate variance components in animal
breeding. Given the prior distributions, the joint posterior distribution of all unknown parameters can be set up. Then, the marginal posterior distribution of a particular variance component can be obtained by integrating out all other parameters in the model from the joint distribution. Reverter et al. (1994) proposed method R, which is based on regression of BLUP solutions from whole data on BLUP solutions from partial data.

\[
\hat{R}_i = \frac{\text{cov}(\hat{u}_i, \hat{u}_i^p)}{\text{var}(\hat{u}_i^p)}
\]

where \( \hat{u}_i \) is a BLUP solution for the \( i^{th} \) random effect that are obtained from whole data, \( \hat{u}_i^p \) is a BLUP solution for the \( i^{th} \) random effect obtained from partial data. The REML method has been popular in estimating variance components in animal breeding because the estimates are within the parameter space, all pedigree information is used, and the estimates are unbiased under selection (Thompson, 1973; Rothschild et al., 1979; Sorensen and Kennedy, 1984). Therefore, this section will focus on this method.

**REML method theory**

Consider the following mixed linear model:

\[
y = X\beta + Zu + e
\]

where \( y \) is a vector of observations, \( \beta \) is a vector of fixed effects, \( u \) is a vector of random effects, \( X \) and \( Z \) are known incidence matrices, and \( e \) is a vector of random residual effects. The first and second moments are as follows:

\[
E[y] = X\beta, E[u] = 0, E[e] = 0, \text{and}
\]

\[
\text{Var} \begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G & 0 \\ 0 & R \end{bmatrix}
\]

and \( \text{Var}(y) = V = ZGZ' + R \).
Under the assumption of a joint multivariate normal distribution for $u$ and $e$, $y \sim \text{MVN}(X\beta, V)$, and the likelihood function to be maximized is:

$$L = L(\hat{\alpha}, V | y) = (2\pi)^{-\frac{N}{2}} |V|^{-\frac{1}{2}} \exp\left\{-\frac{1}{2} (y - X\hat{\alpha})' V^{-1} (y - X\hat{\alpha})\right\}$$

The logarithm of the likelihood function is given by:

$$L = \ln(L) = -\frac{N}{2} \ln(2\pi) - \frac{1}{2} \ln |V| - \frac{1}{2} (y - X\hat{\alpha})' V^{-1} (y - X\hat{\alpha})$$

To obtain the estimates of $\beta$, $G$, and $R$, the logarithm of likelihood function needs to be maximized by equating derivatives with respect to $\beta$, $G$, and $R$, to zero. The maximum likelihood estimator is biased because it does not take into account the degree of freedom used for estimating the fixed effects. Patterson and Thompson (1971) developed the REML method. Restricted maximum likelihood is derived on linear combinations of $y$ such that these combinations do not contain any fixed effects. The likelihood function for REML is based on $K' y \sim \text{MVN}(0, K'VK)$, where $K$ is a matrix of coefficients for linear combinations of $y$ such that $K' X\hat{\alpha} = 0$ for all $\beta$.

Then, the likelihood function ($L$) for $K' y$, is

$$L = L(\hat{\alpha}, V | K' y) = (2\pi)^{-\frac{1}{2} (N - \text{rank}(x))} |K'VK|^{-\frac{1}{2}} \exp\left\{-\frac{1}{2} y' (K'VK)^{-1} K' y\right\}$$

and its logarithm is:

$$L = L(\hat{\alpha}, V | K' y) = -\frac{1}{2} (N - \text{rank}(x)) \ln(2\pi) - \frac{1}{2} \ln |K'VK| - \frac{1}{2} y' (K'VK)^{-1} K' y$$

Searle et al. (1992) showed that:

$$\ln |K'VK| = \ln |V| + \ln |X'V^{-1}X|$$

and
\[ y' K(K'VK)^{-1} K' y = y' P y, \text{ where } P = V^{-1} - V^{-1} X (X' V^{-1} X)' V^{-1}, \]

which allows the simplification of the log-likelihood:

\[ \ln(L) = - \frac{1}{2} (N - \text{rank}(X)) \ln(2\pi) - \frac{1}{2} \ln |V| - \frac{1}{2} \ln |X' V^{-1} X| - \frac{1}{2} y' P y \]

In practice, the alternative form for the logarithm of likelihood function is based on the following equations:

\[ \ln |V| = \ln |R| + \ln |G| + \frac{1}{2} \ln |Z' R^{-1} Z + G^{-1}|, \]

and

\[ \ln |X' V^{-1} X| = \ln |C| - \frac{1}{2} \ln |Z' R^{-1} Z + G^{-1}|, \]

where \( C \) is a coefficient matrix of the mixed model equations.

The quantity \( - \frac{1}{2} (N - \text{rank}(X)) \ln(2\pi) \) is a constant \( k \), therefore, the logarithm of likelihood can be written as:

\[ \ln |L| = - \frac{1}{2} \{k + \ln |R| + \ln |G| + \ln |C| + y' P y\}. \]

Searl et al. (1992) also showed that:

\[ y' P y = (y - X\hat{\alpha})' V^{-1} (y - X\hat{\alpha}) = y' R^{-1} (y - X\hat{\alpha} - Z\hat{u}) \]

It follows that

\[ -2 \ln(L) = k + \ln(R) + \ln(G) + \ln(C) + y' R^{-1} (y - X\hat{\alpha} - Z\hat{u}) \]

The formulas for estimating the variance components are derived by maximizing this function directly. Consider a single trait mixed model with several uncorrected random effects:
\[ y = X\beta + \sum_i Z_i u_i + e \]

where \( y \) is a vector of observations, \( \beta \) is a vector of fixed effects, \( u_i \) is a vector of random effects. The first and second moments are as follows:

\[ E[y] = X\beta, \quad E[u] = 0, \quad E[e] = 0, \text{ and} \]

\[ \text{var}(u_i) = A_i \sigma_i^2, \quad \text{var}(e) = R = I \sigma_e^2, \quad \text{and} \quad \text{var}(y) = \sum_i Z_i G_i + R, \]

where \( \sigma_i^2 \) is random effects variance, \( \sigma_e^2 \) is the variance for the residual effects, \( A_i \) is the known incidence matrix for random effect \( i \), and \( r \) is the number of random effects. The derivatives of the logarithm of likelihood function with respect to particular variance components are:

**Estimations of \( \sigma_i^2 \)**

\[
\ln(L) = -\frac{1}{2} (N - \text{rank}(x)) \ln(2\pi) - \frac{1}{2} \ln |V| - \frac{1}{2} y' V^{-1} X^{-1} X V^{-1} y
\]

\[
\frac{\partial \ln(L)}{\partial \sigma_i^2} = -\frac{1}{2} \text{tr}(V^{-1} \frac{\partial V^{-1}}{\partial \sigma_i^2}) + \frac{1}{2} \text{tr}((X' V^{-1} X X') \frac{\partial V^{-1}}{\partial \sigma_i^2} V^{-1} X) + \frac{1}{2} y' P \frac{\partial V^{-1}}{\partial \sigma_i^2} P y
\]

\[
= -\frac{1}{2} \text{tr}(\frac{\partial V^{-1}}{\partial \sigma_i^2}) + \frac{1}{2} y' P \frac{\partial V^{-1}}{\partial \sigma_i^2} P y
\]

\[
= \frac{1}{2} \text{tr}(P Z_i Z_i' P) + \frac{1}{2} y' P Z_i Z_i' P y
\]

\[
= -\frac{1}{2} \left( \frac{q_i}{\sigma_i^2} - \frac{\hat{\sigma}_i^2}{\hat{\sigma}_i^2} \right) \text{tr}(A_i^{-1} C u_i^i) + \frac{1}{2} \frac{1}{\hat{\sigma}_i^2} \hat{u}_i^i A_i^{-1} \hat{u}_i^i
\]
After equating the derivatives to zero and multiplying by \( \hat{\sigma}_i^4 \), the equation for \( \hat{\sigma}_i^2 \) becomes:
\[
\hat{\sigma}_i^2 = \frac{\hat{u}_i A_i^{-1} \hat{u}_i + \hat{\sigma}_i^2 \text{tr}(A_i^{-1} C^u)}{q_i}
\]

where \( C^u \) is a diagonal block of the inverse of \( C \) corresponding to \( u_i \) and, \( q_i \) is the dimension of \( u_i \).

**Estimation of \( e^2 \)**

\[
\frac{\partial \ln(L)}{\partial \hat{\sigma}_i^2} = -\frac{1}{2} \text{tr}(V^{-1} \frac{\partial V^{-1}}{\partial \hat{\sigma}_i^2}) + \frac{1}{2} \text{tr}(X' X \frac{\partial V^{-1}}{\partial \hat{\sigma}_i^2} V^{-1} X) + \frac{1}{2} y' P \frac{\partial V^{-1}}{\partial \hat{\sigma}_i^2} P y
\]

\[
\frac{\partial \ln(L)}{\partial \hat{\sigma}_i^2} = -\frac{1}{2} \text{tr}(V^{-1} - V^{-1} X(X' V^{-1} X) X' V^{-1} ) \frac{\partial V^{-1}}{\partial \hat{\sigma}_i^2} ) + \frac{1}{2} y' P \frac{\partial V^{-1}}{\partial \hat{\sigma}_i^2} P y
\]

\[
= -\frac{1}{2} \text{tr}(P) + \frac{1}{2} y' P y
\]

\[
= -\frac{1}{2} \left( [N - \text{rank}(X)] - \frac{1}{\hat{\sigma}_i^2} \hat{u}_i A_i^{-1} \hat{u}_i \right) + \frac{1}{2} \frac{1}{\hat{\sigma}_i^2} (y' P y - \hat{u}_i A_i^{-1} \hat{u}_i, a_i)
\]

Equating the derivatives to zero, leads to
\[
(N - \text{rank}(X)) - \frac{1}{\hat{\sigma}_i^2} \hat{u}_i A_i^{-1} \hat{u}_i = \frac{1}{2} \frac{1}{\hat{\sigma}_i^2} (y' P y - \hat{u}_i A_i^{-1} \hat{u}_i, a_i)
\]

Multiply both sides by \( \sigma_i^2 \) to obtain:
\[
(N - \text{rank}(X)) e_i^2 - a_i \hat{u}_i A_i^{-1} \hat{u}_i = y' P y - \hat{u}_i A_i^{-1} \hat{u}_i a_i
\]

Thus, the estimate for \( e_i^2 \) becomes
Several iterative algorithms have been proposed to solve REML equations, generally divided into three categories according to whether or not they require the first- and/or second-order partial derivatives of the log likelihood function to be evaluated at each round of iteration (Takahashi, 1994). Newton-Raphson is an iterative procedure for maximizing or minimizing non-linear functions that uses first and second derivatives. Convergence of the Newton-Raphson algorithm can be very sensitive to the selection of the starting values. Patterson and Thompson (1971) proposed the Fisher scoring (FS) algorithm, which replaces second order partial derivatives with estimates of this expectations. Graser et al. (1987) suggested a derivative-free (DF) algorithm, which does not require formulas for derivatives. Searle et al. (1992) noted that the DF algorithm is efficient and accurate for a small number of variance components. However, Misztal (1997) pointed out that the DF algorithm has at most half the numerical accuracy of the FS algorithm and its high computation costs. Smith (1990) suggested the Expectation Maximization (EM) algorithm as an efficient procedure for obtaining REML estimates of variance components. However, the EM algorithm is especially slow to converge for data from unbalanced design (Meyer, 1989).

The average information (AI) algorithm is similar to the Fisher scoring algorithm proposed by Patterson and Thompson (1971), but avoids computing traces of large matrices. Instead of using the information matrix, the average information matrix and the expectation
of information matrix are used in the equation, resulting in simplification of formula. Johnson and Thomson (1995) showed that AI algorithm performed well compared to the DF and EM algorithms.

Software packages

There are several software packages available to obtain REML estimators in animal breeding. Meyer (1988) wrote a set of computer programs (DFREML) based on the ideas of Graser et al. (1987). Meyer (1988) used the simplex method of Nelder and Mead (1965) to find the maximum point. This simplex method assumes the function surface is continuous and has a unique minimum in the area of the search. However, there is no guarantee that a global maximum will be found with this method. Boldman and Van Vleck (1991) incorporated factorization and SPARSPAK sparse matrix routines in DFREML to decrease the computing time. Misztal and Perez-Enciso (1993) reported that sparse matrix inverse expectation maximization may be more efficient for those models that require many rounds of iteration. Also, there are other software packages available to estimate variance components such as SAS, VCE, and ASREML.

Statistical methods for estimating response to selection

Least-squares method

Lush and Shrode (1950) and Henderson et al. (1959) have shown that least-squares estimators of responses are biased in a selection model if culling is based on the past performance. Sorensen and Kennedy (1984) demonstrated that the least-squares estimator is unbiased provided that the records have been properly adjusted for fixed effects (for example, using a control line), that selection is within generations, and that there is only one record for each candidate for selection.
Consider the following mixed linear model:

\[ y = Xb + Za + e \]

where \( y \) is a vector of observations, \( b \) is a vector of fixed effects, \( a \) is a vector of random effects, \( X \) and \( Z \) are known incidence matrices, and \( e \) is a vector of random residual effects.

Following Henderson (1975), consider a vector \( w \), such that under no selection, the following moments can be defined:

\[
\begin{bmatrix}
  y \\
  a \\
  e \\
  w
\end{bmatrix}
= \begin{bmatrix}
  Xb \\
  0 \\
  0 \\
  0
\end{bmatrix};
\]

\[
\begin{bmatrix}
  y \\
  a \\
  e \\
  w
\end{bmatrix}
= \begin{bmatrix}
  V & Z & R & B \\
  GZ' & G & 0 & B_a \\
  R' & 0 & R & B_e \\
  B' & B_e' & B_e' & H
\end{bmatrix}.
\]

Now assume that selection has operated on \( w \) so that \( E(w) = k \). Using Pearson's (1903) result shown by Henderson (1975), the first order moments become:

\[
\begin{bmatrix}
  y \\
  a \\
  e \\
  w
\end{bmatrix}
= \begin{bmatrix}
  Xb \\
  0 \\
  0 \\
  0
\end{bmatrix} + \begin{bmatrix}
  BH^{-1}K \\
  B_aH^{-1}K \\
  B_eH^{-1}K \\
  k
\end{bmatrix}.
\]

Partition \( X = (1 \ X') \), where \( 1 \) is a column vector of ones, and \( b = (u \ b^*) \), where \( u \) is the population mean before selection. The vector of genetic means is

\[ m = 1, u + K', a, \]
where the order of $I_i$ is $t$, the number of generations, and $K^\prime a$ is average of the breeding values from each generation such that $K^\prime I = I_i$.

Let selection operate on a linear function of the data, such that $w = L^\prime y$ (Henderson, 1975). Then

$$B = GZ^\prime L$$

and

$$E(m) = I_i u + K^\prime GZ^\prime LH^{-1}k$$

When records have been adjusted for fixed effects such that

$$E(y) = Iu + BH^{-1}k,$$

the records are analyzed using,

$$y_{\bar{y}} = g_i + e_{\bar{y}},$$

where $g_i$ is the mean additive genetic value of generation $i$ and $e_{\bar{y}}$ is a random effect.

Therefore, in the matrix form we have

$$y = Qg + e.$$

With $Q$ of full column rank, the least-squares estimator of $g$ is:

$$\hat{g} = (Q^\prime Q)^{-1} Q^\prime y = \bar{y}$$

where $\bar{y}$ is the vector of generation means. With $w = L^\prime y$ and assuming $R = I$, we have,

$$B = (ZGZ^\prime + I)L.$$ Hence,

$$E(\hat{g}) = (Q^\prime Q)^{-1} Q^\prime Iu + (Q^\prime Q)^{-1} Q^\prime ZGZ^\prime LH^{-1}k + (Q^\prime Q)^{-1} Q^\prime LH^{-1}k$$
If selection operates within generations such that \( Q' L = 0 \) and \( Z \) is the identity matrix, then \( E(\hat{g}) = E(m) \), because \( (Q'Q)^{-1}Q'y = K' \). That \( Z \) is equal to the identity matrix implies one record per candidate.

The least-squares method has been used in many selection experiments because of its simplicity (Mrode et al., 1990; Kuhlers and Jungst, 1990, 1991a,b, 1992a,b, 1993; Cameron, 1994; Chen et al., 2001). However, the sampling variance is biased downward because it ignores the correlated error structure of the data. Hill (1971) and Sorensen and Kennedy (1983) proposed methods to correct the sampling variance.

**Mixed model method**

Henderson (1975) has shown that under a culling type of selection model, if the variances before selection are known, the mixed model equations ignoring selection lead to a best linear unbiased predictor (BLUP) and a best linear unbiased estimator (BLUE) under selection if the selection criterion is a linear function of the records and if \( L'X = 0 \). Furthermore, Sorensen and Kennedy (1984) extended Henderson's results to several cycles of selection as long as certain conditions are met. First, the variances, or their ratios, of the trait before selection started operating are known. Second, selection is on a linear function of the records and of the form \( L'X = 0 \). A third condition is that the relationship matrix is complete. If this condition is not met, estimators of fixed effects and of selection response will be biased (Henderson, 1975). Henderson (1985) listed additional requirements of the selected data to produce BLUP: 1) the random variables have a multivariate normal distribution; 2) genetic and environmental variances and covariances are known up to proportionality constant; 3) selection decisions are based on linear translation invariant
functions of the data; 4) the data used in selection decisions are available and included in the mixed model equations. Henderson (1980) described the conditions for $LX = 0$ to satisfy requirement 3.

Several researchers (Mrode et al; 1990; Cameron, 1994; Chen et al., 2001) used both methods to estimate the responses and genetic parameters. There were small differences in the responses estimated by the two methods. However, the heritability estimate for the trait under selection by the least-squares method was lower than that by the mixed model method in these experiments. Sorensen and Kennedy (1984) noted that the least-squares estimator may not be unbiased because it assumes that the response per unit selection differential is linear. The REML can provide unbiased estimators of the base population genetic variances and should be used in the analysis of the selection experiment.
Literature Cited


CHAPTER 2. GENETIC PARAMETERS AND TRENDS FOR LEAN GROWTH RATE AND ITS COMPONENTS IN U.S. YORKSHIRE, DUROC, HAMPSHIRE, AND LANDRACE PIGS

A paper accepted by the Journal of Animal Science

P. Chen, T. J. Baas, J. W. Mabry, J. C. M. Dekkers, and K. J. Koehler

ABSTRACT: Records on 361,300 Yorkshire, 154,833 Duroc, 99,311 Hampshire, and 71,097 Landrace pigs collected between 1985 and April of 2000 in herds on the National Swine Registry Swine Testing and Genetic Evaluation System were analyzed. Animal model and REML procedures were used to estimate random effects of animal genetic, common litter, maternal genetic, and the covariances between animal and maternal for lean growth rate (LGR), days to 113.5 kg (DAYS), backfat adjusted to 113.5 kg (BF), and loin eye area adjusted to 113.5 kg (LEA). Fixed effects of contemporary group and sex were also in the statistical model. Based on the single-trait model, estimates of heritabilities were 0.44, 0.44, 0.46, and 0.39 for LGR; 0.35, 0.40, 0.44, and 0.40 for DAYS; 0.48, 0.48, 0.49, and 0.48 for BF; and 0.33, 0.32, 0.35, and 0.31 for LEA in the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Estimates of maternal genetic effects were low and ranged from 0.01 to 0.05 for all traits across breeds. Estimates of common litter effects ranged from 0.07 to 0.16. A bivariate analysis was used to estimate the genetic correlations between lean growth traits. Average genetic correlations over four breeds were -0.83, -0.37, 0.44, -0.07, 0.08, and -0.37 for LGR with DAYS, BF, and LEA, DAYS with BF and LEA, and BF with LEA, respectively. Average genetic trends were 2.35 g/yr, -0.40 d/yr, -0.39 mm/yr, and 0.37 cm²/yr for LGR, DAYS, BF, and LEA, respectively. Results indicate that selection
based on LGR can improve leanness and growth rate simultaneously and could be a useful biological selection criterion.

**Introduction**

Simultaneous improvement in leanness and growth rate is difficult because the genetic correlation between the two traits is generally unfavorable (McPhee et al., 1988). Fowler et al. (1976) proposed that lean growth can be selected for by using an economic selection index or by using lean growth rate (LGR), which is measured as lean gain per day of age, as a biological index that combines lean percentage and growth rate into one single trait. Several selection experiments demonstrated that selection for LGR will improve leanness and growth rate simultaneously (McPhee et al., 1991; Stern et al., 1993; Cameron, 1994). Clutter and Brascamp (1998) suggested that LGR is the most appropriate expression of the industry's objective for market pigs. Performance traits evaluated in the current National Swine Registry Swine Testing and Genetic Evaluation System (STAGES) are days to 113.5 kg (DAYS), backfat adjusted to 113.5 kg (BF), and loin eye area adjusted to 113.5 kg (LEA) (NSR, 2000). The details of STAGES can be found in Stewart et al. (1991). Lean growth rate, a combination of these three traits, has not been evaluated in the STAGES program. Knowledge of breed-specific genetic parameters of LGR is necessary to accurately estimate breeding values to optimize breeding schemes and to predict genetic responses. Several studies (Stern et al., 1993; Cameron, 1994; Chen et al., 2001) have reported estimates of genetic parameters for LGR based on different selection experiments; however, the data have generally been limited to small sample sizes and specific populations. Breed-specific estimates of genetic parameters for LGR, which could be applied in the STAGES program, have not been reported. Therefore, the objective of this study was to estimate breed-specific

Materials and Methods

Data Source

Data were obtained from the National Swine Registry on Yorkshire, Duroc, Hampshire, and Landrace pigs born from 1985 to April of 2000. Details of data collection can be found in STAGES (NSR, 2000). The data included pedigree information for each pig, contemporary group (CG), sex of the pig, litter identification, birth date, date weighed, and measurements for weight, BF, and LEA at an approximate weight of 113.5 kg. Contemporary groups were defined by breeders as a group of pigs that were raised in a common herd under similar environmental conditions during a similar time. Data on boars, gilts, and barrows were included in the data set. Backfat and loin eye area were measured ultrasonically at the 10th rib. Days to 113.5 kg, backfat, and loin eye area were adjusted to 113.5 kg using recommendations in the Guidelines for Uniform Swine Improvement Programs (NSIF, 1997). Lean growth rate adjusted to 113.5 kg was predicted using the following fat-free lean prediction equation developed by the National Pork Producers Council (NPPC, 2000): LGR (kg/d) = [0.3782 × sex (barrow and boar = 1; gilt = 2) – 2.9488 × (BF, cm) + 0.3817 × (LEA, cm²) + 0.291 × (adjusted live weight, kg) – 0.2424]/(days on test), where days on test is defined as the time from birth to date weighed. Single-sire contemporary group records were removed, as were records from sires not connected across contemporary groups and sires not mated to more than one dam. Numbers of records, contemporary groups, and litters represented by breed are shown in Table 1, along with
means and SD for LGR, DAYS, BF, and LEA. Distributions across years are shown in Table 2 for each breed.

Statistical Analysis

Univariate Analyses. Univariate analyses within breed were conducted using the REMLF90 program of Misztal (2000) to estimate single-trait variance components. The following animal model was fitted using REML: $y = Xb + Za + Sc + Wm + e$, where $y$ represents the vector of observations, $b$ is the vector of fixed effects of CG and sex, $a$ is the vector of random additive genetic effects of animals, which is assumed distributed $N(0, A\sigma_a^2)$, where $A$ is the numerator relationship matrix among animals, $c$ is the vector of common litter effects, assumed distributed $N(0, I\sigma_c^2)$ and uncorrelated with random animal effects, $m$ is the vector of random additive maternal genetic effects, assumed distributed $N(0, I\sigma_m^2)$ and correlated with random animal effects ($\sigma_{am}$), and $e$ is the vector of residual effects, which is assumed distributed $N(0, I\sigma_e^2)$. $X$, $Z$, $S$, and $W$ are incidence matrices relating records to fixed, additive genetic, common litter, and maternal genetic effects, respectively. A simplified model was fitted also, in which maternal genetic effects were excluded. Standard errors of heritability estimates were estimated using the approximate method of Swiger et al. (1964).

Bivariate Analyses. Bivariate REML analyses were conducted to estimate genetic and phenotypic correlations between traits, again using the programs of Misztal (2000). The model for the bivariate analyses was the same as for the univariate analyses, except maternal genetic effects were excluded. Standard errors of genetic correlation estimates ($\hat{\sigma}_{\lambda}$) from REMLF90 were not available; however, they can be approximated by the method of Falconer.
(1989), demonstrated by several studies (Lo et al., 1992; Chen et al., 2001):

\[
\hat{\sigma}_{\lambda} = \frac{1 - \hat{r}_A^2}{\sqrt{2}} \sqrt{\frac{\hat{\sigma}_{\lambda}^2 \hat{\sigma}_{\lambda}^2}{\hat{h}_x^2 \hat{h}_y^2}}
\]

where \( \hat{h}_x^2 \), \( \hat{h}_y^2 \) are the heritability estimates of traits x and y, respectively, and \( \hat{\sigma}_{\lambda} \) and \( \hat{\sigma}_{\lambda} \) are the standard errors of heritability estimates of traits x and y, respectively. In the REML analyses, the convergence criterion was set to \( 10^{-8} \) for all analyses.

**Maternal Effects.** Breeding values for LGR and its components were estimated under two single-trait models with and without maternal effects using the programs of BLUPF90 of Misztal (2000). Spearman rank correlations between two sets of EBV were estimated to examine consequences of ignoring maternal effects.

**Genetic Trends.** Breeding values for LGR and its components were estimated under a multi-trait model without maternal effects using the programs of BLUPF90 of Misztal (2000). The average breeding values per year of birth of the pigs were regressed on year of birth of the pigs and plotted to illustrate trends.

**Results and Discussion**

**Variances**

Estimates of animal genetic, maternal genetic, common litter, and residual variances and covariances between animal genetic and maternal genetic effects are shown in Tables 3 to 6. Genetic variances in LGR, DAYS, and LEA were highest in Hampshires and lowest in Durocs. The Landrace had the highest and the Hampshires had the lowest genetic variance in BF. Total variation in LGR and DAYS was lower in Durocs than in the other three breeds. The Yorkshire and Landrace breeds had greater total variation in BF, while total variation in LEA was the lowest in Durocs and highest in Landrace. The Hampshire and Landrace
breeds had the highest litter variance for LGR, while the Landrace breed had the highest litter variance for BF and LEA.

**Heritabilities**

Results of analyses using single-trait models for LGR, DAYS, BF, and LEA are given in Tables 3 to 6. Average estimates of heritabilities for LGR, DAYS, BF, and LEA from bivariate analyses are given in Table 7. Five estimates of heritability for each trait within breed were obtained by single- and bivariate-trait analyses. Heritability estimates did not differ by more than 2% for any of these analyses; therefore, results of the single-trait analyses are discussed for simplicity. Estimates of heritability for LGR were 0.44, 0.44, 0.46, and 0.39 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 3). These estimates were in the range of previous estimates. Stern et al. (1993) reported an estimate of heritability of 0.37 for LGR from 25 to 90 kg in a selection experiment that was conducted in Swedish Yorkshire pigs free of the stress form of the halothane gene (NN). Mrode and Kennedy (1993) used Yorkshire, Landrace, and Duroc records from Canadian test stations and reported a heritability estimate of 0.39 for LGR from 29 to 90 kg. Cameron (1994) reported an estimate of heritability of 0.38 for LGR from 30 to 85 kg from a selection experiment in Large White pigs. Cameron and Curran (1994) also found an estimate of heritability of 0.25 from a selection experiment in Landrace pigs. Recently, Chen et al. (2001) reported a heritability estimate of 0.37 for LGR from birth to 113.5 kg from a selection experiment in a synthetic line of Yorkshire-Meishan pigs. Estimates may depend on population structure, selection criterion used, breed, sampling error, and appropriateness of the LGR equation for different breeds.
Estimates of heritability for DAYS were 0.35, 0.40, 0.44, and 0.40 for Yorkshires, Durocs, Hampshires, and Landrace, respectively (Table 4). These estimates are consistent with average literature estimates of 0.47 by Hutchens and Hintz (1981). Ducos et al. (1993) reported an estimate of 0.32 for days to 100 kg. Li and Kennedy (1994) also reported estimates of heritability for days to 100 kg ranging from 0.26 to 0.32 based on Yorkshire, Landrace, Duroc, and Hampshire data from the Canadian Swine Improvement Program.

Estimates of heritability for BF in this study were 0.48, 0.48, 0.49, and 0.48 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 5). These estimates were in the range of estimates from previous studies. Kennedy et al. (1985) reported heritabilities for ultrasonic measure of BF at 90 kg ranging from 0.40 to 0.44 for different breeds of Canadian performance tested pigs. Lo et al. (1992) found an estimate of 0.54 for ultrasonic measure of BF. Bryner et al. (1992) used Yorkshire records from U.S. Central test stations and reported a heritability estimate for ultrasonic measure of BF of 0.56. Ferraz and Johnson (1993), using four animal models for herds of Landrace and Large White pigs, reported estimates of heritability that ranged from 0.39 to 0.50 for ultrasonic measure of BF. Mrode and Kennedy (1993) reported an average heritability for three breeds of 0.59 for ultrasonic measure of BF adjusted to 100 kg. Johnson et al. (1999) reported a heritability estimate of 0.36 for ultrasonic measure of BF in Large White boars.

Estimates of heritability for LEA were 0.33, 0.32, 0.35, and 0.31 for Yorkshires, Durocs, Hampshires, and Landrace, respectively (Table 6). These estimates were lower than previous estimates of 0.46 by Lo et al. (1992). Some previous studies did not properly account for common litter effects, which may be substantial as found in this study (Tables 3 to 6), and this could have contributed to an upward bias in previous estimates. Johnson et al.
(1999) reported an estimate of heritability of 0.24 for LEA, with a common litter effect of 0.18.

The magnitude of the estimated heritability for LGR was in the range of its components for each breed. It was expected that estimates of heritability for LGR would be a compromise between heritability estimates of the three traits, since LGR is a combination of its components. Standard errors of heritability estimates from REMLF90 were not available; however, they can be approximated by the method of Swiger et al. (1964), as demonstrated by several studies (Lo et al., 1992; See, 1994). Standard errors of heritability estimates ranged from 0.01 to 0.02.

Common Litter Effects

Common litter effects were significant sources of variation for all traits and breeds, and the proportion of phenotypic variation accounted for by common litter effects ranged from 0.07 to 0.16 (Tables 3 to 6). Estimates of common litter effects were not greatly affected by including random maternal genetic effects in the model for any trait or breed. Also, estimates of common litter effects were similar for all traits and all breeds except a relatively large estimate of 0.16 for DAYS in Durocs and a small estimate of 0.07 for LEA in Hampshires. Ferraz and Johnson (1993) reported that approximately 7% of the variation in ADG and 5% of the variation in BF was due to common litter effects in Landrace and Large White pigs. Li and Kennedy (1994) reported average common litter effects, which were expressed as a proportion of the total variance, of 0.26 for days to 100 kg and 0.10 for BF in Yorkshire, Landrace, Duroc, and Hampshire pigs. Crump et al. (1997) reported average estimates over various analyses of 0.05, 0.11, 0.06, and 0.06 for BF, average daily food
intake, average daily gain, and food conversion ratio, respectively. Johnson et al. (1999) reported common litter effects of 0.13 and 0.18 for BF and LEA in Large White boars.

The magnitude of common litter effects reported in this and in previous studies indicates that common litter effects must be included in the model for estimation of variance components and breeding values. Several studies (Crump et al., 1997) reported that estimates of heritabilities with common litter effects in the model were approximately 10% less than those obtained with only random animal effects in the model. The use of models without common litter effects for genetic evaluation would, therefore, lead to biases in estimation of breeding values and overprediction of potential genetic gain.

**Additive Maternal Genetic Effects**

Additive maternal genetic effects were not large sources of variation in this study. Fractions of variance accounted for by maternal effects ranged from 0.01 to 0.05 for all traits across breeds (Tables 3 to 6). Correlations between maternal and direct genetic effects were negative for all traits and all four breeds. Estimated correlations ranged from -0.31 to -0.61 for LGR, from -0.28 to -0.58 for DAYS, from -0.35 to -0.60 for BF, and from -0.28 to -0.41 for LEA. Crump et al. (1997) reported an average correlation of -0.18 for ultrasonic backfat depth. Ferraz and Johnson (1993) reported estimated correlations of -0.26 for BF and -0.34 for ADG. The estimates in this study were of greater magnitude than estimates reported in previous studies.

The correlations between two sets of EBV for direct genetic effects for LGR and its components under the models with and without maternal genetic effects over 15 yr ranged from 0.92 to 0.96. The correlations with a year ranged from 0.88 to 0.97. Therefore, maternal effects could be ignored in the model to estimate breeding values in practice. This
result agrees with the findings of Ferraz and Johnson (1993) and Crump et al. (1997), who reported that, for all practical purposes, the maternal effect and the correlation between maternal effects and direct effects could be ignored for performance traits in pigs. Robison (1972), however, indicated that maternal effects account for a significant proportion of the variance for 140-d weight and carcass BF in Yorkshire pigs. Bryner et al. (1992) also reported that maternal effects were significant for both BF and ADG, accounting for 11 and 23% of the variance, respectively. Their relatively large estimates of maternal effects could be due to confounding between common litter effects and maternal effects, since common litter effects were not included in those studies (Robison, 1972; Bryner et al., 1992).

Genetic Correlations

Genetic and phenotypic correlations among LGR and its components are given in Table 7. Lean growth rate was estimated to have high negative genetic correlations with DAYS of -0.84, -0.86, -0.80, and -0.83 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively, and these estimates were not significantly different from each other (P > 0.05). Lean growth rate was estimated to have moderately favorable genetic correlations with BF of -0.32, -0.40, -0.35, and -0.41 for Yorkshires, Durocs, Hampshires, and Landrace, respectively. Lean growth rate was estimated to have moderately favorable genetic correlations with LEA of 0.44, 0.43, 0.50, and 0.38 for Yorkshires, Durocs, Hampshires, and Landraces, respectively. Moderate genetic correlation estimates between LGR and LEA (Table 7) indicate that selection for increased LGR would result in increased LEA. Genetic correlation estimates of DAYS with BF and LEA were not different from zero (Table 7). Kennedy et al. (1985) also reported genetic correlations between days to 100 kg and BF to be -0.11 for Durocs and -0.17 for Yorkshires.
Moderate unfavorable genetic correlation estimates between BF and LEA, which ranged from $-0.35$ to $-0.45$, were found for all breeds (Table 7). This is confirmed by other studies (NPPC, 1995; Johnson et al., 1999). The estimated genetic correlations between LGR and its components suggest that selection in pigs based on LGR can be accomplished without adverse effects on DAYS, BF, and LEA.

There are small differences in genetic parameter estimates between breeds. Use of estimates pooled across breeds might be appropriate.

**Genetic Trends**

The average breeding values for animals in 1990 were adjusted to zero to illustrate genetic changes in later generations. All estimated genetic trends for DAYS, BF, LEA, and LGR were favorable (Figures 1 to 4, and Table 8). The Duroc breed showed the largest genetic changes of $3.28$ g/d per year and $-0.54$ d/yr for LGR and DAYS, while Yorkshires had the largest genetic changes of $-0.45$ mm/yr and $0.41$ cm$^2$/yr for BF and LEA, respectively. Average genetic change in DAYS over four breeds was $-0.40$ d/yr or $-0.23\%$ of the mean. The estimates were lower than the estimates of $-0.63$ or $-0.36\%$ of the mean for four Canadian breeds reported by Kennedy et al. (1996). The average genetic change in BF over the four breeds was $-0.40$ mm/yr or $-2.3\%$ of the mean. The average estimate of genetic change expressed as the percentage of the mean was higher than the estimate of $2.0\%$ reported by Kennedy et al. (1996) in Canada and $0.5\%$ reported by Tibau i Font et al. (1994) in Spain, but lower than the estimate of $3.9\%$ reported by Mantysaari et al. (1994) in Finland. Kennedy et al. (1996) suggested that 1.7 to 2.9% improvement per year for BF and 1.5% per year for days to 110 kg would be realistic for industry breeding programs, although Smith (1984) suggested that 3 to 5% and 2.7% for BF and growth rate were possible.
Estimates of rates of genetic changes in LEA and LGR were 0.42 and 0.91% of their means per year, respectively, over the entire period. Some selection experiments have achieved greater rates of genetic change for LGR (Stern et al., 1993; Cameron, 1994; Chen et al., 2001). The current rates for LGR and its components being achieved in the U.S. Yorkshire, Duroc, Hampshire, and Landrace breeds are positive but still offer room for further improvement.

**Lean Growth Rate**

If LGR could be predicted on individual animals, as other traits, the breeding objective would be a single-trait biological selection criterion (BLUP EBV). Therefore, the use of LGR could simplify the selection procedures for breeders when selecting for leanness and growth simultaneously.

Estimated breeding values for LGR in this study were estimated from a phenotypic trait that was calculated based on the lean prediction equation (NPPC, 2000). Therefore, lean growth rate used in this study was the predicted LGR. Bennett et al. (1992) explained that the relationships between predicted LGR and other traits could be different from the relationships of actual LGR to the same traits. The accuracy of predicted LGR would rely on maximizing the correlation between actual LGR and a prediction equation consisting of its component traits. The equation used in this study might predict biased LGR due to sex, breed, and weight. Several researchers have demonstrated biases in estimation of carcass lean of swine associated with genotype, sex, and treatments (Gu et al., 1992; Hicks et al., 1998). Further research is needed to develop a sex-breed-weight-specific prediction equation, which can predict LGR more accurately.
An alternative method is to estimate EBVs for the components of LGR, DAYS, BF, and LEA, and then combine these EBVs to obtain the EBV for LGR. Goddard (1998), however, suggested that if there are complex relationships between the traits in the phenotypic profit function, calculating profit on individual animals directly may be more robust than using a complex bioeconomic model. Similarly, since the relationships between the traits of DAYS, BF, and LEA and LGR are complex, it might be better to use the trait of LGR than to use an index that consists of its components as a biological selection criterion. The results of a simulation study (our unpublished observations) show that direct selection for EBV for LGR with a multi-trait model yielded higher LGR when compared to a linear index of EBVs for DAYS, BF, and LEA.

Meuwissen and Goddard (1997) found that, when profit was recorded as a trait in a multi-trait BLUP, the EBV for profit provided a robust and accurate selection criterion. They further suggested that even if profit cannot be calculated for all individual animals, it may still be possible and useful to define traits (e.g., milk per day of herd life in dairy cattle) that are major components of profit. Since LGR expressed as lean gain per day is the major component of profit in the swine industry and can be predicted and included as a trait in a multi-trait BLUP, the EBV for LGR could be a useful biological selection criterion when economic values are uncertain.

Implications

Results of this study indicate that lean growth rate is highly heritable and should respond to selection. Genetic correlations indicate that it should be possible to select for lean growth rate without adversely affecting growth rate and leanness. Lean growth rate as a trait could be a useful biological selection criterion when the relationships between the
components of lean growth rate are complex. Use of an appropriate model including litter effects, along with breed-specific genetic parameters, will increase the accuracy of EBV.

**Literature Cited**


<table>
<thead>
<tr>
<th>Item</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td>Records</td>
<td>361,300</td>
<td>154,833</td>
<td>99,311</td>
<td>71,097</td>
</tr>
<tr>
<td>Contemporary groups</td>
<td>8,067</td>
<td>4,270</td>
<td>4,155</td>
<td>2,785</td>
</tr>
<tr>
<td>Litters</td>
<td>76,514</td>
<td>30,654</td>
<td>25,215</td>
<td>15,841</td>
</tr>
<tr>
<td>Lean growth rate, g/d</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \bar{x} )</td>
<td>256.51</td>
<td>263.05</td>
<td>251.97</td>
<td>259.46</td>
</tr>
<tr>
<td>SD</td>
<td>30.40</td>
<td>29.06</td>
<td>28.60</td>
<td>30.14</td>
</tr>
<tr>
<td>Days to 113.5 kg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \bar{x} )</td>
<td>176.34</td>
<td>173.93</td>
<td>184.93</td>
<td>175.54</td>
</tr>
<tr>
<td>SD</td>
<td>17.99</td>
<td>16.98</td>
<td>17.62</td>
<td>16.58</td>
</tr>
<tr>
<td>Backfat, cm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \bar{x} )</td>
<td>1.79</td>
<td>1.68</td>
<td>1.65</td>
<td>1.78</td>
</tr>
<tr>
<td>SD</td>
<td>0.52</td>
<td>0.47</td>
<td>0.42</td>
<td>0.58</td>
</tr>
<tr>
<td>Loin eye area, cm²</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \bar{x} )</td>
<td>42.65</td>
<td>43.12</td>
<td>45.94</td>
<td>43.20</td>
</tr>
<tr>
<td>SD</td>
<td>5.55</td>
<td>5.22</td>
<td>6.59</td>
<td>5.65</td>
</tr>
</tbody>
</table>
Table 2. Distributions of records by year and breed

<table>
<thead>
<tr>
<th>Year</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>1,351</td>
<td>0</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>1986</td>
<td>3,663</td>
<td>0</td>
<td>0</td>
<td>340</td>
</tr>
<tr>
<td>1987</td>
<td>4,627</td>
<td>48</td>
<td>15</td>
<td>382</td>
</tr>
<tr>
<td>1988</td>
<td>5,234</td>
<td>478</td>
<td>387</td>
<td>606</td>
</tr>
<tr>
<td>1989</td>
<td>7,934</td>
<td>1,216</td>
<td>1,881</td>
<td>783</td>
</tr>
<tr>
<td>1990</td>
<td>17,509</td>
<td>2,229</td>
<td>3,221</td>
<td>2,372</td>
</tr>
<tr>
<td>1991</td>
<td>29,877</td>
<td>5,850</td>
<td>6,028</td>
<td>4,038</td>
</tr>
<tr>
<td>1992</td>
<td>35,722</td>
<td>10,844</td>
<td>10,759</td>
<td>5,204</td>
</tr>
<tr>
<td>1993</td>
<td>41,132</td>
<td>13,273</td>
<td>12,702</td>
<td>6,819</td>
</tr>
<tr>
<td>1994</td>
<td>41,664</td>
<td>16,358</td>
<td>14,318</td>
<td>7,766</td>
</tr>
<tr>
<td>1995</td>
<td>42,156</td>
<td>20,207</td>
<td>14,602</td>
<td>8,901</td>
</tr>
<tr>
<td>1996</td>
<td>39,526</td>
<td>19,408</td>
<td>12,223</td>
<td>8,808</td>
</tr>
<tr>
<td>1997</td>
<td>39,532</td>
<td>21,153</td>
<td>10,970</td>
<td>8,825</td>
</tr>
<tr>
<td>1998</td>
<td>25,241</td>
<td>19,454</td>
<td>6,523</td>
<td>8,064</td>
</tr>
<tr>
<td>1999</td>
<td>20,451</td>
<td>17,935</td>
<td>4,264</td>
<td>6,174</td>
</tr>
<tr>
<td>2000*</td>
<td>5,681</td>
<td>6,380</td>
<td>1,418</td>
<td>2,001</td>
</tr>
</tbody>
</table>

*Partial year - records included through April 2000.
Table 3. Estimates of (co)variance components and genetic parameters from univariate analyses for lean growth rate (g/d) by breed using models without (model 1) and with (model 2) maternal genetic effects

<table>
<thead>
<tr>
<th>Component</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Model 1</td>
<td>Model 2</td>
<td>Model 1</td>
<td>Model 2</td>
</tr>
<tr>
<td>$\sigma^2_a$</td>
<td>200.71</td>
<td>207.62</td>
<td>172.19</td>
<td>173.59</td>
</tr>
<tr>
<td>$\sigma_{am}$</td>
<td>-37.76</td>
<td>-18.18</td>
<td>-19.29</td>
<td>-10.08</td>
</tr>
<tr>
<td>$\sigma^2_m$</td>
<td>18.45</td>
<td>8.27</td>
<td>15.56</td>
<td>4.87</td>
</tr>
<tr>
<td>$\sigma^2_e$</td>
<td>36.49</td>
<td>36.91</td>
<td>31.31</td>
<td>37.19</td>
</tr>
<tr>
<td>$\sigma^2_p$</td>
<td>218.94</td>
<td>198.39</td>
<td>187.84</td>
<td>194.26</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.44</td>
<td>0.45</td>
<td>0.44</td>
<td>0.42</td>
</tr>
<tr>
<td>$m^2$</td>
<td>0.04</td>
<td>0.02</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.08</td>
<td>0.08</td>
<td>0.09</td>
<td>0.10</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>-0.61</td>
<td>-0.48</td>
<td>-0.31</td>
<td>-0.34</td>
</tr>
</tbody>
</table>

*a = animal genetic; m = maternal genetic; e = residual; p = phenotypic; $m^2$ = fraction of variance due to maternal genetic effects; $c^2$ = fraction of variance due to common litter effects; standard errors of $h^2$ ranged from approximately 0.01 to 0.02.
Table 4. Estimates of (co)variance components and genetic parameters from univariate analyses for days to 113.5 kg by breed using models without (model 1) and with (model 2) maternal genetic effects

<table>
<thead>
<tr>
<th>Component(^a)</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\sigma^2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 1</td>
<td>61.25</td>
<td>62.72</td>
<td>81.81</td>
<td>76.20</td>
</tr>
<tr>
<td>Model 2</td>
<td>64.74</td>
<td>61.32</td>
<td>83.71</td>
<td>74.20</td>
</tr>
<tr>
<td>(\sigma_{an})</td>
<td>-3.02</td>
<td>-8.15</td>
<td>-10.94</td>
<td>-11.57</td>
</tr>
<tr>
<td>(\sigma_m^2)</td>
<td>1.80</td>
<td>3.22</td>
<td>7.73</td>
<td>9.76</td>
</tr>
<tr>
<td>(\sigma_e^2)</td>
<td>21.00</td>
<td>25.08</td>
<td>22.31</td>
<td>22.86</td>
</tr>
<tr>
<td></td>
<td>19.78</td>
<td>24.20</td>
<td>25.13</td>
<td>23.43</td>
</tr>
<tr>
<td>(\sigma_{c}^2)</td>
<td>92.76</td>
<td>69.00</td>
<td>81.82</td>
<td>91.43</td>
</tr>
<tr>
<td></td>
<td>93.51</td>
<td>72.63</td>
<td>76.71</td>
<td>87.88</td>
</tr>
<tr>
<td>(\sigma_p^2)</td>
<td>175.01</td>
<td>156.80</td>
<td>185.94</td>
<td>190.49</td>
</tr>
<tr>
<td></td>
<td>179.83</td>
<td>161.37</td>
<td>193.28</td>
<td>195.27</td>
</tr>
<tr>
<td>(h^2)</td>
<td>0.35</td>
<td>0.40</td>
<td>0.44</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>0.36</td>
<td>0.38</td>
<td>0.43</td>
<td>0.38</td>
</tr>
<tr>
<td>(m^2)</td>
<td>0.01</td>
<td>0.02</td>
<td>0.04</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(c^2)</td>
<td>0.12</td>
<td>0.16</td>
<td>0.12</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>0.11</td>
<td>0.15</td>
<td>0.13</td>
<td>0.12</td>
</tr>
<tr>
<td>(r_{an})</td>
<td>-0.28</td>
<td>-0.58</td>
<td>-0.43</td>
<td>-0.43</td>
</tr>
</tbody>
</table>

\(^a\) = animal genetic; \(m\) = maternal genetic; \(c\) = residual; \(p\) = phenotypic; \(m^2\) = fraction of variance due to maternal genetic effects; \(c^2\) = fraction of variance due to common litter effects; standard errors of \(h^2\) ranged from approximately 0.01 to 0.02.
Table 5. Estimates of (co)variance components and genetic parameters from univariate analyses for backfat (mm) by breed using models without (model 1) and with (model 2) maternal genetic effects

<table>
<thead>
<tr>
<th>Component&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Model 1</td>
<td>Model 2</td>
<td>Model 1</td>
<td>Model 2</td>
</tr>
<tr>
<td>$\sigma_a^2$</td>
<td>6.01</td>
<td>6.54</td>
<td>5.22</td>
<td>5.51</td>
</tr>
<tr>
<td>$\sigma_{am}$</td>
<td>-0.72</td>
<td>-0.67</td>
<td>-0.46</td>
<td>-1.03</td>
</tr>
<tr>
<td>$\sigma_m^2$</td>
<td>0.26</td>
<td>0.44</td>
<td>0.38</td>
<td>0.42</td>
</tr>
<tr>
<td>$\sigma_e^2$</td>
<td>1.00</td>
<td>1.05</td>
<td>0.97</td>
<td>1.10</td>
</tr>
<tr>
<td>$\sigma_p^2$</td>
<td>5.52</td>
<td>5.23</td>
<td>4.69</td>
<td>3.96</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.48</td>
<td>0.50</td>
<td>0.48</td>
<td>0.50</td>
</tr>
<tr>
<td>$m^2$</td>
<td>0.02</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.08</td>
<td>0.08</td>
<td>0.09</td>
<td>0.10</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>-0.55</td>
<td>-0.43</td>
<td>-0.35</td>
<td>-0.60</td>
</tr>
</tbody>
</table>

<sup>a</sup>a = animal genetic; m = maternal genetic; e = residual; p = phenotypic; $m^2$ = fraction of variance due to maternal genetic effects; $c^2$ = fraction of variance due to common litter effects; standard errors of $h^2$ ranged from approximately 0.01 to 0.02.
Table 6. Estimates of (co)variance components and genetic parameters from univariate analyses for loin eye area (cm$^2$) by breed using models without (model 1) and with (model 2) maternal genetic effects

<table>
<thead>
<tr>
<th>Component*</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Model 1</td>
<td>Model 2</td>
<td>Model 1</td>
<td>Model 2</td>
</tr>
<tr>
<td>$\sigma_a^2$</td>
<td>5.09</td>
<td>5.67</td>
<td>4.52</td>
<td>4.94</td>
</tr>
<tr>
<td>$\sigma_{am}$</td>
<td>-0.55</td>
<td>-0.47</td>
<td>-0.67</td>
<td>-0.47</td>
</tr>
<tr>
<td>$\sigma_m^2$</td>
<td>0.49</td>
<td>0.56</td>
<td>0.50</td>
<td>0.52</td>
</tr>
<tr>
<td>$\sigma_e^2$</td>
<td>1.39</td>
<td>1.46</td>
<td>1.27</td>
<td>1.27</td>
</tr>
<tr>
<td>$\sigma_p^2$</td>
<td>8.96</td>
<td>8.56</td>
<td>8.27</td>
<td>7.33</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.33</td>
<td>0.35</td>
<td>0.32</td>
<td>0.35</td>
</tr>
<tr>
<td>$m^2$</td>
<td>0.03</td>
<td>0.04</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>$c^2$</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.07</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>-0.31</td>
<td>-0.28</td>
<td>-0.41</td>
<td>-0.29</td>
</tr>
</tbody>
</table>

* $a$ = animal genetic; $m$ = maternal genetic; $e$ = residual; $p$ = phenotypic; $m^2$ = fraction of variance due to maternal genetic effects; $c^2$ = fraction of variance due to common litter effects; standard errors of $h^2$ were around 0.01.
Table 7. Estimates of heritability ($h^2$) (diagonal), genetic correlations ($r_g$) (above diagonal), and phenotypic correlations (below diagonal) by breed

<table>
<thead>
<tr>
<th>Trait</th>
<th>Lean growth rate</th>
<th>Days to 113.5 kg</th>
<th>Backfat</th>
<th>Loin eye area</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lean growth rate, kg/d</td>
<td>0.43</td>
<td>-0.84</td>
<td>-0.32</td>
<td>0.44</td>
</tr>
<tr>
<td>Days to 113.5 kg</td>
<td>-0.80</td>
<td>0.35</td>
<td>-0.04</td>
<td>0.10</td>
</tr>
<tr>
<td>Backfat, cm</td>
<td>-0.40</td>
<td>-0.05</td>
<td>0.49</td>
<td>-0.35</td>
</tr>
<tr>
<td>Loin eye area, cm$^2$</td>
<td>0.56</td>
<td>0.15</td>
<td>-0.45</td>
<td>0.34</td>
</tr>
</tbody>
</table>

Yorkshire

| Lean growth rate, kg/d          | 0.42             | -0.86            | -0.40   | 0.43          |
| Days to 113.5 kg                | -0.91            | 0.38             | -0.10   | 0.08          |
| Backfat, cm                     | -0.45            | -0.08            | 0.49    | -0.41         |
| Loin eye area, cm$^2$            | 0.53             | 0.13             | -0.47   | 0.33          |

Duroc

| Lean growth rate, kg/d          | 0.47             | -0.80            | -0.35   | 0.50          |
| Days to 113.5 kg                | -0.90            | 0.44             | -0.08   | -0.02         |
| Backfat, cm                     | -0.40            | -0.03            | 0.48    | -0.45         |
| Loin eye area, cm$^2$            | 0.47             | 0.05             | -0.43   | 0.34          |

Hampshire
Table 7. Estimates of heritability\(^a\) (\(h^2\)) (diagonal), genetic correlations\(^b\) (\(r_g\)) (above diagonal), and phenotypic correlations (below diagonal) by breed

<table>
<thead>
<tr>
<th>Breed</th>
<th>Lean growth rate, kg/d</th>
<th>Days to 113.5 kg</th>
<th>Backfat, cm</th>
<th>Loin eye area, cm(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.38</td>
<td>-0.80</td>
<td>-0.40</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>-0.83</td>
<td>0.39</td>
<td>-0.08</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>-0.41</td>
<td>-0.04</td>
<td>0.48</td>
<td>-0.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.38</td>
<td>0.10</td>
<td>-0.35</td>
<td>0.30</td>
</tr>
</tbody>
</table>

\(^a\)\(h^2\) is the average of three estimates from bivariate analyses.

\(^b\)Standard errors ranged from approximately 0.005 to 0.009 for days to 113.5 kg with lean growth rate, from 0.01 to 0.02 for backfat with lean growth rate, from 0.02 to 0.03 for backfat with days to 113.5 kg, from 0.02 to 0.03 for lean eye area to lean growth rate, from 0.02 to 0.03 for lean eye area to days to 113.5 kg, and from 0.02 to 0.03 for lean eye area to backfat, respectively.
Table 8. Overall regressions of EBV for lean growth rate, days to 113 kg, backfat, and loin eye area on birth year by breed

<table>
<thead>
<tr>
<th>Item</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lean growth rate, g/d</td>
<td>2.46</td>
<td>3.28</td>
<td>1.42</td>
<td>2.24</td>
</tr>
<tr>
<td>Days to 113 kg</td>
<td>-0.41</td>
<td>-0.54</td>
<td>-0.13</td>
<td>-0.52</td>
</tr>
<tr>
<td>Backfat, mm</td>
<td>-0.45</td>
<td>-0.43</td>
<td>-0.31</td>
<td>-0.37</td>
</tr>
<tr>
<td>Loin eye area, cm²</td>
<td>0.41</td>
<td>0.40</td>
<td>0.29</td>
<td>0.37</td>
</tr>
</tbody>
</table>
Figure 1. Genetic trend for days to 113.5 kg by breed from 1990 to 2000
Figure 2. Genetic trend for backfat by breed from 1990 to 2000
Figure 3. Genetic trend for loin eye area by breed from 1990 to 2000
Figure 4. Genetic trend for lean growth rate by breed from 1990 to 2000
CHAPTER 3. GENETIC PARAMETERS AND TRENDS FOR LITTER TRAITS IN U.S. YORKSHIRE, DUROC, HAMPSHIRE, AND LANDRACE PIGS

A paper accepted by the Journal of Animal Science

P. Chen, T. J. Baas, J. W. Mabry, K. J. Koehler, and J. C. M. Dekkers

ABSTRACT: Records on 251,296 Yorkshire, 75,262 Duroc, 83,338 Hampshire, and 53,234 Landrace litters born between 1984 and April of 1999 in herds on the National Swine Registry Swine Testing and Genetic Evaluation System (STAGES) were analyzed. Animal model and REML procedures were used to estimate variances of animal genetic (a), maternal genetic (m), permanent environmental, and service sire, and the covariances between a and m for number born alive (NBA), litter weight at 21 d (L21WT), and number weaned (NW). Fixed effects of contemporary groups were included in the analysis. Based on a single-trait model, estimates of heritabilities were 0.10, 0.09, 0.08, and 0.08 for NBA; 0.08, 0.07, 0.08, and 0.09 for L21WT; and 0.05, 0.07, 0.05, and 0.05 for NW in the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Estimates of maternal genetic effects were low and ranged from 0.00 to 0.02 for all traits and all breeds. Estimates of permanent environmental effects ranged from 0.03 to 0.08. Estimates of service sire effects ranged from 0.02 to 0.05. A bivariate analysis was used to estimate the genetic correlations among traits. Average genetic correlations over the four breeds were 0.13, 0.15, and 0.71 for NBA with L21WT, NBA with NW, and L21WT with NW, respectively. Average genetic trends were 0.018 pigs/yr, 0.114 kg/yr, and 0.004 pigs/yr for NBA, L21WT, and NW, respectively. Although estimates of heritabilities for litter traits were low and similar across breeds, genetic variances for litter traits were sufficiently large to indicate that litter traits could be improved through selection. This study presents the first set of breed-specific estimates of
genetic parameters available from large numbers of field records. It provides information for use in national genetic evaluations.

**Introduction**

Selection for litter traits is attractive to breeders because lean growth traits, which have been selection objectives for many years, may be approaching an optimum point (Webb, 1998). A successful genetic improvement program requires accurate genetic parameter estimates. Several studies (Southwood and Kennedy, 1990; Crump et al., 1997; Kaufmann et al., 2000) have reported estimates of genetic parameters for litter traits based on different commercial populations and limited field data. Parameter estimates in the literature for litter traits vary substantially among studies or breeds (Southwood and Kennedy, 1990; Ferraz and Johnson, 1993; Kaufmann et al., 2000). Genetic parameters currently recommended by the National Swine Improvement Federation (NSIF, 1997) for genetic evaluation programs are not breed-specific. Therefore, the objective of this study was to estimate breed-specific genetic parameters and genetic trends for number born alive (NBA), number weaned (NW), and litter weight at 21 d (L21WT) for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations.

**Materials and Methods**

*Data Source*

Data were obtained from the National Swine Registry (NSR) Swine Testing and Genetic Evaluation System (STAGES) on Yorkshire, Duroc, Hampshire, and Landrace litters born from 1984 to April 1999. Details of data collection can be found in STAGES (NSR, 2000). Data included pedigree information for each sow, contemporary group (CG), parity of the sow, farrowing and weighing dates, NBA, number after transfer (NAT), NW,
and L21WT. The NW included adopted pigs but excluded pigs transferred to other sows.

Contemporary groups were defined by the breeder as a group of sows that were bred, gestated, and farrowed in a group under the same management and environmental conditions. The traits NBA and L21WT were adjusted according to breed-specific procedures developed by Culbertson et al. (1997). Number weaned was adjusted according to breed-specific procedures developed by Culbertson (1997). Both NBA and L21WT were adjusted for parity and age at farrowing. Litter weight at 21 d was also adjusted for NAT and age at weighing. Number weaned was adjusted for parity and NAT. Single-sire contemporary group records were removed, as were records from sires not connected across contemporary groups. Numbers of records, animals, sires, dams, service sires, and contemporary groups by breed are in Table 1, along with means and SD for NBA, L21WT, and NW. After editing, distribution of records across years for each breed is shown in Table 2. In the Yorkshire dataset, only records since 1992 were used to estimate variance components due to computational limitations on dataset size.

**Statistical Analysis**

**Univariate Analysis.** Within-breed univariate analyses were conducted using REMLF90 (Misztal, 2000) to estimate single-trait variance components. The model fitted was: \( y = Xb + Za + Pm + W_1ss + W_2pe + e \), where \( y \) represents a vector of observations; \( b \) is a vector of fixed contemporary group effects; \( a \) is a vector of random additive genetic effects of animals, which is assumed to be distributed \( N(0, \sigma_a^2) \); \( A \) is the numerator relationship matrix among animals; \( m \) is a vector of random additive maternal genetic effects, assumed to be distributed \( N(0, \sigma_m^2) \) and correlated with random animal effects \( (\sigma_{am}) \); \( ss \) is a vector of service sires, assumed to be distributed \( N(0, \sigma_{ss}^2) \) and uncorrelated
with other random effects; \( \mathbf{pe} \) is a vector of permanent environmental effects, assumed to be distributed \( \mathbf{N}(\mathbf{0}, \mathbf{I} \sigma_{pe}^2) \) and uncorrelated with other random effects; and \( \mathbf{e} \) is a vector of residual effects, which is assumed to be distributed \( \mathbf{N}(\mathbf{0}, \mathbf{I} \sigma_e^2) \). Incidence matrices of \( \mathbf{X}, \mathbf{Z}, \mathbf{P}, \mathbf{W}_1, \) and \( \mathbf{W}_2 \) relate records to fixed, additive genetic, maternal genetic, service sire, and permanent environmental effects, respectively. A simplified model in which maternal genetic effects were excluded was also fitted. Standard errors of heritability estimates were calculated using the approximation of Swiger et al. (1964).

**Bivariate Analyses.** Bivariate analyses were conducted to estimate genetic and phenotypic correlations among traits using REMLF90 ((Misztal, 2000). The model was the same as for the univariate analyses except maternal genetic effects were excluded. Standard errors of genetic correlations (\( \hat{\sigma}_{ij} \)) were calculated using the approximate formula given by Falconer (1989):

\[
\hat{\sigma}_{ij} = \frac{1 - \hat{r}_{ij}^2}{\sqrt{2}} \sqrt{\frac{\hat{h}_i^2 \hat{h}_j^2}{\hat{h}_i^2 + \hat{h}_j^2}}
\]

where \( \hat{h}_i^2, \hat{h}_j^2 \) are the heritability estimates of traits \( x \) and \( y \), respectively, and \( \hat{\sigma}_{ki} \) and \( \hat{\sigma}_{kj} \) are the standard errors of the heritability estimates of traits \( x \) and \( y \), respectively. In the REML analyses, the convergence criterion was set to \( 10^{-8} \) for all analyses.

**Maternal Effects.** Breeding values for litter traits were estimated using two single-trait models with and without maternal effects using BLUPF90 (Misztal, 2000). Spearman rank correlations between the two sets of EBV for sows were estimated to examine the consequences of ignoring maternal effects.
Genetic Trends. Breeding values for litter traits were estimated using a three-trait model without maternal effects using BLUPF90 (Misztal, 2000). The average breeding values per birth year were regressed on birth year of the sows and plotted to illustrate trends.

Results and Discussion

Genetic Variances

Estimates of genetic variances and covariances are in Tables 3 to 5. Differences in estimates of variance components among breeds were found. Genetic variances for NBA, L21WT, and NW were highest in the Yorkshire breed. Landrace had the highest additive maternal genetic variance for NBA, and Yorkshire had the highest for NW and L21WT. Interpreting differences in variance component estimates from the literature is difficult because these estimates depend on the population and the data collected. Estimates of animal genetic variance for NBA in Tables 3 to 5 generally tend to be smaller than those reported in the literature (Southwood and Kennedy, 1990; Crump et al., 1997; Kaufmann et al., 2000). However, estimates of animal genetic variances for L21WT are in agreement with the values reported by Ferraz and Johnson (1993). Negative genetic covariances between direct and maternal genetic effects were found for all traits in each breed.

Heritabilities

Estimates of heritabilities from single-trait models are in Tables 3 to 5, and those from bivariate analyses are in Table 6. Estimates of heritability for each trait within breed obtained from single- and bivariate-trait analyses differed by 1% or less; therefore, only those from single-trait analyses are discussed. Very little difference in the estimates of heritability with and without maternal genetic effects occurred. This result agrees with the findings of Southwood and Kennedy (1990) in Canadian Yorkshire. However, the results of this study
are not consistent with the findings of Southwood and Kennedy (1990) in Canadian Landraces who found estimates of heritability were reduced considerably by not accounting for maternal effects and their covariance with animal direct effects. Crump et al. (1997) also reported that the estimates of heritability for litter traits changed very little with maternal genetic effects in the model.

Estimates of heritability for NBA are 0.10, 0.09, 0.08, and 0.08 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 3). These are in agreement with literature estimates of approximately 0.10 (Southwood and Kennedy, 1990; Crump et al., 1997). See et al. (1993) reported estimates of 0.12 to 0.13 from field data of Hampshire, Landrace, and Spotted breeds, which were included in the current analysis. However, the estimates in this study are much lower than the estimate of 0.22 reported by Kaufmann et al. (2000). These results are also consistent with the heritability of 0.10 recommended by NSIF (1997).

Estimates of heritability for L21WT are 0.08, 0.07, 0.08, and 0.09 for Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 4). These estimates are similar to those reported by Kaplon et al. (1991a) in Polish Large White sows; however, the data in that study was not adjusted for litter size, and cross-fostering was stated to be infrequent. However, Ferraz and Johnson (1993) reported an average heritability of 0.19 over four models for L21WT in Landrace and Large White sows. The results in this study are also lower than the heritability of 0.15 recommended by NSIF (1997).

Estimates of heritability for NW are 0.05, 0.07, 0.05, and 0.05 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 5). These estimates are in the range of previous estimates (Kaplon et al., 1991a; Roehe and Kennedy, 1995), but lower than
the estimated heritability of 0.10 reported by Southwood and Kennedy (1990) in Canadian sows and Chen et al. (2001) from a selection experiment with a synthetic line of Yorkshire-Meishan pigs. The estimates from this study are also similar to the value of 0.06 recommended by NSIF (1997).

*Additive Maternal Genetic Effects*

Additive maternal genetic effects were not large sources of variation. The percentage of the variance accounted for by maternal genetic effects ranged from 0.00 to 0.02 for all traits and breeds (Tables 3 to 5). This result is in agreement with the results of Perez-Enciso and Gianola (1992), Roehe and Kennedy (1995), and Crump et al. (1997). However, these estimates of maternal genetic effects are considerably lower than those reported by Southwood and Kennedy (1990), Ferraz and Johnson (1993), and See et al. (1993). Negative correlations between direct and maternal additive genetic effects were found for all traits across breeds (Tables 3 to 5). The estimated correlations ranged from -0.27 to -0.70 for NBA; from -0.11 to -0.21 for L21WT; and from -0.53 to -0.71 for NW. These results are in the range of previous estimates reported by Southwood and Kennedy (1990), Haley and Lee (1992), and Crump et al. (1997). These correlations were stronger for NW than for NBA in the Yorkshire, Duroc, and Hampshire breeds, but they were relatively strong for both NW and NBA in the Landrace.

Spearman rank correlations between the two sets of EBV for direct genetic effects for litter traits under the models with and without maternal genetic effects ranged from 0.93 to 0.98 across breeds. Little change in ranking of sows on estimating breeding values from models with and without maternal genetic effects occurred. This result is consistent with
those of other studies (Southwood and Kennedy, 1990; Crump et al., 1997) indicating models with only direct genetic effects are sufficient.

In this dataset, 50% of litters had cross-fostering. The small maternal genetic effects may be explained by the large amount of cross-fostering practiced, as argued by Crump et al. (1997), which means that sows that are littermates at birth do not share the same postnatal environment. This implies the maternal genetic effect applies postnatally rather than in utero or cytoplasmically. This was supported by Southwood and Kennedy (1990) who found that estimates of maternal genetic effects for NW were generally higher than for NBA. However, in this study, estimates of maternal genetic effects for NW are similar to those for NBA. Roehe and Kennedy (1993) showed that with small maternal heritability ($h^2_m$) and a negative correlation between maternal and direct effects, the response to direct selection for litter size can be reduced.

Estimates of maternal genetic effects and their correlations with direct effects have high sampling variances (Meyer, 1992). Also, Gerstenmayr (1992) found that estimates of small magnitude have greater relative and absolute sampling variances than larger estimates. Additionally, Roehe and Kennedy (1993) found substantial confounding between estimates of maternal and direct effects. Therefore, estimates of maternal genetic effects in this study likely have high sampling variances and may be confounded with direct genetic effects.

**Permanent Environmental Effects**

Estimates of the fraction of the total phenotypic variation for litter traits due to permanent environmental effects associated with the sow ranged from 0.03 to 0.08 (Tables 3 to 5). These estimates are consistent with those reported by Crump et al. (1997) and Kaufmann et al. (2000). However, these results for NBA are lower than the estimates of 16
to 17% reported by Ferraz and Johnson (1993) and the estimate of 12.6% reported by Haley and Lee (1992).

**Service Sire Effects**

The proportion of the total variation in litter traits due to the effect of service sire ranged from 0.02 to 0.05 (Tables 3 to 5) across breeds. See et al. (1993) estimated variation due to service sire effects at 0.01 to 0.02 for NBA from field data in the Spotted, Landrace, and Hampshire breeds. Mabry et al. (1988) also reported that service sire effects accounted for 3% of the total variation in NBA, and Buytels and Long (1991) found service sire effects accounted for 1% of the total variation. In general, results from this study indicate stronger service sire effects than these previous studies. The service sire could influence litter size either by semen quality and quantity, or by genetic effects that influence embryo development and survival (See et al., 1993).

**Correlations**

Estimates of phenotypic and genetic correlations among traits for each breed are in Table 6. Estimates of phenotypic correlations between NBA and L21WT ranged from 0.03 in the Duroc breed to 0.07 in the Landrace breed. Strong, positive phenotypic correlations between NW and L21WT ranging from 0.77 in the Duroc breed to 0.80 in the Yorkshire breed were found. Small positive correlations between NBA and NW were also found. The weak correlations between NBA and L21WT and between NBA and NW may be due to cross-fostering of pigs. McCarter et al. (1987) reported estimates of phenotypic correlations of 0.08 between NBA and L21WT, 0.48 between NW and L21WT, and 0.59 between NBA and NW.
Estimated genetic correlations between NBA and L21WT were lowest for the Duroc breed (0.10) and highest for the Landrace breed (0.15). A genetic correlation of 0.12 between NBA and L21WT is recommended by NSIF (1997). Estimated genetic correlations between L21WT and NW ranged from 0.65 in the Duroc breed to 0.75 in the Yorkshire breed, while genetic correlations between NBA and NW ranged from 0.07 in the Duroc breed to 0.20 in the Hampshire breed. McCarter et al. (1987) reported estimates of genetic correlations of 0.12 for NBA and L21WT, 0.55 for NW and L21WT, and 0.58 for NBA and NW. Kaplon et al. (1991a) reported estimates of pooled genetic correlations of 0.68 for NBA and L21WT, 0.80 for NW and L21WT, and 0.91 for NBA and NW. These differences, especially between NW and NBA, may be due to the fact that cross-fostering was not practiced in their populations.

Genetic Trends

All estimated genetic trends for NBA, L21WT, and NW were positive (Figures 1 to 3, Table 7). Estimates of genetic trends were greatest in Yorkshire, averaging 0.029 pigs/yr for NBA, 0.279 kg/yr for L21WT, and 0.008 pigs/yr for NW. Average genetic change in NBA over the four breeds was 0.018 pigs/yr, or 0.18% of the mean, higher than the estimate of 0.01 pigs/yr reported by Kaplon et al. (1991b), Southwood and Kennedy (1991), and Ferraz and Johnson (1993). Average genetic change in L21WT was 0.11 kg/yr or 0.20% of the mean. This is lower than the estimates of 0.245 kg/yr or 0.44% of the mean in Landrace and Large White breeds by Ferraz and Johnson (1993), but larger than the average of 0.045 kg/yr reported by Kaplon et al. (1991b). Genetic trends in NW across breeds were positive and very small (Figure 3, Table 7), which is consistent with the values reported by Southwood and Kennedy (1991) in Canadian breeds and Kaplon et al. (1991b) in Polish sows. Low rates
of genetic trends could be because breeders were applying very little selection for them, or
the selection that was applied was ineffective because of the low heritabilities.

Implications

This report of breed-specific genetic estimates for litter traits is based on the U.S.
national database. Based on this study, use of a direct model that ignores maternal breeding
values would seem sufficient. Genetic variance for litter traits was sufficiently large to
indicate that litter traits could be improved through selection. Estimated annual rates of
genetic change for litter traits indicate that further improvement in these traits is still
possible. Use of appropriate models that include permanent environmental and service sire
effects, along with breed-specific genetic parameters, will increase the accuracy of EBV.

Literature Cited

303-306 in. Proc. 9th Conf. Australian Assoc. of Anim. Breed. and Genet. Univ. of
Melbourne, Victoria, Australia.

rate and correlated responses in litter traits in a synthetic line of Yorkshire-Meishan pigs.

University of Georgia, Athens, GA.

adjustment factors for reproductive traits in Duroc, Hampshire, Landrace, and


Table 1. Number of records and means for litter traits by breed

<table>
<thead>
<tr>
<th>Item</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td>Records</td>
<td>251,296</td>
<td>75,262</td>
<td>83,332</td>
<td>53,234</td>
</tr>
<tr>
<td>Animals</td>
<td>128,773</td>
<td>45,970</td>
<td>46,861</td>
<td>26,134</td>
</tr>
<tr>
<td>Sires</td>
<td>12,415</td>
<td>4,729</td>
<td>4,982</td>
<td>2,815</td>
</tr>
<tr>
<td>Dams</td>
<td>48,875</td>
<td>18,413</td>
<td>18,795</td>
<td>9,241</td>
</tr>
<tr>
<td>Service sires</td>
<td>12,415</td>
<td>5,299</td>
<td>5,947</td>
<td>3,737</td>
</tr>
<tr>
<td>Contemporary groups</td>
<td>31,487</td>
<td>10,404</td>
<td>12,086</td>
<td>7,191</td>
</tr>
<tr>
<td>Number born alive</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>10.61</td>
<td>9.16</td>
<td>9.54</td>
<td>10.44</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>2.67</td>
<td>2.37</td>
<td>2.36</td>
<td>2.54</td>
</tr>
<tr>
<td>Litter weight, kg</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>59.48</td>
<td>55.64</td>
<td>54.57</td>
<td>62.41</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>14.34</td>
<td>14.11</td>
<td>13.81</td>
<td>13.84</td>
</tr>
<tr>
<td>Number weaned</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>11.31</td>
<td>10.77</td>
<td>10.49</td>
<td>11.42</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>2.45</td>
<td>1.85</td>
<td>1.71</td>
<td>1.81</td>
</tr>
</tbody>
</table>

*aMean adjusted for parity and age at farrowing.

*bMean adjusted for parity, age at farrowing, number after transfer, and age at weighing.

*cMean adjusted for parity and number after transfer.
Table 2. Data distribution by year and breed

<table>
<thead>
<tr>
<th>Year</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>8,636</td>
<td>15</td>
<td>444</td>
<td>1,400</td>
</tr>
<tr>
<td>1985</td>
<td>14,469</td>
<td>34</td>
<td>994</td>
<td>1,759</td>
</tr>
<tr>
<td>1986</td>
<td>16,138</td>
<td>1,123</td>
<td>2,323</td>
<td>2,484</td>
</tr>
<tr>
<td>1987</td>
<td>18,137</td>
<td>3,019</td>
<td>3,844</td>
<td>3,423</td>
</tr>
<tr>
<td>1988</td>
<td>19,697</td>
<td>3,294</td>
<td>4,823</td>
<td>3,255</td>
</tr>
<tr>
<td>1989</td>
<td>20,434</td>
<td>3,638</td>
<td>5,751</td>
<td>3,555</td>
</tr>
<tr>
<td>1990</td>
<td>21,870</td>
<td>4,150</td>
<td>6,799</td>
<td>4,128</td>
</tr>
<tr>
<td>1991</td>
<td>20,913</td>
<td>5,026</td>
<td>8,240</td>
<td>4,520</td>
</tr>
<tr>
<td>1992</td>
<td>20,392</td>
<td>5,474</td>
<td>9,113</td>
<td>5,231</td>
</tr>
<tr>
<td>1993</td>
<td>18,349</td>
<td>6,860</td>
<td>8,725</td>
<td>4,479</td>
</tr>
<tr>
<td>1994</td>
<td>16,960</td>
<td>7,969</td>
<td>8,815</td>
<td>4,218</td>
</tr>
<tr>
<td>1995</td>
<td>14,907</td>
<td>7,686</td>
<td>7,830</td>
<td>3,959</td>
</tr>
<tr>
<td>1996</td>
<td>14,939</td>
<td>8,909</td>
<td>6,914</td>
<td>4,027</td>
</tr>
<tr>
<td>1997</td>
<td>12,400</td>
<td>8,471</td>
<td>5,010</td>
<td>3,417</td>
</tr>
<tr>
<td>1998</td>
<td>7,404</td>
<td>5,796</td>
<td>2,762</td>
<td>2,108</td>
</tr>
<tr>
<td>1999*</td>
<td>5,651</td>
<td>3,798</td>
<td>951</td>
<td>1,271</td>
</tr>
</tbody>
</table>

*Partial year—records included the litters born up to April 1999.
### Table 3. Estimates of (co)variance components and genetic parameters from univariate analyses for number born alive by breed using models without (model 1) and with (model 2) maternal genetic effects

<table>
<thead>
<tr>
<th>Component</th>
<th>Yorkshire Model 1</th>
<th>Yorkshire Model 2</th>
<th>Duroc Model 1</th>
<th>Duroc Model 2</th>
<th>Hampshire Model 1</th>
<th>Hampshire Model 2</th>
<th>Landrace Model 1</th>
<th>Landrace Model 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \sigma_e^2 )</td>
<td>0.5931</td>
<td>0.5917</td>
<td>0.4627</td>
<td>0.4113</td>
<td>0.4046</td>
<td>0.4045</td>
<td>0.5050</td>
<td>0.4418</td>
</tr>
<tr>
<td>( \sigma_m^2 )</td>
<td>0.0592</td>
<td>0.0514</td>
<td>-0.0495</td>
<td>-0.0618</td>
<td>0.0450</td>
<td>0.0553</td>
<td>0.1262</td>
<td>-0.1653</td>
</tr>
<tr>
<td>( \sigma_{am} )</td>
<td>0.2372</td>
<td>0.2368</td>
<td>0.1542</td>
<td>0.1542</td>
<td>0.1011</td>
<td>0.1010</td>
<td>0.2525</td>
<td>0.2525</td>
</tr>
<tr>
<td>( \sigma_{pe}^2 )</td>
<td>0.4152</td>
<td>0.4142</td>
<td>0.4113</td>
<td>0.4113</td>
<td>0.3034</td>
<td>0.3035</td>
<td>0.4417</td>
<td>0.4418</td>
</tr>
<tr>
<td>( \sigma_c^2 )</td>
<td>4.6856</td>
<td>4.6149</td>
<td>4.1129</td>
<td>4.1131</td>
<td>4.248</td>
<td>4.2478</td>
<td>5.1132</td>
<td>5.0498</td>
</tr>
<tr>
<td>( \sigma_p^2 )</td>
<td>5.9311</td>
<td>5.9168</td>
<td>5.1411</td>
<td>5.1413</td>
<td>5.0571</td>
<td>5.0568</td>
<td>6.3124</td>
<td>6.3121</td>
</tr>
<tr>
<td>( h^2 )</td>
<td>0.10</td>
<td>0.10</td>
<td>0.09</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>( m^2 )</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.02</td>
<td>0.02</td>
</tr>
<tr>
<td>( ss^2 )</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
<td>0.03</td>
<td>0.02</td>
<td>0.02</td>
<td>0.04</td>
<td>0.04</td>
</tr>
<tr>
<td>( pe^2 )</td>
<td>0.07</td>
<td>0.07</td>
<td>0.08</td>
<td>0.08</td>
<td>0.06</td>
<td>0.06</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>( r )</td>
<td>0.17</td>
<td>0.17</td>
<td>0.17</td>
<td>0.16</td>
<td>0.14</td>
<td>0.14</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>( r_{am} )</td>
<td>-0.27</td>
<td>-0.43</td>
<td>-0.41</td>
<td>-0.41</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*\( \sigma_e^2 \) = Animal genetic variance; \( \sigma_m^2 \) = maternal genetic effect; \( \sigma_{am} \) = covariance between animal genetic and maternal genetic effects; \( \sigma_{ss}^2 \) = service sire variance; \( \sigma_{pe}^2 \) = permanent environmental variance; \( \sigma_c^2 \) = residual variance; \( \sigma_p^2 \) = phenotypic variance; \( h^2 \) = heritability (standard errors ranged from approximately 0.004 to 0.008); \( m^2 \) = fraction of variance due to maternal genetic effects; \( ss^2 \) = fraction of variance due to service sire effects; \( pe^2 \) = fraction of variance due to permanent environmental effects; \( r_{am} \) = genetic correlation between animal genetic and maternal genetic effects; \( r \) = repeatability.
Table 4. Estimates of (co)variance components and genetic parameters from univariate analyses for litter weight at 21d (kg) by breed using models without (model 1) and with (model 2) maternal genetic effects

<table>
<thead>
<tr>
<th>Component</th>
<th>Yorkshire</th>
<th></th>
<th>Duroc</th>
<th></th>
<th>Hampshire</th>
<th></th>
<th>Landrace</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Model 1</td>
<td>Model 2</td>
<td>Model 1</td>
<td>Model 2</td>
<td>Model 1</td>
<td>Model 2</td>
<td>Model 1</td>
<td>Model 2</td>
</tr>
<tr>
<td>( \sigma^2_a )</td>
<td>14.8214</td>
<td>15.2861</td>
<td>8.5931</td>
<td>8.5071</td>
<td>9.0515</td>
<td>8.9656</td>
<td>13.0831</td>
<td>12.9783</td>
</tr>
<tr>
<td>( \sigma^2_m )</td>
<td>3.7140</td>
<td>1.3125</td>
<td>0.9921</td>
<td>0.9921</td>
<td>0.9921</td>
<td>0.9921</td>
<td>1.7971</td>
<td>1.7971</td>
</tr>
<tr>
<td>( \sigma_{am} )</td>
<td>-0.8355</td>
<td>-0.5013</td>
<td>-0.6264</td>
<td>-0.6279</td>
<td>-0.6264</td>
<td>-0.6279</td>
<td>-0.6264</td>
<td>-0.6279</td>
</tr>
<tr>
<td>( \sigma^2_e )</td>
<td>7.7908</td>
<td>7.7374</td>
<td>3.7837</td>
<td>3.6988</td>
<td>4.3866</td>
<td>4.5214</td>
<td>5.8671</td>
<td>5.7834</td>
</tr>
<tr>
<td>( \sigma^2_{pe} )</td>
<td>7.4107</td>
<td>7.5134</td>
<td>8.1471</td>
<td>8.4952</td>
<td>6.8137</td>
<td>6.8117</td>
<td>7.5534</td>
<td>7.5134</td>
</tr>
<tr>
<td>( \sigma^2_s )</td>
<td>159.9955</td>
<td>154.4059</td>
<td>102.2471</td>
<td>97.3011</td>
<td>91.0826</td>
<td>88.9876</td>
<td>123.9932</td>
<td>121.7461</td>
</tr>
<tr>
<td>( \sigma^2_p )</td>
<td>190.0184</td>
<td>188.6568</td>
<td>122.7710</td>
<td>119.3147</td>
<td>111.3344</td>
<td>110.2784</td>
<td>150.4968</td>
<td>149.8183</td>
</tr>
<tr>
<td>( h^2 )</td>
<td>0.08</td>
<td>0.08</td>
<td>0.07</td>
<td>0.07</td>
<td>0.08</td>
<td>0.08</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>( m^2 )</td>
<td>0.02</td>
<td>0.01</td>
<td>0.03</td>
<td>0.03</td>
<td>0.04</td>
<td>0.04</td>
<td>0.04</td>
<td>0.04</td>
</tr>
<tr>
<td>( ss^2 )</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
<td>0.03</td>
<td>0.04</td>
<td>0.04</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>( pe^2 )</td>
<td>0.04</td>
<td>0.04</td>
<td>0.07</td>
<td>0.07</td>
<td>0.06</td>
<td>0.06</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>( r )</td>
<td>0.12</td>
<td>0.12</td>
<td>0.14</td>
<td>0.14</td>
<td>0.14</td>
<td>0.14</td>
<td>0.14</td>
<td>0.14</td>
</tr>
<tr>
<td>( r_{am} )</td>
<td>-0.11</td>
<td>-0.15</td>
<td>-0.21</td>
<td>-0.13</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\( \sigma^2_a \) = Animal genetic variance; \( \sigma^2_m \) = maternal genetic effect; \( \sigma_{am} \) = covariance between animal genetic and maternal genetic effects; \( \sigma^2_{ss} \) = service sire variance; \( \sigma^2_{pe} \) = permanent environmental variance; \( \sigma^2_e \) = residual variance; \( \sigma^2_p \) = phenotypic variance; \( h^2 \) = heritability (standard errors ranged from approximately 0.004 to 0.008); \( m^2 \) = fraction of variance due to maternal genetic effects; \( ss^2 \) = fraction of variance due to service sire effects; \( pe^2 \) = fraction of variance due to permanent environmental effects; \( r_{am} \) = genetic correlation between animal genetic and maternal genetic effects; \( r \) = repeatability.
Table 5. Estimates of (co)variance components and genetic parameters from univariate analyses for number weaned by breed using models without (model 1) and with (model 2) maternal genetic effects

<table>
<thead>
<tr>
<th>Component*</th>
<th>Yorkshire Model 1</th>
<th>Yorkshire Model 2</th>
<th>Duroc Model 1</th>
<th>Duroc Model 2</th>
<th>Hampshire Model 1</th>
<th>Hampshire Model 2</th>
<th>Landrace Model 1</th>
<th>Landrace Model 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma_s^2$</td>
<td>0.2554</td>
<td>0.2597</td>
<td>0.2216</td>
<td>0.2118</td>
<td>0.1363</td>
<td>0.1383</td>
<td>0.1577</td>
<td>0.1540</td>
</tr>
<tr>
<td>$\sigma_m^2$</td>
<td></td>
<td>0.0583</td>
<td>0.0279</td>
<td></td>
<td>0.0257</td>
<td></td>
<td>0.0126</td>
<td></td>
</tr>
<tr>
<td>$\sigma_{am}$</td>
<td>-0.0652</td>
<td></td>
<td>-0.0469</td>
<td></td>
<td>-0.0423</td>
<td></td>
<td>-0.0299</td>
<td></td>
</tr>
<tr>
<td>$\sigma_{sm}^2$</td>
<td>0.1996</td>
<td>0.2118</td>
<td>0.1547</td>
<td>0.1517</td>
<td>0.1055</td>
<td>0.1044</td>
<td>0.1072</td>
<td>0.0944</td>
</tr>
<tr>
<td>$\sigma_{pe}^2$</td>
<td>0.2557</td>
<td>0.2612</td>
<td>0.1234</td>
<td>0.1214</td>
<td>0.1061</td>
<td>0.1037</td>
<td>0.1041</td>
<td>0.0951</td>
</tr>
<tr>
<td>$\sigma_e^2$</td>
<td>4.6116</td>
<td>4.5108</td>
<td>2.6220</td>
<td>2.6056</td>
<td>2.3252</td>
<td>2.2893</td>
<td>2.7824</td>
<td>2.7887</td>
</tr>
<tr>
<td>$\sigma_p^2$</td>
<td>5.3223</td>
<td>5.3018</td>
<td>3.1217</td>
<td>3.1184</td>
<td>2.6731</td>
<td>2.6614</td>
<td>3.1514</td>
<td>3.1448</td>
</tr>
<tr>
<td>$h^2$</td>
<td>0.05</td>
<td>0.05</td>
<td>0.07</td>
<td>0.07</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>$m^2$</td>
<td></td>
<td>0.01</td>
<td></td>
<td>0.01</td>
<td></td>
<td>0.01</td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>$ss^2$</td>
<td>0.04</td>
<td>0.04</td>
<td>0.05</td>
<td>0.05</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>$pe^2$</td>
<td>0.05</td>
<td>0.05</td>
<td>0.04</td>
<td>0.04</td>
<td>0.04</td>
<td>0.04</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>$r$</td>
<td>0.10</td>
<td>0.10</td>
<td>0.11</td>
<td>0.11</td>
<td>0.09</td>
<td>0.09</td>
<td>0.08</td>
<td>0.08</td>
</tr>
<tr>
<td>$r_{am}$</td>
<td>-0.53</td>
<td>-0.61</td>
<td>-0.71</td>
<td>-0.68</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* $\sigma_s^2$ = Animal genetic variance; $\sigma_m^2$ = maternal genetic effect; $\sigma_{am}$ = covariance between animal genetic and maternal genetic effects; $\sigma_{sm}^2$ = service sire variance; $\sigma_{pe}^2$ = permanent environmental variance; $\sigma_e^2$ = residual variance; $\sigma_p^2$ = phenotypic variance; $h^2$ = heritability (standard errors ranged from approximately 0.003 to 0.007); $m^2$ = fraction of variance due to maternal genetic effects; $ss^2$ = fraction of variance due to service sire effects; $pe^2$ = fraction of variance due to permanent environmental effects; $r_{am}$ = genetic correlation between animal genetic and maternal genetic effects; $r$ = repeatability.
### Table 6. Estimates of heritability\(^a\) (diagonal), genetic\(^b\) (above diagonal), and phenotypic (below diagonal) correlations from bivariate analysis by breed

<table>
<thead>
<tr>
<th>Trait</th>
<th>Number born alive</th>
<th>Litter weight at 21 d</th>
<th>Number Weaned</th>
</tr>
</thead>
<tbody>
<tr>
<td>- Yorkshire</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number born alive</td>
<td>0.10</td>
<td>0.14</td>
<td>0.19</td>
</tr>
<tr>
<td>Litter weight at 21d</td>
<td>0.06</td>
<td>0.08</td>
<td>0.75</td>
</tr>
<tr>
<td>Number weaned</td>
<td>0.06</td>
<td>0.80</td>
<td>0.04</td>
</tr>
<tr>
<td>- Duroc</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number born alive</td>
<td>0.09</td>
<td>0.10</td>
<td>0.07</td>
</tr>
<tr>
<td>Litter weight at 21d</td>
<td>0.03</td>
<td>0.07</td>
<td>0.65</td>
</tr>
<tr>
<td>Number weaned</td>
<td>0.02</td>
<td>0.77</td>
<td>0.06</td>
</tr>
<tr>
<td>- Hampshire</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number born alive</td>
<td>0.08</td>
<td>0.13</td>
<td>0.20</td>
</tr>
<tr>
<td>Litter weight at 21d</td>
<td>0.04</td>
<td>0.08</td>
<td>0.71</td>
</tr>
<tr>
<td>Number weaned</td>
<td>0.06</td>
<td>0.79</td>
<td>0.03</td>
</tr>
<tr>
<td>- Landrace</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number born alive</td>
<td>0.08</td>
<td>0.15</td>
<td>0.14</td>
</tr>
<tr>
<td>Litter weight at 21d</td>
<td>0.07</td>
<td>0.09</td>
<td>0.73</td>
</tr>
<tr>
<td>Number weaned</td>
<td>0.05</td>
<td>0.78</td>
<td>0.02</td>
</tr>
</tbody>
</table>

\(^a\) \(h^2\) is the average of two estimates from bivariate analyses.

\(^b\) Standard errors of \(r_g\) ranged from 0.05 to 0.09 for number born alive with litter weight at 21 d; from 0.06 to 0.10 for number born alive with number weaned; and from 0.02 to 0.04 for litter weight at 21 d with number weaned, respectively.
Table 7. Overall regressions of EBV for number born alive, litter weight at 21 d, and number weaned on birth year by breed

<table>
<thead>
<tr>
<th>Item</th>
<th>Yorkshire</th>
<th>Duroc</th>
<th>Hampshire</th>
<th>Landrace</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number born alive, pigs/yr</td>
<td>0.029 ± 0.002</td>
<td>0.013 ± 0.001</td>
<td>0.007 ± 0.001</td>
<td>0.021 ± 0.002</td>
</tr>
<tr>
<td>Litter weight at 21 d, kg/yr</td>
<td>0.279 ± 0.025</td>
<td>0.087 ± 0.020</td>
<td>0.007 ± 0.009</td>
<td>0.081 ± 0.020</td>
</tr>
<tr>
<td>Number weaned, pigs/yr</td>
<td>0.008 ± 0.0006</td>
<td>0.004 ± 0.0005</td>
<td>0.001 ± 0.0005</td>
<td>0.004 ± 0.0003</td>
</tr>
</tbody>
</table>
Figure 1. Genetic trend for number born alive by breed from 1984 to 1999 National Swine Registry STAGES data
Figure 2. Genetic trend for litter weight at 21 d by breed from 1984 to 1999 National Swine Registry STAGES data
Figure 3. Genetic trend for number weaned by breed from 1984 to 1999 National Swine Registry STAGES data
CHAPTER 4. GENETIC CORRELATIONS BETWEEN LEAN GROWTH AND LITTER TRAITS IN U.S. YORKSHIRE, DUROC, HAMPSHIRE, AND LANDRACE PIGS

A paper submitted to the Journal of Animal Science

P. Chen, T. J. Baas, J. W. Mabry, and K. J. Koehler

ABSTRACT: Records for lean growth and litter traits on Yorkshire, Duroc, Hampshire, and Landrace pigs collected between 1990 and April of 2000 in herds on the National Swine Registry Swine Testing and Genetic Evaluation System were analyzed. A bivariate animal model and restricted maximum likelihood procedures were used to estimate genetic and environmental correlations between lean growth rate, days to 113.5 kg, backfat, and loin eye area with litter traits of number born alive, litter weight at 21 d, and number weaned. Most genetic correlation estimates between lean growth and litter traits were small in magnitude and consistent across breeds. Backfat had the largest within-breed genetic correlations with number born alive (0.18 to 0.20) and litter weight at 21 d (-0.27 to -0.30). Estimates of genetic correlations between lean growth traits and number weaned were very small. Estimates of the environmental correlations between lean growth and litter traits were also very small for all traits and for all four breeds. Results indicate that selection for lean growth traits could have a long-term effect on litter traits. Including lean growth traits in a maternal line evaluation using a multiple trait model could increase the accuracy of the genetic evaluation for litter traits. Estimates from this study should be recommended for use in genetic evaluation programs.

Introduction
The genetic improvement of both lean growth and litter traits is important for increasing the efficiency of pork production. However, in general, there are negative relationships between lean growth and litter traits (Clutter and Brascamp, 1998). Multiple-trait BLUP EBV has been widely used in swine genetic evaluations for lean growth and litter traits (Hofer et al., 1992; Kennedy et al., 1996). Reliable estimates of the genetic correlations between lean growth and litter traits are required for optimum use of BLUP procedures. Currently, most genetic evaluation programs evaluate lean growth and litter traits separately using multi-trait models, and their EBVs are then combined into a bio-economic index using appropriate economic values (NSR, 2000). Thus, the genetic correlation between lean growth and litter traits has not been taken into account in current evaluations. In order to increase the accuracy of evaluations, especially for traits with low heritability (e.g., litter traits), it is necessary to evaluate lean growth and litter traits jointly using multiple trait analyses.

Clutter and Brascamp (1998) reviewed estimates of genetic correlations between lean growth and litter traits, and concluded that, in general, estimates have been plagued by insufficient precision. Estimates of genetic correlations in the literature for total number born with lean growth traits range from −0.15 to 0.44 (Vangen, 1980; Short et al., 1994) for ADG, and from −0.54 to 0.62 for backfat (Bereskin, 1984; Short et al., 1994). Estimates of the genetic correlation between number born alive and backfat include 0.21 by Crump et al. (1997) and from 0.13 to 0.22 by Johannson and Kennedy (1983). Chen et al. (2001) reported non-significant genetic correlations between lean growth rate with litter traits from a selection experiment in a synthetic line of Yorkshire-Meishan pigs. Use of parameter estimates from the literature could be very misleading because they are population-specific.
Genetic correlations between lean growth and litter traits currently recommended by the National Swine Improvement Federation (NSIF, 1997) for genetic evaluation programs are based on the results from the literature and are not breed-specific. Therefore, the objective of this study was to estimate breed-specific genetic correlations between lean growth and litter traits for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations.

**Materials and Methods**

**Data Source**

Lean growth and litter data were obtained from the National Swine Registry on Yorkshire, Duroc, Hampshire, and Landrace pigs. Details of data collection can be found in Swine Testing and Genetic Evaluation System (STAGES) (NSR, 2000). Lean growth data included pedigree information for each pig, contemporary group (CG), sex of the pig, litter identification, birth date, date weighed, and measurements for weight, backfat (BF), and loin eye area (LEA) at an approximate weight of 113.5 kg. Contemporary groups were defined by breeders as a group of pigs that were raised under the same management and environmental conditions. Data on boars, gilts, and barrows were included in the lean growth data set. Backfat and LEA were measured ultrasonically at the 10th rib. Days to 113.5 kg (DAYS), BF, and LEA were adjusted using recommendations in the Guidelines for Uniform Swine Improvement Programs (NSIF, 1997). Kilograms of lean was estimated using the following fat-free lean prediction equation developed by the National Pork Producers Council (NPPC, 2000): \[ \text{Lean (kg)} = 0.3782 \times \text{sex (barrow and boar = 1; gilt = 2)} - \]
2.9488 \times (BF, \text{cm}) + 0.3817 \times (LEA, \text{cm}^2) + 0.291 \times (\text{adjusted live weight, kg}) - 0.2424.

Then, lean growth rate per day (LGR), was calculated by dividing by DAYS.

Litter data included pedigree information for each sow, CG, parity of the sow, farrowing and weighing dates, number born alive (NBA), number after transfer (NAT), number weaned (NW), and litter weight at 21 d (L21WT). Number weaned included the number of adopted pigs but excluded pigs transferred to other sows. Contemporary groups were defined by the breeders as a group of sows that were bred, gestated, and farrowed in a group under the same management and environmental conditions. Litter traits were adjusted according to breed-specific procedures developed by Culbertson et al. (1997). Both NBA and L21WT were adjusted for parity and age at farrowing. Litter weight at 21 d was also adjusted for NAT and age at weighing. Number weaned was adjusted for parity and NAT.

In both data sets, single-sire contemporary group records were removed, as were records from sires not connected across contemporary groups and sires not mated to more than one dam. Numbers of records and contemporary groups, and litters represented by breed in the lean growth data set, along with means and SD for LGR, DAYS, BF, and LEA, can be found in Chen et al. (2002a). Number of records, animals, sires, dams, service sires, and contemporary groups represented by breed in the litter data, along with means and SD for NBA, L21WT, and NW can be found in Chen et al. (2002b).

Statistical Analysis

Bivariate REML analyses were conducted to estimate genetic correlations between lean growth and litter traits using REMLF90 (Misztal, 2000). Each analysis contained one lean growth trait and one litter trait. Different fixed and random effects, along with the environmental correlation between traits, were considered in two models. Models used for
bivariate analyses were as follows: \( y_1 = X_1b_1 + Z_1a_1 + Sc + e_1, y_2 = X_2b_2 + Z_2a_2 + W_1ss + W_2pe + e_2 \), where \( y_1, y_2 \) = observations for lean growth and litter traits, \( b_1, b_2 \) = fixed effects of contemporary group and sex for lean growth rates and fixed effects of contemporary group, \( a_1, a_2 \) = random additive genetic effects of animals, \( c \) = common litter effects, \( ss \) = service sire effects, \( pe \) = permanent environmental effects, \( X_1, X_2 \) = incidence matrices relating to fixed effects, \( Z_1, Z_2 \) = incidence matrices relating to animal effects, \( S \) = incidence matrix relating to common litter effects, \( W_1, W_2 \) = service sire and permanent environmental effects, \( e_1, e_2 \) = residual effects for lean growth and litter traits. It was assumed that the covariances between additive, common litter, service sire, permanent environmental, and residual effects were zero and that levels of each were independently distributed with variances \( \sigma_{a1}^2 \) and \( \sigma_{a2}^2 \) for animal effects, \( \sigma_c^2 \) for common litter effects, \( \sigma_{ss}^2 \) for service sire effects, \( \sigma_{pe}^2 \) for permanent environmental effects, and \( \sigma_{e1}^2 \) and \( \sigma_{e2}^2 \) for residual effects.

Standard errors of genetic correlations were estimated using formulas by Falconer (1989). In the REML analysis, the convergence criterion was set to \( 10^{-8} \) for all analyses.

Results and Discussion

Estimates of variance components for lean growth and litter traits are similar to the results from univariate analyses given in the previous papers in this series (Chen et al., 2002a,b). Estimates of covariances between lean growth and litter traits are in Table 1. The Landrace had the highest absolute value of genetic covariances between BF, LEA, and LGR with NBA; between BF and L21WT; and between DAYS and BF with NW. The Duroc breed had the lowest absolute value of genetic covariances between LEA and LGR with
NBA; between DAYS, BF and LGR with L21WT; and between DAYS and NW. In general, the genetic covariance was not consistent among breeds. Estimates of correlations between lean growth and litter traits are in Table 2. Genetic correlations between DAYS and litter traits were low in magnitude and inconsistent across breeds. Estimates of the genetic correlation of DAYS with NBA are \(-0.041, 0.051, -0.072,\) and \(-0.061\) for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Crump et al. (1997) reported an estimate of 0.084 for the genetic correlation between ADG and NBA in British Landrace pigs. Short et al. (1994) reported positive values for three of the four estimates of the genetic correlation between ADG and total number born in two dam lines from two farms (0.04, 0.05, 0.23, and \(-0.15\)). The estimates from this study are also lower than the value of \(-0.20\) recommended by NSIF (1997). Estimates from this study revealed positive genetic correlations between DAYS and L21WT for three breeds, the exception being the Hampshire breed (Table 2). The largest absolute value of the estimate of genetic correlation of DAYS with L21WT is 0.095 in the Hampshire breed. Estimates of the genetic correlation of DAYS with L21WT from this study are much lower than the value of 0.43 recommended by NSIF (1997). Estimates of the genetic correlation between DAYS and NW are very low, which supports the value of 0 recommended by NSIF (1997). Even though the correlations between DAYS and litter traits are small, the signs indicate that selection for increased gain could slightly increase litter size but decrease litter weight in most breeds.

Estimates of genetic correlations between BF and NBA and L21WT are relatively high, and consistent across breeds (Table 2). Estimates of the genetic correlation of BF with NBA are 0.19, 0.18, 0.18, and 0.20 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. This result agrees with the value of 0.21 reported by Crump et al.
(1997) in British Landrace pigs. Johannson and Kennedy (1983) also reported positive estimates of 0.13 to 0.22 for BF with NBA in Swedish Landrace and Yorkshire pigs. Löbke et al. (1986) reported positive correlations of 0.03 and 0.28 for BF with NBA for the first litter and the first three litters, respectively. However, Morris (1975) and Bereskin (1984) reported negative genetic correlations between BF and litter size. Short et al. (1994) also reported three of four estimates of the genetic correlation between BF and total number born were negative, -0.12, -0.03, -0.08, and 0.06. The estimates from this study disagree with the value of 0.00 recommended by NSIF (1997). Estimates of the genetic correlation between BF and L21WT were -0.27, -0.29, -0.30, and -0.29 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 2). These estimates are lower than the value of -0.40 recommended by NSIF (1997). Estimates of the genetic correlation between BF and NW are very low (Table 2) and support the value of 0 recommended by NSIF (1997). The signs of the correlations indicate that selection for decreased BF could slightly decrease litter size but increase litter weight.

Estimates of genetic correlations between LEA and litter traits are also low in magnitude and inconsistent across breeds. Estimates of the genetic correlation between LEA and NBA are -0.015, -0.016, 0.019, and -0.028 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 2). Estimates of the genetic correlation between LEA and L21WT are -0.054, 0.083, -0.031, and -0.017 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively (Table 2). Estimates of the genetic correlation between LEA and NW are very low (Table 2). There are no previously reported estimates of genetic correlations between LEA and litter traits.
Negative genetic correlations were found for LGR with litter traits across breeds. Estimates of the genetic correlation of LGR with NBA are -0.087, -0.082, -0.098, and -0.113 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Estimates of the genetic correlation of LGR with L21WT are -0.061, -0.059, -0.071, and -0.049 for the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Estimates of the genetic correlation between LGR and NW are very low (Table 2). Chen et al. (2001) reported negative genetic correlations of -0.18 and -0.05 for LGR with NBA and NW, respectively, and a positive correlation of 0.13 for LGR with L21WT from a selection experiment in a synthetic line of Yorkshire-Meishan pigs.

Environmental correlation estimates are very low across all traits and all breeds. The largest absolute value found is 0.032 for the environmental correlation for BF with NBA in Yorkshires. This result agrees with the findings of Crump et al. (1997) who reported that environmental correlations between performance and litter traits were, in general, low.

This study was the first to provide breed-specific genetic correlation estimates between lean growth and litter traits based on a large amount of field data. These breed-specific estimates could be used for jointly evaluating lean growth and litter traits using multiple trait analyses in genetic evaluation programs. One of the reasons for including the relationship between lean growth traits and litter traits in a maternal line evaluation is to increase the accuracy of the genetic evaluation for litter traits.

In general, the genetic correlations between lean growth and litter traits are unfavorable. This might in part explain the relatively slow genetic progress in litter traits in these populations demonstrated by Chen et al. (2002b). It also indicates that long-term selection for LGR would harm litter traits. Because the genetic correlations and heritabilities
for litter traits are low, the effect of selection for lean growth traits on litter traits without accounting for these correlations would not be observed in the short term.

As selection for lean growth traits continues, it is unknown whether relationships between them in these populations will change. It is possible that genetic relationships between components of LGR and litter traits are not linear, and that correlations may change as lean growth traits reach new thresholds. Therefore, it will be necessary to evaluate these relationships periodically and incorporate them into the evaluation program.

**Implications**

Unfavorable genetic correlations between lean growth and litter traits indicate that selection for lean growth traits could harm litter traits if selection is practiced for many generations. Although breed-specific estimates for genetic correlations between lean growth and litter traits were found to be low, including them in maternal line evaluations using a multiple-trait model within breed could increase the accuracy of the genetic evaluation for litter traits. These estimates should be recommended for use in genetic evaluation programs. This relationship should be evaluated periodically, however, if selection for lean growth traits continues.
Literature Cited


Table 1. Estimates of genetic and residual covariance of lean growth traits with litter traits by breed

<table>
<thead>
<tr>
<th>Item²</th>
<th>Number born alive</th>
<th>Litter weight at 21 d</th>
<th>Number weaned</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>σ_a1²</td>
<td>σ_e12</td>
<td>σ_a1²</td>
</tr>
<tr>
<td>DAYS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>-0.2472</td>
<td>0.0626</td>
<td>2.3200</td>
</tr>
<tr>
<td>Duroc</td>
<td>0.2748</td>
<td>-0.0337</td>
<td>1.9269</td>
</tr>
<tr>
<td>Hampshire</td>
<td>-0.4142</td>
<td>0.0186</td>
<td>-2.5851</td>
</tr>
<tr>
<td>Landrace</td>
<td>-0.3784</td>
<td>0.0649</td>
<td>2.3681</td>
</tr>
<tr>
<td>BF</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>0.3644</td>
<td>-0.1627</td>
<td>-2.5577</td>
</tr>
<tr>
<td>Duroc</td>
<td>0.2735</td>
<td>-0.1362</td>
<td>-1.9088</td>
</tr>
<tr>
<td>Hampshire</td>
<td>0.2461</td>
<td>-0.0907</td>
<td>-1.9146</td>
</tr>
<tr>
<td>Landrace</td>
<td>0.3675</td>
<td>0.0907</td>
<td>-2.7175</td>
</tr>
<tr>
<td>LEA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>-0.0262</td>
<td>0.0129</td>
<td>-0.4690</td>
</tr>
<tr>
<td>Duroc</td>
<td>-0.0231</td>
<td>0.0175</td>
<td>0.5173</td>
</tr>
<tr>
<td>Hampshire</td>
<td>0.0287</td>
<td>-0.0252</td>
<td>-0.2216</td>
</tr>
<tr>
<td>Landrace</td>
<td>-0.0462</td>
<td>-0.0579</td>
<td>-0.1426</td>
</tr>
<tr>
<td>LGR</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>-0.9492</td>
<td>-0.0397</td>
<td>-3.3599</td>
</tr>
<tr>
<td>Duroc</td>
<td>-0.7243</td>
<td>0.3074</td>
<td>-2.2625</td>
</tr>
<tr>
<td>Hampshire</td>
<td>-0.9700</td>
<td>-0.2705</td>
<td>-3.2997</td>
</tr>
<tr>
<td>Landrace</td>
<td>-1.1069</td>
<td>-0.1787</td>
<td>-2.4352</td>
</tr>
</tbody>
</table>

¹DAYS = days to 113.5 kg; BF = backfat; LEA = loin eye area; LGR = lean growth rate.
²σ_a1² = genetic covariance between lean growth and litter traits; σ_e12 = residual covariance between lean growth and litter traits.
Table 2. Estimates of genetic ($r_g$) and residual correlations ($r_c$) of lean growth with litter traits

<table>
<thead>
<tr>
<th>Item</th>
<th>Number born alive</th>
<th>Litter weight at 21 d</th>
<th>Number weaned</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r_g$</td>
<td>$r_c$</td>
<td>$r_g$</td>
</tr>
<tr>
<td>DAYS</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>$-0.041 \pm 0.025$</td>
<td>0.003</td>
<td>$0.077 \pm 0.025$</td>
</tr>
<tr>
<td>Duroc</td>
<td>$0.051 \pm 0.031$</td>
<td>$-0.002$</td>
<td>$0.083 \pm 0.037$</td>
</tr>
<tr>
<td>Hampshire</td>
<td>$-0.072 \pm 0.036$</td>
<td>0.001</td>
<td>$-0.095 \pm 0.037$</td>
</tr>
<tr>
<td>Landrace</td>
<td>$-0.061 \pm 0.044$</td>
<td>0.003</td>
<td>$0.075 \pm 0.041$</td>
</tr>
<tr>
<td>BF</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>$0.193 \pm 0.023$</td>
<td>$-0.032$</td>
<td>$-0.271 \pm 0.024$</td>
</tr>
<tr>
<td>Duroc</td>
<td>$0.176 \pm 0.032$</td>
<td>$-0.031$</td>
<td>$-0.285 \pm 0.034$</td>
</tr>
<tr>
<td>Hampshire</td>
<td>$0.183 \pm 0.034$</td>
<td>$-0.023$</td>
<td>$-0.301 \pm 0.032$</td>
</tr>
<tr>
<td>Landrace</td>
<td>$0.201 \pm 0.042$</td>
<td>0.017</td>
<td>$-0.292 \pm 0.053$</td>
</tr>
<tr>
<td>LEA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>$-0.015 \pm 0.025$</td>
<td>0.002</td>
<td>$-0.054 \pm 0.027$</td>
</tr>
<tr>
<td>Duroc</td>
<td>$-0.016 \pm 0.035$</td>
<td>0.003</td>
<td>$0.083 \pm 0.038$</td>
</tr>
<tr>
<td>Hampshire</td>
<td>$0.019 \pm 0.037$</td>
<td>$-0.004$</td>
<td>$-0.031 \pm 0.037$</td>
</tr>
<tr>
<td>Landrace</td>
<td>$-0.028 \pm 0.046$</td>
<td>$-0.008$</td>
<td>$-0.017 \pm 0.044$</td>
</tr>
<tr>
<td>LGR</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yorkshire</td>
<td>$-0.087 \pm 0.019$</td>
<td>$-0.013$</td>
<td>$-0.061 \pm 0.021$</td>
</tr>
<tr>
<td>Duroc</td>
<td>$-0.082 \pm 0.033$</td>
<td>0.011</td>
<td>$-0.059 \pm 0.037$</td>
</tr>
<tr>
<td>Hampshire</td>
<td>$-0.098 \pm 0.035$</td>
<td>$-0.009$</td>
<td>$-0.071 \pm 0.035$</td>
</tr>
<tr>
<td>Landrace</td>
<td>$-0.113 \pm 0.062$</td>
<td>$-0.005$</td>
<td>$-0.049 \pm 0.039$</td>
</tr>
</tbody>
</table>

*DAYS = days to 113.5 kg; BF = backfat; LEA = loin eye area; LGR = lean growth rate.*
CHAPTER 5. SELECTION FOR LEAN GROWTH RATE AND CORRELATED RESPONSES IN LITTER TRAITS IN A SYNTHETIC LINE OF YORKSHIRE-MEISHAN PIGS

A paper published in the Canadian Journal of Animal Science 81:205-214

P. Chen, T. J. Baas, J. C. M. Dekkers, and L. L. Christian

ABSTRACT: Selection for lean growth rate (LGR) was conducted for four generations in a synthetic line of Yorkshire-Meishan pigs to study the effectiveness of selection for LGR and correlated responses in litter traits. Lean growth rate was estimated from ultrasound measurements of 10th-rib backfat thickness and longissimus muscle area. In the selection line, 7 boars and 20 gilts with the highest LGR were selected to produce the next generation. The generation interval was 13 mo and the average selection differential per generation was 1.1 phenotypic standard deviation units. A contemporaneous control line was maintained by randomly selecting 5 boars and 15 gilts. Data from a total of 1,057 pigs sired by 58 boars and out of 133 sows were available from the two lines. Selection responses were estimated from deviations of the selection line from the control line using least squares (LS) and by multiple trait derivative-free restricted maximum likelihood analysis using an animal model (AM). The estimate of response to selection per generation using LS was 9.4 ± 0.95 gd\textsuperscript{-1} for LGR. The corresponding estimate from the AM was 9.8 ± 0.51 gd\textsuperscript{-1}. Correlated responses in litter traits were regressed on generation. For the LS method, regression coefficients were negative but not significant ($P > 0.05$) for total number born, number born alive, and number at 21 d and at 42 d. Significant, positive correlated responses occurred in 42-d litter weight and 21-d piglet weight ($P < 0.05$). For the AM method, the regression coefficients were also negative but not significant ($P > 0.05$) for number alive at birth, at 21 d, and at 42 d. A
significant positive correlated response occurred only for 42-d litter weight ($P < 0.05$).

Although results are based on a population of limited size, it can be concluded that selection for LGR in a synthetic line is effective and should have little effect on litter traits.

**Introduction**

Lean growth rate (LGR) and litter traits are economically important traits of swine production and both should be emphasized in selection programs. Selection for LGR has been practiced for several decades and has been effective (Vangen 1977; Cleveland et al. 1982; Cameron and Curran 1994). An important question for the pork industry is how to improve lean growth rate and litter traits simultaneously.

Several studies have documented the superior reproduction of some breeds that are native to the People's Republic of China, relative to American and European breeds (Legault and Caritez 1983; Rothschild et al. 1990; Young 1993). One way to improve litter traits is to incorporate these prolific breeds as a component of the maternal line in a crossbreeding program (Bidanel et al. 1991). Sellier and Legault (1986) proposed various crossbreeding schemes to take advantage of the high prolificacy of Chinese breeds. Several studies have demonstrated the usefulness of crossbred females produced from these Chinese breeds when crossed with American and European breeds (Legault and Caritez 1983; Christian et al. 1992, 1993; Young 1992, 1993, 1995). Unfortunately, low growth rate and poor carcass composition of Chinese breeds have hampered the realization of a commercial boost to litter productivity through the use of these breeds (Legault 1985; Bidanel et al. 1991). This problem could be overcome by creating a synthetic line that contains a highly prolific native Chinese breed such as the Meishan (Bolet et al. 1986; Bazer et al. 1988; Bidanel et al. 1989), along with American and European breeds, and then selecting the resulting line for LGR.
(Bidanel et al. 1991; Webb 1998). Moreover, several studies (Vangen 1980; Cleveland et al. 1988; Kerr and Cameron 1996) have demonstrated that selection for LGR in purebred lines does not result in significant negative correlated responses in litter traits.

To our knowledge, no results have been reported on: (1) selection for LGR in a synthetic line of pigs that includes Chinese breeds; or (2) selection on LGR using the National Pork Producers Council (NPPC) prediction equation for lean growth (NPPC 1991). Therefore, the objectives of this study were to investigate the effectiveness of selection for LGR using the NPPC prediction equation and evaluate the correlated responses in litter traits in a synthetic line of pigs based on a Meishan-Yorkshire cross.

**MATERIALS AND METHODS**

**Source of Data**

A LGR selection experiment with a control line was conducted at the Iowa State University Bilsland Memorial Research Farm from 1993 to 1998. Utilization and care of pigs involved in the study was in accordance with guidelines of the Canadian Council on Animal Care (1993). Foundation stock consisted of nine Meishan sows that were descendants of a representative sample of animals imported from the People's Republic of China in 1989. Semen from six selected American Yorkshire boars from two commercial companies was used to randomly inseminate Meishan sows to produce the base population (generation 0) in 1994. Selection of the Yorkshire boars emphasized low adjusted 10th-rib backfat thickness. From the base population and in each subsequent generation, 5 boars and 15 gilts were randomly selected to produce the next generation of the control line. Two additional boars, also randomly selected, were kept as alternatives and used when any of the originally designated boars were unable to service sows. In the selection line, seven boars, along with
two or three alternatives, and 20 gilts with the highest LGR were selected each generation without regard to pedigree to produce the next generation of selection line pigs. In the base population, one of the seven designated control line boars was also used to sire select line pigs for generation one. In each of the succeeding generations selection was within lines. Matings were assigned to minimize inbreeding. Generation intervals were designed to be 13 mo by allowing females to farrow only one litter and retaining boars for one 5-wk breeding period.

During gestation, sows were housed in open-front buildings with concrete floor pens. Before farrowing, sows were moved to farrowing pens in an environmentally controlled building. Approximately 1 wk after farrowing, sows and litters were moved to an open-front, concrete floor nursery and no cross fostering was practiced in this experiment. Pigs were weaned at approximately 6 wk of age and moved to growing pens to start the test.

Commercially prepared corn-soybean meal diets containing 18, 16, and 14% CP were fed to pigs weighing up to 30, 70, and 105 kg, respectively. Pigs were allowed ad libitum access to feed and water. Pigs were taken off test on an individual basis at weekly intervals upon reaching a weight of 105 kg. Ultrasound measurements of 10th-rib backfat thickness (BF10) and longissimus muscle area (LMA) were obtained at a minimum weight of 105 kg by an Iowa State University certified ultrasound technician according to the procedure described by Moeller (1994). An Aloka 500V (Corometrics Medical Systems, Wallingford, CT) real-time ultrasonic machine equipped with a 3.5 Mhz, 12.5 cm linear-array transducer was used. Ultrasound fat thickness was measured using calipers of the ultrasound unit. LGR adjusted to 105 kg was estimated using the following equation (NPPC 1991): \[
\text{LGR (kgd}^{-1}) = (38.59 - 0.042*(\text{live weight, kg}) + 0.322*(\text{LMA, cm}^2) - 2.9125*(\text{BF10, cm})) \text{ (d on test)}^{-1}
\]
Selection
of boars and gilts for the selection line was based on adjusted LGR. In total, ultrasound LMA and BF10 data were collected on 1,057 pigs, which were sired by 58 boars and out of 133 sows.

The following traits were recorded on all litters born: total number born (TNB), number born alive (NBA), litter birth weight (LBWT), piglet birth weight (PBWT), litter alive weight (LAWT), number piglets nursed at 21 d (N21), adjusted 21-d litter weight (L21WT), adjusted 21-d piglet weight (P21WT), number piglets weaned at 42 d (N42), adjusted 42-d litter weight (L42WT), adjusted 42-d piglet weight (P42WT), and number of nipples (NN). L21WT, P21WT, L42WT, and P42WT were adjusted to a constant age.

Statistical Analyses
Response to selection was evaluated based on analysis of the data by least-squares (LS) and by an animal model (AM) using multiple trait derivative-free restricted maximum likelihood (MTDFREML) (Boldman et al. 1993).

Least Squares Analysis
In the LS method, phenotypic traits were analyzed with a statistical model that included the effects of generation by line (GL), sire within GL, dam within sire and GL, sex, and the interaction of GL and sex:

\[ Y_{ijkl} = GL_i + X_l + GL^*X_l + S_{ij} + D_{ijk} + e_{ijkl} \]

where \( Y_{ijkl} \) = phenotypic observation for the ijklth pig, GL\(_i\) = the fixed effect of the \(i^{th}\) generation by line, S\(_{ij}\) = the random effect of the \(j^{th}\) sire in the \(i^{th}\) GL, D\(_{ijk}\) = the random effect of the \(k^{th}\) dam of the \(j^{th}\) sire in the \(i^{th}\) GL, X\(_l\) = the fixed effect of the \(l^{th}\) sex, GL\(^*\)X\(_l\) = the interaction between GL and sex, and e\(_{ijkl}\) = random residual effect. Sires and dams were
assumed unrelated. Models for analysis of litter size and litter weight traits included only GL as a fixed effect and sire within GL as a random effect.

Cumulative responses to selection by generation were calculated for each trait as deviations of least square means of the selection line from the control line. To provide a measure of average response over generations, cumulative genetic responses by generation were regressed on generation of selection (Falconer 1981). Response was averaged across sex.

Realized heritability for LGR was estimated by the weighted regression of cumulative response on weighted cumulative selection differentials (WCSD). Weighted cumulative selection differentials were calculated by deviating the phenotypic record of each selected individual from its generation-line-sex subclass mean and adding it to the average cumulative selection mean of the individual’s parents. Individual cumulative selection differentials were weighted by the number of progeny alive at the time of ultrasound scanning. A weighted regression of cumulative response on WCSD was used to estimate realized heritability, using the variance–covariance matrix of cumulative responses (Hill 1972) to take into account the covariances between cumulative responses: $\mathbf{b} = (\mathbf{S}'\mathbf{C}'\mathbf{S})^{-1}\mathbf{S}'\mathbf{C}'\mathbf{R}$, with variance $(\mathbf{S}'\mathbf{C}'\mathbf{S})^{-1}$, where $\mathbf{b}$ is the realized heritability; $\mathbf{R}$ and $\mathbf{S}$ are the vectors of cumulative responses and WCSD, respectively; and $\mathbf{C}$ is the variance–covariance matrix of cumulative responses. Matrix $\mathbf{C}$ was calculated following Hill (1971, 1972), using estimates of heritability and phenotypic variance obtained from a single–trait analysis by MTDFREML from the animal model analysis (see following), and accounting for the different selection intensities in the two sexes and the different numbers of animals selected in each generation and sex.
Diagonal elements of the $C$ matrix are the variances of the direct responses in each generation.

**Animal Model Analysis**

In the AM analysis, MTDFREML was used to estimate (co-)variance components and genetic trends. The model fitted for LGR and all individual piglet traits can be expressed as

$$Y_{ijkl} = YM_i + X_l + a_i + L_j + e_{ijkl},$$

where $YM_i$ is the fixed effect of year-month at the start of the test, $a_i$ is the random genetic effect of animal $i$, and $L_j$ a random common effect due to litter. All other variables were as defined under the LS model. The relationship matrix based on pedigree information on all animals back to generation 0 was included in the analysis.

Litter size, litter weight traits, and NN were analyzed as a trait of the sow with year-month of farrowing as the only fixed effect. A common litter effect of the litter in which the sow was born was not included because variance explained by common litter effects was very low in our preliminary analyses of this population (less than 2%).

All analyses were conducted using the combined data from the selection line and the control line. LGR was analyzed in a single-trait analysis. To account for selection bias, LGR was included in a bivariate analysis of each of the other traits. Estimates of genetic change per generation were obtained by regressing the mean EBV by generation on generation number.

**RESULTS AND DISCUSSION**

The number of animals tested and number of litters per generation were slightly smaller in the selection than the control line (Table 1). On average, the selection and control lines had
7.3 and 5.8 sires, with 17.3 and 12.8 dams per generation, respectively. The mean WCSD for LGR by generation and line are illustrated in Figure 1. Total WCSD over the four generations of selection was 141 \text{gd}^{-1} in the selection line and 16.2 \text{gd}^{-1} in the control line, a difference of 124.8 \text{gd}^{-1}. This corresponds to a standardized WCSD of 4.1 phenotypic SD units, where the phenotypic SD for LGR was calculated from the sum of squares of means pooled across generation by line subclasses. The regression of WCSD on generation showed that the average increase in WCSD was 33.9 \text{gd}^{-1}, or 1.1 phenotypic SD units per generation.

**Direct Response**

Direct cumulative responses for LGR derived using the LS and AM methods are presented in Figure 2. Average responses were 9.4 \text{gd}^{-1} per generation by the LS method and 9.8 \text{gd}^{-1} per generation by the AM method, which was higher than the annual rate of 8.28 \text{gd}^{-1} and 7.67 \text{gd}^{-1} in the high and low protein lines in Swedish Yorkshire pigs reported by Stern et al. (1993). This result was also higher than responses reported by Cameron (1994) and Cameron and Curren (1994), who used selection on an index of ADG and average backfat thickness. One explanation for the relatively high responses in this experiment could be the higher selection intensities for lean growth rate compared with other selection experiments. On average, the selected percentage was 15\% for sires and 26\% for dams in this experiment, compared with 17\% and 54\% in the study of Stern et al. (1993). Another explanation for the high response in this study could be that other studies were carried out in purebred lines, for which genetic variance is expected to be lower than in cross between divergent breeds. The realized rate of genetic change in this study indicates that selection for LGR can be effective.
Correlated Responses

Estimates of cumulative correlated responses per generation are illustrated in Figures 3 to 5. Correlated responses were scaled to the corresponding phenotypic SD units. Phenotypic SD were calculated from the sum of squares of means pooled across generation by line subclasses. Estimates of regression coefficients on generation number, reflecting average responses per generation, are in Table 2. It must be noted that the SE for regression coefficients do not reflect genetic drift and will, therefore, underestimate the true SE.

Litter Size Traits. Regression coefficients for correlated responses for litter size traits were negative but not significantly different from zero ($P > 0.05$) for all traits and for both the LS and AM methods (Figure 3, Table 2). The only exception was a slight positive but non-significant response for TNB based on the AM method. These results suggest that selection for LGR in a synthetic line of Yorkshire-Meishan pigs will not have a large effect on litter size.

Correlated responses in litter size traits to selection for LGR were variable among other experiments reported in the literature. Correlated responses reported here (Figure 3, Table 2) agree with those of Cleveland et al. (1988), who reported that index selection for ADG and backfat thickness for lean growth resulted in negative but non-significant correlated responses for TNB, NBA, and N42. Vangen (1980) reported positive correlated responses for TNB and NBA but negative correlated responses for N42 to index selection for lean growth in a Norwegian Landrace line. However, none of the correlated responses in their study were significant. Fredeen and Mikami (1986) noted significant negative phenotypic trends for NBA over years in a Lacombe line selected for rate of lean growth. Selection for weight of lean cuts at a constant age in a Yorkshire line (DeNise et al. 1983)
resulted in negative ($P > 0.05$) correlated responses for litter size at 1 and 7 d in first-parity gilts. Correlated responses were negative ($P < 0.05$) in second-parity sows for litter size at 1, 7, and 21 d. Kerr and Cameron (1996) also did not observe significant differences in litter size at birth and at 21 d between a selection line and a control line after seven generations of selection for lean growth with ad libitum or restricted feeding in a population of Large White pigs.

**Litter Weight Traits.** Based on the two methods of analysis, litter weight traits showed positive correlated responses (Figure 4), but only the response for litter weight at 42 d was significantly different from zero (Table 2).

Vangen (1974) reported that correlated responses to index selection for rate of lean growth were positive ($P > 0.05$) for litter weight at birth but negative for litter weight at 42 d. DeNise et al. (1983) found that selection for weight of lean cuts resulted in negative correlated responses for litter weights at birth and 21 d in first and second parity, but responses were significant only for second parity sows. Fredeen and Mikami (1986) observed a significant negative phenotypic trend over years for litter weight at birth in a Lacombe line. Cleveland et al. (1988) noted consistently heavier LBWT and L42WT in a line selected for rate of lean growth compared with a control line, but regressions on cumulative selective differential were not significant. Kerr and Cameron (1996) also found that there were no significant differences for LBWT, L21WT, and L42WT between selection and control lines after seven generations of selection for lean growth rate with ad libitum or restricted feeding. Our results and those of similar experiments reported above, therefore, indicate that selection for LGR in a synthetic line will have very little effect on litter weights.
**Individual Piglet Traits.** Coefficients of correlated response were positive but not significant \((P > 0.05)\) for both methods of analysis for PBWT and P42WT (Table 2). Correlated responses were positive and significant \((P < 0.05)\) for P21WT based on the LS method but zero based on the AM method (Figure 5, Table 2).

Vangen (1980) reported positive correlated responses to index selection for rate of lean growth for PBWT \((P < 0.05)\) and P42WT \((P > 0.05)\). Cleveland et al. (1988) observed positive but non-significant correlated responses for PBWT and P42WT. Kerr and Cameron (1996) also reported no differences in PBWT and P21WT between selection and control lines after seven generations of selection for LGR.

In both methods of analysis, regression coefficients of NN on generation were positive but not significant (Table 2). This is consistent with the results of Cleveland et al. (1988).

**Heritability of LGR**

The estimate of realized heritability for LGR from the LS method was 0.29 ± 0.12. The estimate of heritability was 0.37 ± 0.11 by the AM method. Estimates from both methods were within the range of literature estimates of heritability for LGR of 0.25 to 0.49 (Vangen 1979; Cleveland et al. 1982; Stern et al. 1993; Cameron 1994; Cameron and Curren 1994). Differences may be due to differences in population structures, selection criteria, breed differences, and sampling errors.

Although the LS method resulted in a lower estimate of heritability than the AM method, which agrees with the work of Cameron (1994), the difference in two estimates was not significant \((P > 0.05)\). However, Mrode et al. (1990) found similar estimates of
heritability for LGR in beef cattle based on these two methods. The regression method uses only between-line information and the fact that animals are selected on their phenotype using mass selection. Hill (1972) showed that linear estimators of realized heritability, such as regression of response on WCSD, are efficient and unbiased over a range of parameter values. However, Sorensen and Kennedy (1984) mentioned that the regression of response on WCSD may not give unbiased estimates of base population parameters because of changes in genetic variance, random drift, and gametic phase disequilibrium generated by selection. The AM method incorporates information from between- and within-lines, parent-offspring relationships, and relationships between collateral relatives. It accounts for changes in genetic variance due to selection, assuming an additive genetic model with an infinite number of loci, and gives unbiased estimates of base population parameters (Rothschild et al. 1979; Thompson and Meyer 1986).

In a selection experiment, the standard error for the estimate of heritability using the LS method can be computed from formulas provided by Hill (1972), as demonstrated by many researchers (e.g. Mrode et al. 1990). Standard errors of heritability estimates from MTDFREML were not available. An approximate standard error was obtained by assuming data conformed to a paternal half-sib design (Falconer 1981). The resulting SE for the estimate of heritability was slightly smaller for the AM (0.11) than the LS method (0.12). Both these SE will overestimate the true standard error of the estimate based on the AM because the AM uses more information than either the LS or paternal half-sib methods (Thompson 1982; Cameron 1994).

**Common litter effects**
The estimates of common litter of birth effects for individual piglet traits were around 0.05 (Table 3), which agree with those reported by Crump et al. (1997a), however, considerably lower than those reported by Kaufmann et al. (2000) for birth and weaning weight.

Therefore, the use of models that omit common litter of birth effects and heritability estimates from these models in breeding value estimation using BLUP in this population, would lead to biases in the breeding value estimates and over prediction of genetic gain. The estimates of common litter effects of the litter in which the sow was born for litter traits in this study were generally very low (Table 3), which agree with those reported by Crump et al. (1997b), however, considerably lower than those reported by Kaufmann et al. (2000) on litter size. Heritability for litter traits in this population do not appear to be biased by common litter of birth effects, which can therefore omitted from breeding value estimation and prediction of genetic gain models.

**Heritabilities and genetic correlations of litter size and weight traits**

Estimates of heritabilities and genetic correlations for correlated traits from the AM method are shown in Table 3. The low estimates of heritabilities for litter traits and of genetic correlations between LGR and litter traits in this study (Table 3) were in agreement with several reports regarding the genetic relationship between growth traits and litter traits (Short et al. 1994; Crump et al. 1997c; Kaufmann et al. 2000). This implies that selection for LGR is not expected to harm reproduction in the short term. Estimates from this study, however, have relatively larger SE than estimates from other studies (e.g. Cameron 1994). This is largely due to the small population size. This may also be the cause of non-significance of the correlated responses in litter traits to selection for LGR in this study.
CONCLUSIONS

This study is the first to report direct and correlated responses to selection for LGR in a synthetic line of pigs including a Chinese breed using the NPPC lean growth prediction equation. Although the genetic base population and line sizes were relatively small, based on standard errors of responses, it appears that selection for LGR in this synthetic line was effective and correlated responses on litter traits were small. Although results are based on a small population, this provides useful information for designing improvement programs for a synthetic line while maintaining the advantage of litter traits from Chinese breeds.

ACKNOWLEDGEMENT

The authors are grateful to John Newton for data collection.


Table 1. Number of parents and offspring by line and generation

<table>
<thead>
<tr>
<th>Generation</th>
<th>Selection line</th>
<th>Control line</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Offspring</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sires</td>
<td>Dams</td>
</tr>
<tr>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1</td>
<td>7</td>
<td>16</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>17</td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>18</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>18</td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>69</td>
</tr>
</tbody>
</table>
Table 2. Estimated response per generation by least squares and animal model methods

<table>
<thead>
<tr>
<th>Trait²</th>
<th>Least squares</th>
<th>Animal model</th>
</tr>
</thead>
<tbody>
<tr>
<td>LGR</td>
<td>9.4 ± 0.95*</td>
<td>9.8 ± 0.51*</td>
</tr>
<tr>
<td>TNB</td>
<td>-0.17 ± 0.30</td>
<td>0.06 ± 0.13</td>
</tr>
<tr>
<td>NBA</td>
<td>-0.24 ± 0.08</td>
<td>-0.14 ± 0.08</td>
</tr>
<tr>
<td>N21</td>
<td>-0.21 ± 0.14</td>
<td>-0.11 ± 0.27</td>
</tr>
<tr>
<td>N42</td>
<td>-0.16 ± 0.24</td>
<td>-0.18 ± 0.21</td>
</tr>
<tr>
<td>LBWT</td>
<td>0.05 ± 0.14</td>
<td>0.14 ± 0.13</td>
</tr>
<tr>
<td>LAWT</td>
<td>0.30 ± 0.73</td>
<td>0.13 ± 0.17</td>
</tr>
<tr>
<td>L21WT</td>
<td>0.25 ± 1.37</td>
<td>0.36 ± 0.37</td>
</tr>
<tr>
<td>L42WT</td>
<td>1.2 ± 0.20*</td>
<td>0.96 ± 0.14*</td>
</tr>
<tr>
<td>PBWT</td>
<td>0.04 ± 0.04</td>
<td>0.11 ± 0.08</td>
</tr>
<tr>
<td>P21WT</td>
<td>0.23 ± 0.003*</td>
<td>-0.03 ± 0.05</td>
</tr>
<tr>
<td>P42WT</td>
<td>0.23 ± 0.12</td>
<td>0.86 ± 0.22</td>
</tr>
<tr>
<td>NN</td>
<td>0.08 ± 0.03</td>
<td>0.04 ± 0.03</td>
</tr>
</tbody>
</table>

*P < 0.05

²Lean growth rate (LGR), total number born (TNB), number born alive (NBA), number piglets nursed at 21d (N21), number piglets weaned at 42d (N42), litter birth weight (LBWT), litter alive weight (LAWT), adjusted 21-d litter weight (L21WT), adjusted 42-d litter weight (L42WT), piglet birth weight (PBWT), adjusted 21-d piglet weight (P21WT), adjusted 42-d piglet weight (P42WT), number of nipples (NN).
Table 3. Estimates of heritability and genetic correlations between lean growth rate and reproductive traits based on bivariate animal model analyses

<table>
<thead>
<tr>
<th>Trait</th>
<th>Heritability(^z)</th>
<th>Genetic correlation</th>
<th>Common litter effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>TNB</td>
<td>0.13 ± 0.06</td>
<td>0.08</td>
<td>0.01</td>
</tr>
<tr>
<td>NBA</td>
<td>0.11 ± 0.06</td>
<td>-0.18</td>
<td>0.01</td>
</tr>
<tr>
<td>N21</td>
<td>0.08 ± 0.05</td>
<td>-0.05</td>
<td>0.00</td>
</tr>
<tr>
<td>N42</td>
<td>0.09 ± 0.05</td>
<td>-0.07</td>
<td>0.00</td>
</tr>
<tr>
<td>LBWT</td>
<td>0.12 ± 0.06</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>LWT</td>
<td>0.11 ± 0.06</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>L21WT</td>
<td>0.06 ± 0.04</td>
<td>0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>L42WT</td>
<td>0.09 ± 0.05</td>
<td>0.23</td>
<td>0.01</td>
</tr>
<tr>
<td>PBWT</td>
<td>0.15 ± 0.05</td>
<td>0.09</td>
<td>0.05</td>
</tr>
<tr>
<td>P21WT</td>
<td>0.14 ± 0.07</td>
<td>-0.04</td>
<td>0.06</td>
</tr>
<tr>
<td>P42WT</td>
<td>0.13 ± 0.06</td>
<td>0.18</td>
<td>0.05</td>
</tr>
<tr>
<td>NN</td>
<td>0.05 ± 0.04</td>
<td>0.09</td>
<td>0.00</td>
</tr>
</tbody>
</table>

\(^z\)Standard errors were approximated based on formula for a paternal half-sib design (Falconer 1988).
Figure 1. Cumulative selection differential for lean growth rate in the selection (Δ) and control line ( ).
Figure 2. Cumulative response for lean growth rate by least squares (○) and by animal model (△) methods.
Figure 3. Correlated responses (in phenotypic SD units) for litter size traits by least squares (\(\gamma\)) and animal model (\(\Delta\)) methods; total number born pigs (3a); number born alive pigs (3b); number at 21 d pigs (3c); number at 42 d pigs (3d).
Figure 4. Correlated responses (in phenotypic SD units) for litter weight traits by least squares ( ) and animal model (A) methods; litter birth weight (kg) (4a); litter weight alive (kg) (4b); litter weight at 21 d (kg) (4c); litter weight at 42 d (kg) (4d).

(a) (c)
Figure 5. Correlated responses (in phenotypic SD units) for individual piglet traits and number of nipples by least squares (•) and animal model (△) methods; piglet birth weight (kg) (5a); piglet weight at 21 d (kg) (5b), piglet weight at 42 d (kg) (5c), number of nipples (5d).
CHAPTER 6. EVALUATION OF STRATEGIES FOR SELECTION ON LEAN GROWTH RATE IN PIGS

A paper submitted to the Journal of Animal Science

P. Chen, T. J. Baas, J. C. M. Dekkers, K. J. Koehler, and J. W. Mabry

ABSTRACT: Lean growth rate (LGR) in pigs is a non-linear biological function of growth rate and carcass composition. According to animal breeding theory, genetic progress for LGR is maximized with selection on a linear index of its component traits, but selection on direct EBV for LGR is not common. In this study, five strategies for selection on LGR in pigs were evaluated through simulation over five generations. A linear index with updating of the index weights in each generation yielded the highest response in LGR. A linear index without updating index weights resulted in 1.8% lower ($P < 0.05$) response in LGR in generation 5. A non-linear index of component traits of LGR performed almost as well as the linear index with updating. Direct selection on single-trait EBV for LGR yielded the lowest responses in generation 5. Direct selection on EBV for LGR based on a multiple-trait animal model that also included component traits, yielded 3.1% greater response in LGR ($P < 0.05$), but 2.4% lower response than the linear index with updating in generation 5. Although differences in response in LGR were limited, alternative selection criteria resulted in substantially different responses in component traits. Linear index selection for LGR placed more emphasis on carcass composition while direct selection for LGR emphasized growth rate. Selection for LGR based on a linear index with updating or a non-linear index is recommended for use in the swine industry.
**Introduction**

Lean growth rate (LGR) is an important trait for genetic improvement programs in pigs because lean tissue can be deposited more efficiently than fat tissue and consumer demands are for lean products. The future competitiveness of pork producers, therefore, depends in part on genetic improvement of efficiency of quality lean production. Simultaneous improvement in leanness and growth rate is important, but difficult to achieve, because the genetic correlation between the two traits is generally unfavorable, as demonstrated by several studies (McPhee et al., 1988; Cameron and Curren, 1994a). Fowler et al. (1976) proposed that selection for lean tissue growth could be accomplished by using LGR as a biological index that combines lean percentage and growth rate into one single trait. Clutter and Brascamp (1998) suggested that LGR is the most appropriate expression of the industry's objective for market pigs. Several selection experiments have demonstrated that selection for LGR is effective (Stern et al., 1993; Cameron, 1994; Chen et al., 2001).

Since LGR is a non-linear biological function of component traits, several alternative strategies exist for selection for LGR. Most selection experiments for LGR selected on a classical linear selection index that combines ultrasonic measures of backfat thickness and ADG (McKay, 1990, 1992; Cameron, 1994; Cameron and Curran, 1994). Stern et al. (1993) and Chen et al. (2001) selected on phenotypes for LGR that were estimated based on a non-linear function of ultrasonic measurements of fat depth and loin muscle area, along with growth rate.

Several studies have evaluated strategies for selection for profitability when biological traits contribute to profit in a non-linear manner (Goddard, 1983; Dekkers et al., 1995; Meuwissen and Goddard, 1997). In theory, a linear index of biological traits is expected to
give the greatest increase in profit (Goddard, 1983; Dekkers et al., 1995). Meuwissen and Goddard (1997), however, showed by simulation that direct selection on EBV for profit or selection on a non-linear index of EBV for biological traits can result in similar responses to selection when compared to selection on a linear index of EBV for biological traits. Linear indexes have also been proposed for selection on ratio traits (Gunsett, 1984). Similar considerations apply to selection for LGR as a non-linear function of carcass composition and ADG. Therefore, the objective of this study was to evaluate strategies for selection on LGR based on simulation, including linear indexes of component traits, a non-linear index of component traits, and direct selection for LGR.

**Materials and Methods**

*Lean Growth Rate*

In this study, kg of fat-free lean in the carcass was predicted using the following fat-free lean prediction equation developed by the National Pork Producers Council (NPPC, 2000):

\[
\text{Lean (kg)} = [33.1643 - 0.29488 \times \text{BF (mm)} + 0.3817 \times \text{LEA (cm}^2\text{)}],
\]

where BF is backfat thickness and LEA is loin eye area, both measured by ultrasound. Then, LGR, denoted as lean gain per day, was calculated by dividing by days from birth to 113.5 kg (DAYS), resulting in the following biological function for LGR:

\[
LGR \text{ (kg/d)} = \frac{[33.1643 - 0.29488 \times \text{BF (mm)} + 0.3817 \times \text{LEA (cm}^2\text{)}]}{\text{DAYS}} \quad [1].
\]

Figure 1 illustrates the non-linear relationship between DAYS and LGR based on equation [1], when setting BF and LEA equal to population means of 16.94 mm and 44.06 cm², respectively.
Selection Criteria

Five criteria for selection for LGR were derived. All criteria used EBV derived using BLUP based on an animal model.

Linear Index. The most common approach to select for LGR is to include EBV for the component traits of LGR in a linear index as follows:

\[ I_{\text{lin}} = v^\top \hat{\mathbf{u}}, \]

where \( v \) is a vector of biological values for DAYS, BF, and LEA in relation to LGR and \( \hat{\mathbf{u}} \) is a vector of multi-trait EBVs for DAYS, BF, and LEA. The biological value of a trait \( i \) is defined as the increase in LGR if the population mean for the trait is improved by one unit, similar to the concept of economic values in selection index theory (Hazel, 1943). Biological values were derived as first derivatives of the biological relationship of LGR with ADG, BF, and LEA, using either the relationship at the individual animal level or the relationship at the population level. In the individual animal approach, biological values were derived as first derivatives of the LGR prediction equation [1]. In the population average approach, the LGR equation [1] was converted to a population-level function that describes the relationship of the population average for LGR with the population average for ADG, BF and LEA. Biological values were then derived as first derivatives of the population-level function. Derivation of the population-average function is given in Appendix 1.

Biological values for the linear index were either updated or not updated over generations. Without updating, biological values were derived as first derivatives evaluated at the population means in the base population. With updating, biological values were updated each generation \( t \) by evaluating first derivatives at the mean in generation \( t \).
Non-Linear Index. Using Equation [1], the following non-linear index is obtained: 
\[ I_{NL} = [33.1643 - 0.29488 \times (\mu_{BF} + \hat{u}_{BF}) + 0.3817 \times ((\mu_{LEA} + \hat{u}_{LEA}))]/( (\mu_{DAYS} + \hat{u}_{DAYS}), \] where \( \mu_i \) = the population mean of trait i in generation 0, \( \hat{u}_i \) = the individual's multi-trait EBV for trait i.

Direct Selection for LGR. It is assumed that all three traits are recorded such that the LGR of every animal can be predicted using equation [1]. A very simple strategy then is direct selection on EBV for LGR, \( I_{LGR, ST} = \hat{u}_{LGR}, \) where \( \hat{u}_{LGR} \) is the single-trait EBV for LGR. In order to increase the accuracy of EBV for LGR, records for DAYS, BF, and LEA can be included in a multi-trait animal model for LGR and selection for LGR can be on the multi-trait EBV for LGR, \( I_{LGR, MT} = \hat{u}_{LGR, MT}. \)

Data Simulation

Selection in a closed nucleus breeding scheme over five generations was simulated and replicated 600 times for each selection strategy. Population parameters are summarized in Table 1. Phenotypes for the component traits DAYS, BF, and LEA were simulated as: 
\[ Y_i = G_i + E_i, \] where \( Y_i \) is a vector of the phenotypic records of the three component traits for animal i; \( G_i \) is a vector of genetic values for animal i, which is assumed to be distributed \( N(\mu, \Sigma_g) \), where \( \Sigma_g \) is the genetic variance–covariance matrix among the three component traits; and \( E_i \) is a vector of residuals for animal i, which is assumed to be distributed \( N(0, \Sigma_e) \), where \( \Sigma_e \) is the residual variance–covariance matrix among traits. The values for \( G_i \) and \( E_i \) were assumed to be independent. Phenotypic and genetic parameters for DAYS, BF, and LEA were obtained from Chen et al. (2002) and are in Table 2. Phenotypes for LGR were calculated using Equation [1].

Genetic Evaluation
Breeding values for evaluated traits were estimated under a single-trait or multi-trait model, depending on the selection criterion, with a fixed sex effect and a random animal effect and using the true genetic parameters as listed in Table 2. Since it is not easy to derive the appropriate genetic parameters for LGR because of the non-linear relationships, true genetic values for LGR were obtained for 10,000 individuals by inserting simulated true breeding values for DAYS, BF, and LEA and their base population means into Equation [1]. Then, heritability of LGR was derived as the ratio of the variance of LGR genetic values over the phenotypic variance of LGR, and genetic correlations were obtained as correlations of the simulated genetic values for LGR, with the true breeding values for DAYS, BF, and LEA.

Results

Simulated genetic parameters for LGR that were used in genetic evaluations based on LGR phenotypes are in Table 2. Simulated parameters were similar to those observed in the literature (Chen et al., 2002).

Figure 2 shows biological values for DAYS as a function of the population mean when derived based on the population-average biological function for LGR (see Appendix 1). Biological values for BF and LEA did not depend on population means for the traits because the relationships of BF and LEA with LGR are linear in Equation [1]. Table 3 shows two sets of biological values at the base population means, one based on the individual biological function and one based on the average biological function. These two sets of biological values are nearly identical, which indicates that there is not a high degree of non-linearity in LGR as a function of DAYS (Figure 2).

Figures 3 through 6 show responses in LGR, DAYS, BF, and LEA from alternative selection criteria relative to responses to the linear index without updating, $I_{LIN}$. The linear
index with updating (ILIN, UP) yielded the highest LGR in generation 5. The linear index selection without updating resulted in 1.8% lower response in LGR in generation 5 ($P < 0.05$). The non-linear index performed almost as well as the linear index with updating in generation 5.

Direct selection for LGR with a multi-trait model yielded the highest LGR at generation 1 but lower responses in later generations (Figure 3). This might be due to the fact that genetic parameter estimates for LGR that were used in genetic evaluation were obtained from the base population and not updated over generations. To illustrate these changes, Table 4 shows genetic parameters for LGR derived by simulation but using means in generation 5 instead of the base population means, which are shown in Table 2. Parameters from Table 2 were used for genetic evaluation. Direct selection on EBV for LGR based on a single-trait model yielded 3.1% lower response in LGR in generation 5 than selection on a multi-trait EBV for LGR ($P < 0.05$).

Although the alternative selection strategies resulted in limited differences in LGR, the responses in component traits were substantially different, as indicated in Figures 4, 5, and 6. Direct selection for LGR resulted in large responses in DAYS (Figure 4), but this was at the cost of selection for BF and LEA (Figures 5 and 6). The linear indexes put more emphasis on BF and LEA and less on DAYS (Figures 4, 5, 6). The non-linear index resulted in intermediate responses in DAYS, BF, and LEA (Figures 4, 5, 6).

**Discussion**

In the current paper, selection for LGR over multiple generations was formulated as selection for a non-linear biological function. The results for the linear index in this study agree with the findings of Meuwissen and Goddard (1997) for selection on non-linear profit.
They found that the selection response achieved by the linear index with updating of index weights was greater than responses by direct selection on single-trait or multi-trait EBV for profit. The efficiency of linear indexes over direct selection on single-trait EBV in this study is consistent with the findings of Gunsetts (1986) who found that a linear index of feed intake and ADG was superior to direct selection for feed conversion as a ratio of these two traits when component traits have different genetic parameters. Meuwissen and Goddard (1997), however, found that a non-linear index resulted in a slightly larger response in non-linear profit than a linear index with updating. In this study, the linear index with updating gave the greatest response to selection, although the difference with the non-linear index was small.

A linear selection index of growth rate and lean percentage has been used to select for LGR in many experiments (Fredeen and Mikami, 1990; Cameron, 1994; Cameron and Curran, 1994). In most cases, the linear index for LGR was derived by approximating LGR by a linear function at the base population mean. Goddard (1983) demonstrated that a linear selection index is optimal for a non-linear profit function, when biological traits exhibit no non-additive variance. Pasternak and Weller (1993) developed an iterative algorithm to derive linear selection indexes that maximize average profit in the last generation of a planning horizon. Groen et al. (1994) used a general derivative-free search algorithm to derive linear selection indexes that maximize average profit in the last generation of a planning horizon. Dekkers et al. (1995) showed that optimal indexes are derived from economic values that are obtained as first derivatives of the profit function at future rather than the current population mean. In the present study, linear indexes were derived from biological values evaluated at the base population means or at means in the current generation for the linear index with updating. Following Dekkers et al. (1995), the optimal
linear index has to be linearized at the mean of the population after 5 generations of selection if the objective is to maximize response over 5 generations. The difference between linearization at the current versus future means is, however, not expected to be large for LGR because non-linearity is not very strong.

An attractive alternative to linear index selection is to substitute the EBVs of component traits into the non-linear biological function. This yields maximum likelihood estimates of genetic values for LGR, rather than of breeding values for LGR because LGR will have non-additive genetic variation as a result of the non-linearity of the biological function (Meuwissen and Goddard, 1997). Therefore, the non-linear index might not be an optimal selection procedure. Many researchers (Goddard, 1983; Groen et al., 1994; Weller, 1994) already have shown that non-linear indexes are theoretically suboptimal. In our study, the response by the non-linear index was, however, not significantly different from the response by the linear index with updating at generation 5 ($P > 0.05$).

Direct selection for phenotypes for LGR has been used in several selection experiments (Stern et al., 1993; Chen et al., 2001) because of its simplicity. In this study, direct selection for LGR based on single-trait EBV was the poorest selection strategy for selection for LGR in pigs. Direct selection on multi-trait EBV for LGR yielded higher responses in LGR than selection on single-trait EBV for LGR at generation 5. This agrees with Meuwissen and Goddard (1997) who found that direct selection for single-trait EBV for profit was worse than direct selection for multi-trait profit, the linear indexes, and the non-linear index.

All five selection strategies for LGR that were evaluated in this study resulted in increased ADG, decreased BF, and increased LEA. These results are consistent with the results of several selection experiments (Stern et al., 1993; Cameron and Curren, 1994b).
Stem et al. (1993) reported increased lean percentage and growth rate using direct selection on phenotypes for LGR that were estimated from ultrasonic measurements of fat depth and loin muscle area, along with growth rate, in the line on a high protein diet. Cameron and Curren (1994b) also reported decreased BF and increased ADG using a linear index of BF and ADG. However, McKay (1990) reported that the main effect of selection on a linear index of BF and ADG was a reduction in BF.

The results of this study demonstrate that linear indexes for LGR would select lean pigs with relatively slow growth. On the contrary, direct selection for LGR would select pigs with relatively fast growth. The non-linear index resulted in balanced responses in both leanness and growth rate. Gunsett (1984) found that responses in component traits when selecting on a ratio of traits are difficult to predict and are mediated by the complex relationships between heritabilities and phenotypic and genetic correlations of component traits, as well as selection intensity.

Most studies on selection for non-linear profit functions use profit evaluated at trait means as the objective function. However, Elsen et al. (1986) argued that the objective should be to maximize average profit, which is not necessarily equal to maximizing profit evaluated at the mean of component traits in the case of a non-linear function. Chen et al. (1998) derived economic values of meat quality traits based on individual and average profit functions, and found there were only small differences in two sets of economic values because the degree of non-linearity of the non-profit function is not high. Here we quantified biological values of component traits at the population level, accounting for the distribution and inherent variability in traits within a population of pigs. Although differences between biological values derived from average versus individual biological functions were small
(Table 3), differences between the two methods of deriving biological values will be greater if the individual biological function exhibits a greater degree of non-linearity.

Implications

Lean growth rate is an important biological criterion for selection. Results of this study indicate that alternative methods for selection for LGR result in different responses to selection in LGR, but in particular in its component traits. Selection on a linear index of component traits, with updating of index weight over generations, yielded the highest response in LGR. However, a non-linear index of component trait EBV yielded almost the same response in LGR and does not require updating of index weights. These two indexes are useful selection criteria in genetic evaluation programs in the industry. Direct selection on EBV for LGR is not advocated.

Literature Cited


Appendix I

Equation [1] gives \( f(x) \) for LGR from birth to 113.5 kg. The next step is to apply this individual biological function to the distribution of the trait that is represented in a population or herd of animals. This step is needed because the extra LGR that can be obtained by improving a trait differs across the range of trait values that are present among animals in a population due to the non-linear relationship between LGR and its component traits. Therefore, an average biological function is defined as the relationship between the population average for the trait and the average LGR for animals in the population. Given the distribution of the trait in the population, \( g(x \mid \mu) \), the average LGR of the population for a given population mean of the trait, \( \mu \), can be derived by integrating the individual biological function \( f(x) \) over the distribution of the trait in the population to obtain

\[
AP(\mu) = \frac{\int f(x) g(x \mid \mu) \varnothing(x) \, dx}{\int g(x \mid \mu) \varnothing(x) \, dx},
\]

where \( U \) and \( L \) are the upper and lower bounds for the trait in the population, respectively, and where

\[
g(x \mid \mu) = \frac{1}{\sqrt{2\pi} \sigma} e^{-\frac{1}{2} \left(\frac{x - \mu}{\sigma}\right)^2}.
\]

Here, distributions for each trait were assumed to be truncated normal distributions. According to the above definition, average LGR levels can be calculated based on Equations [1] and [2] for a range of population means. Average LGR levels will depend on the population mean (\( \mu \)), the standard deviation of component traits (\( \sigma \)), the upper and lower bounds of the population range, and the individual biological function \( f(x) \).
According to the definition, the biological value of a trait is the marginal change in the LGR mean if the population mean of the trait is changed one unit by selection. Therefore, the biological value can be found as the first derivative of Equation [2] with regard to μ and evaluated at the given population mean. Because AP(μ) is non-linear in μ, the biological value is a function of μ as well

\[ BV(\mu) = \frac{\partial}{\partial \mu} \left\{ \int_{\mu}^\infty f(x) g(x | \mu) \, dx \right\} \]  

[4].

The parameters of the distribution were based on the results of the national genetic evaluation program (Chen et al., 2002), as shown in Table 1. Based on Equation [2], an average LGR function can be derived for each trait by integrating Equation [1] over the distribution of the trait for a range of population means. The biological values of DAYS, BF, and LEA are then obtained from equation [4] as the first derivatives of Equation [2] by substituting the appropriate \( f(x) \) and \( g(x | \mu) \). Integrals in all equations were solved numerically using Matlab 5.2 (The Math Works, Inc., Natick, MA).
Table 1. Parameters of the closed nucleus breeding schemes used for simulation

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of animals per generation</td>
<td>500 males and 500 females</td>
</tr>
<tr>
<td>No. of sires selected per generation</td>
<td>20</td>
</tr>
<tr>
<td>No. of dams selected per generation</td>
<td>100</td>
</tr>
<tr>
<td>DAYS (d)</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>173.27</td>
</tr>
<tr>
<td>Phenotypic variance</td>
<td>175.01</td>
</tr>
<tr>
<td>Lower bound</td>
<td>119.97</td>
</tr>
<tr>
<td>Upper bound</td>
<td>258.54</td>
</tr>
<tr>
<td>BF (mm)</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>16.94</td>
</tr>
<tr>
<td>Phenotypic variance</td>
<td>12.53</td>
</tr>
<tr>
<td>Lower bound</td>
<td>5.59</td>
</tr>
<tr>
<td>Upper bound</td>
<td>48.51</td>
</tr>
<tr>
<td>LEA (cm$^2$)</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>44.06</td>
</tr>
<tr>
<td>Phenotypic variance</td>
<td>15.44</td>
</tr>
<tr>
<td>Lower bound</td>
<td>27.09</td>
</tr>
<tr>
<td>Upper bound</td>
<td>71.80</td>
</tr>
</tbody>
</table>

$^a$DAYS = days to 113.5 kg; BF = backfat thickness; LEA = loin eye area.
Table 2. Heritability (diagonal), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) assumed for traits in the simulation and genetic evaluation

<table>
<thead>
<tr>
<th>Traits(^a)</th>
<th>LGR(^b)</th>
<th>DAYS</th>
<th>BF</th>
<th>LEA</th>
</tr>
</thead>
<tbody>
<tr>
<td>LGR(^b)</td>
<td>0.35</td>
<td>-0.82</td>
<td>-0.39</td>
<td>0.41</td>
</tr>
<tr>
<td>DAYS</td>
<td>-0.83</td>
<td>0.35</td>
<td>-0.06</td>
<td>0.08</td>
</tr>
<tr>
<td>BF</td>
<td>-0.36</td>
<td>-0.08</td>
<td>0.48</td>
<td>-0.40</td>
</tr>
<tr>
<td>LEA</td>
<td>0.45</td>
<td>0.11</td>
<td>-0.43</td>
<td>0.33</td>
</tr>
</tbody>
</table>

\(^a\)LGR = lean growth rate; DAYS = days to 113.5 kg; BF = backfat thickness; LEA = loin eye area.

\(^b\)All parameter estimates involving LGR are derived by simulation.
Table 3. Biological values for DAYS, BF, and LEA using the biological function at the population average or at the individual animal level and evaluated at the mean of the base population.

<table>
<thead>
<tr>
<th>Biological function</th>
<th>DAYS, d</th>
<th>BF, mm</th>
<th>LEA, cm²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population average</td>
<td>-0.00152</td>
<td>-0.0016</td>
<td>0.0022</td>
</tr>
<tr>
<td>Individual animal</td>
<td>-0.00149</td>
<td>-0.0016</td>
<td>0.0022</td>
</tr>
</tbody>
</table>

* DAYS = days to 113.5 kg; BF = backfat thickness; LEA = loin eye area.
Table 4. Heritability (diagonal), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) from the simulation based on the mean in generation 5 for the non-linear index

<table>
<thead>
<tr>
<th>Traits&lt;sup&gt;a&lt;/sup&gt;</th>
<th>LGR&lt;sup&gt;b&lt;/sup&gt;</th>
<th>DAYS</th>
<th>BF</th>
<th>LEA</th>
</tr>
</thead>
<tbody>
<tr>
<td>LGR&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.33</td>
<td>-0.89</td>
<td>-0.29</td>
<td>0.31</td>
</tr>
<tr>
<td>DAYS</td>
<td>-0.89</td>
<td>0.35</td>
<td>-0.06</td>
<td>0.08</td>
</tr>
<tr>
<td>BF</td>
<td>-0.27</td>
<td>-0.08</td>
<td>0.48</td>
<td>-0.40</td>
</tr>
<tr>
<td>LEA</td>
<td>0.34</td>
<td>0.11</td>
<td>-0.43</td>
<td>0.33</td>
</tr>
</tbody>
</table>

<sup>a</sup>LGR = lean growth rate; DAYS = days to 113.5 kg; BF = backfat thickness; LEA = loin eye area.

<sup>b</sup>All parameter estimates involving LGR are derived by simulation.
Figure 1. Non-linear relationship between phenotypes for days to 113.5 kg and lean growth rate at base population means for backfat and loin eye area.
Figure 2. Biological values based on biological functions for days to 113.5 kg as function of population mean.

\(^a\)ABF = biological values based on the average biological function; IBF = biological values based on the individual biological function.
Figure 3. Responses of lean growth rate for different selection strategies relative to $I_{LIN}$ (means of 600 replicate simulations)$^a$

$a$ $I_{LGR, ST} = $ direct selection for LGR based on a single-trait model; $I_{LGR, MT} = $ direct selection for LGR based on a multi-trait model; $I_{LIN} = $ linear index without updating; $I_{LIN, UP} = $ linear index with updating; $I_{NL} = $ non-linear index.

$b, c, d$ Means with different letters differ in generation 5 ($P < 0.05$).
Figure 4. Responses of days to 113.5 kg for different selection strategies relative to \( I_{L}_{IN} \) (means of 600 replicate simulations)\(^a\)

\[ I_{LGR, ST} = \text{direct selection for LGR based on a single-trait model; } I_{LGR, MT} = \text{direct selection for LGR based on a multi-trait model; } I_{LIN} = \text{linear index without updating; } I_{LIN, UP} = \text{linear index with updating; } I_{NL} = \text{non-linear index.} \]

\(^a\)Means with different letters differ in generation 5 \((P < 0.05)\).
Figure 5. Responses of backfat thickness for different selection strategies relative to $l_{\text{LIN}}$ (means of 600 replicate simulations)*

*a $l_{\text{LGR, ST}}$ = direct selection for LGR based on a single-trait model; $l_{\text{LGR, MT}}$ = direct selection for LGR based on a multi-trait model; $l_{\text{LIN}}$ = linear index without updating; $l_{\text{LIN, UP}}$ = linear index with updating; $l_{\text{NL}}$ = non-linear index.

*Means with different letters differ in generation 5 ($P < 0.05$).
Figure 6. Responses of loin eye area for different selection strategies relative to $I_{LIN}$ (means of 600 replicated simulations)

- $I_{LGR, ST}$ = direct selection for LGR based on a single-trait model; $I_{LGR, MT}$ = direct selection for LGR based on a multi-trait model; $I_{LIN}$ = linear index without updating; $I_{LIN, UP}$ = linear index with updating; $I_{NL}$ = non-linear index.

Means with different letters differ in generation 5 ($P < 0.05$).
CHAPTER 7. GENERAL CONCLUSIONS

Introduction

Lean growth rate (LGR) is an important trait for genetic improvement programs in pigs because lean tissue can be deposited more efficiently than fat tissue and consumer demands are for lean products. The future competitiveness of pork producers, therefore, depends in part on genetic improvement of efficiency of quality lean production.

Reproductive traits have always been important to the industry. Simultaneous improvement in LGR and reproductive traits is important, but difficult to achieve, because the genetic correlation between the two traits is generally unfavorable. To investigate the potential genetic improvement of two groups of traits, certain information is necessary such as the heritabilities of LGR and reproductive traits, genetic correlations between LGR and reproductive traits, the possibility of producing a synthetic line, and selection strategies. This dissertation describes a study of these topics.

Genetic Parameters of LGR

Knowledge of breed-specific genetic parameters of LGR and correlations with its component traits is necessary to investigate possibilities for improving LGR by selection and to investigate correlated responses of component traits by selection for LGR. Therefore, breed-specific genetic parameters for LGR and its components were estimated for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations (Chapter 2).

Records on 361,300 Yorkshire, 154,833 Duroc, 99,311 Hampshire, and 71,097 Landrace pigs collected between 1985 and April of 2000 in herds on the National Swine Registry Swine Testing and Genetic Evaluation System were analyzed. Lean growth rate was estimated using the lean prediction equation developed by the NPPC, and the component
traits of days to 113.5 kg (DAYS), backfat adjusted to 113.5 kg (BF), and loin eye area adjusted to 113.5 kg (LEA) were considered. Parameters were estimated using an animal model by REML method.

Estimates of heritabilities were 0.44, 0.44, 0.46, and 0.39 for LGR in the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Average genetic correlations over four breeds were −0.83, −0.37, and 0.44 for LGR with DAYS, BF, and LEA, respectively, and −0.07, 0.08, and −0.37 for DAYS with BF and LEA, and BF with LEA, respectively.

Considering the heritabilities and genetic correlations between LGR and its component traits, it was concluded that selection based on LGR can improve leanness and growth rate simultaneously and could be a useful biological selection criterion.

**Genetic Parameters of Reproductive Traits**

A successful genetic improvement program requires accurate estimation of heritabilities for reproductive traits. Therefore, breed-specific genetic parameters for reproductive traits were estimated for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations (Chapter 3).

Records on 251,296 Yorkshire, 75,262 Duroc, 83,338 Hampshire, and 53,234 Landrace litters born between 1984 and April of 1999 in herds on the National Swine Registry Swine Testing and Genetic Evaluation System were analyzed. Litter traits of number born alive (NBA), litter weight at 21 d (L21WT), and number weaned (NW) were considered.

Estimates of heritabilities were 0.10, 0.09, 0.08, and 0.08 for NBA; 0.08, 0.07, 0.08, and 0.09 for L21WT; and 0.05, 0.07, 0.05, and 0.05 for NW in the Yorkshire, Duroc, Hampshire, and Landrace breeds, respectively. Average genetic correlations over the four
breeds were 0.13, 0.15, and 0.71 for NBA with L21WT, NBA with NW, and L21WT with NW, respectively. Although estimates of genetic parameters for litter traits were low and similar across breeds, differences in genetic variances indicate that litter traits could be improved through selection.

This study presents the first set of breed-specific estimates of genetic parameters available from large numbers of field records. It provides valuable information for use in national genetic evaluations.

**Genetic Correlations between LGR and Litter Traits**

The genetic correlation between lean growth and litter traits has not been accounted for in most genetic evaluation programs because of the lack of understanding of the relationships between lean growth and litter traits. In order to determine the optimum emphasis on LGR in selection objectives and increase the accuracy of the evaluations, especially for traits with low heritability (e.g., litter traits), the genetic relationships of LGR with litter traits must be known. Therefore, genetic correlations between lean growth and litter traits were estimated for the U.S. Yorkshire, Duroc, Hampshire, and Landrace populations (Chapter 4).

Records for lean growth and litter traits on Yorkshire, Duroc, Hampshire, Landrace pigs collected between 1990 and April of 2000 in herds on the National Swine Registry Swine Testing and Genetic Evaluation System were analyzed. A bivariate animal model and REML procedures were used to estimate genetic and environmental correlations between lean growth traits of LGR, DAYS, BF, and LEA with litter traits of NBA, L21WT, and NW.

Most genetic correlation estimates between lean growth and litter traits were small in magnitude and consistent across breeds. **Backfat had the largest genetic correlations with**
NBA (0.176 to 0.201) and L21WT (−0.271 to −0.301). Estimates of genetic correlations between lean growth traits and number weaned were very small.

Considering the genetic correlations between LGR and litter traits, it was concluded that selection for lean growth traits could have a long-term effect on litter traits. Including lean growth traits in a maternal line evaluation using a multiple trait model could increase the accuracy of EBVs for litter traits. Estimates from this study should be recommended for use in genetic evaluation programs.

**Synthetic Line**

Several studies have documented the superior reproduction of some breeds that are native to the People's Republic of China, relative to American and European breeds. One way to improve litter traits is to incorporate these prolific breeds as a component of the maternal line in a crossbreeding program. Several studies have demonstrated the usefulness of crossbred females produced from these Chinese breeds when crossed with American and European breeds. Unfortunately, low growth rate and poor carcass composition of Chinese breeds have hampered the realization of a commercial boost to litter productivity through the use of these breeds. This problem could be overcome by creating a synthetic line that contains a highly prolific native Chinese breed such as the Meishan, along with American and European breeds, and then selecting the resulting line for LGR. Therefore, the objectives of this study were to investigate the effectiveness of selection for LGR using the NPPC prediction equation and evaluate the correlated responses in litter traits in a synthetic line of pigs based on a Meishan-Yorkshire cross (Chapter 5).

In the selection line, 7 boars and 20 gilts with the highest LGR were selected to produce the next generation. A contemporaneous control line was maintained by randomly
selecting 5 boars and 15 gilts. Data from a total of 1,057 pigs sired by 58 boars and out of 133 sows were available from the two lines. Selection for LGR was conducted for four generations.

Selection responses were estimated from deviations of the selection line from the control line using least squares (LS) estimation and by multiple trait derivative-free restricted maximum likelihood analysis using an animal model (AM). The estimate of response to selection per generation using LS was $9.4 \pm 0.95$ gd$^{-1}$ for LGR. The corresponding estimate from the AM was $9.8 \pm 0.51$ gd$^{-1}$. Correlated responses in litter traits were regressed on generation. For the LS method, regression coefficients were negative but not significant ($P > 0.05$) for total number born, number born alive, and number at 21 d and at 42 d. Significant, positive correlated responses occurred in 42-d litter weight and 21-d piglet weight ($P < 0.05$). For the AM method, the regression coefficients were also negative but not significant ($P > 0.05$) for number alive at birth, at 21 d, and at 42 d. A significant, positive correlated response occurred only for 42-d litter weight ($P < 0.05$). Although results are based on a population of limited size, it can be concluded that selection for LGR in a synthetic line is possible and should have little effect on litter traits.

**Selection Strategies**

Since LGR is a non-linear biological function of component traits, several strategies exist for selection for LGR. In theory, a linear index of biological traits is expected to give the greatest increase in profit. Several studies, however, showed that direct selection on EBV for profit or selection on a non-linear index of EBV for biological traits can result in similar responses to selection when compared to selection on a linear index of EBV for biological traits. Similar considerations apply to selection for LGR as a non-linear function of carcass
composition and ADG. This study was conducted to evaluate strategies for selection on LGR, including linear indexes of component traits, a non-linear index of component traits, and direct selection for LGR (Chapter 6).

In this study, five strategies for selection on LGR in pigs that maximize average LGR at the last generation with a planning horizon based on a non-linear biological function were evaluated through simulation over five generations. A linear index with updating index weights yielded the highest LGR at the last generation. The difference in responses in LGR between selection for linear component traits of LGR with and without updating index weights at generation 5 was 1.8% ($P < 0.05$). The non-linear index performed almost as well as the linear index with updating. Direct selection on single-trait EBV for LGR yielded the lowest responses at generation 5. Direct selection on multi-trait EBV for LGR yielded 3.1% higher responses in LGR than selection on single-trait EBV for LGR ($P < 0.05$). Selection for LGR based on linear indexes put more emphasis on carcass composition while direct selection for LGR emphasized growth rate. It was concluded that selection for LGR based on a linear index with updating or a non-linear index should be recommended for use in the swine industry.

**Conclusion**

Heritability estimates obtained in this study indicate that there is sufficient genetic variation to allow improvement in LGR and litter traits by selection. Based on the genetic correlation estimates obtained, selection for LGR would be expected to harm litter traits in the long term, but this would not be observed in the short term. Including the relationship between lean growth traits and litter traits in maternal line genetic evaluation will be increasing important. This study has demonstrated that creating a synthetic line could be an
alternative way to improve LGR and litter traits simultaneously. Selection for LGR should be expected to be more effective by using a linear index with updating index weights or a non-linear index

**Further Research**

The LGR prediction equation used was adopted from the equation developed by National Pork Producers Council and is not breed-specific. Potential bias in predicting LGR could be caused by this equation. Further research is needed to develop breed-specific prediction equations for LGR.

Improvement of the genetic potential for LGR increases both lean percentage and growth rate. Since several studies have shown that deterioration of meat quality occurs when selecting for LGR, investigation of the correlated responses to selection for LGR, especially in meat quality traits, will be necessary in the future.
ACKNOWLEDGEMENTS

It is a time to look back through each step I have made and thanks to all the people who supported, encouraged, and challenged me over my numerous years as a graduate student.

I wish to extend my sincere thanks to Dr. Tom J. Baas and Dr. Kenneth J. Koehler for serving my co-major professors during my studies at Iowa State University. You have never refused whenever I need help, always sharing your incredible experiences with me. I look forward to learning even more from you in the future.

My thanks also go out to my committee members, Dr Jack C.M. Dekkers, Dr. Michael J. Daniels, Dr. John W. Mabry, and Dr. David Topel. Each of you provided me with guidance in developing a better understanding of knowledge both in and out of the classroom. Thank you all for giving the excellent advice that makes me successful.

To all my fellow graduate students, the animal science staff, the statistics staff, and the pork industry center staff I extend my sincere thanks. Without your help I could not accomplished this task.

My special thanks must be given to my late major professor, Dr. Lauren L. Christian, and former Dean of the College of the Agriculture, Dr. David Topel, for initiating my program at Iowa State University. I am truly in debt to you for all you have done for my family and me.

Thanks you Mom and Dad for setting the stage for my development through your love and support. Thanks also to my father-in-law and mother-in-law for taking care of my son during my studies.
And finally, to my wife and my son. Wenyu, thank you for the endless love and support. Tim, you have been such a wonderful joy in my life. Watching you grow from the little baby to the little boy who runs to see me with a great smile when I get home is the most enjoyable part in my life. I love you both so very much!!