

**Quantitative genetic and statistical aspects of feed efficiency by analysis of the
selection experiment for residual feed intake in Yorkshire pigs**

by

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CHAPTER 1. GENERAL INTRODUCTION

Introduction

Profit from pig production depends on not only income but also costs. The income from the sale of a pig for slaughter mainly depends on its body weight (BW) and body composition. Typically, measures of backfat (BF) thickness and loin muscle area (LMA) are used as proxy indicators for the body composition of fat and lean meat content of the whole carcass, with high BF getting a penalty and high LMA getting an appreciation on the price per unit weight. On the other side, feed costs represent a major part of the total cost of swine production. Therefore, feed efficiency (FE), i.e. using the feed to produce lean pigs efficiently, is an important consideration in swine breeding programs. For production purposes, feed efficiency is usually measured as the ratio of average daily body weight gain (ADG: kg/d) to average daily feed intake (ADFI: kg/d) or as its reciprocal, feed conversion ratio. Residual Feed Intake (RFI) is an alternative measure of feed efficiency defined as the difference between observed feed intake and that predicted from average requirements for the pig's achieved growth and maintenance (Koch et al., 1963).

For many years, most swine breeding programs have mainly focused on intense selection of output traits, such as ADG, BF, and LMA, to improve lean tissue growth rate. This traditional selection strategy rarely includes direct measurements of feed intake (FI) although the breeding objective often includes feed efficiency or feed intake, besides leanness and growth rate (Clutter and Brascamp, 1998). These years of intense selection of lean tissue growth rate have significantly improved feed efficiency, but further improvement of feed efficiency requires more attention to input traits, i.e. feed intake. To include feed intake or efficiency into selection programs requires direct measurement of feed intake on individual pigs. Webb (1998) specified that individual measurement of feed intake can increase the rate for the genetic improvement of efficient lean meat production by 15 to 20%.

Before electronic feeding equipment was introduced in breeding programs, the only way to measure individual feed intake on growing pigs in the breeding herd was by penning pigs individually. This individual penning method to measure feed intake was not broadly used in breeding programs because this is labor intensive and results in genotype by environment

interactions for production traits compared to group-housing (De Haer and Merks, 1992). With electronic feeding equipment, recording individual feed intake in group-housed pigs became possible. Although the expense of electronic swine feeders is high, to improve FE, the swine industry has increasingly used electronic feeders in breeding programs (De Haer et al., 1992; McDonald and Nienaber, 1994; Roehe et al., 1994).

Computerized feeders automatically record repeated measurements of BW and FI, as well as feeding behavior traits for individual pigs. Due to the wide application of ultrasound technology in swine breeding, BF and LMA can also be repeatedly measured on individual pigs across different ages. These repeated measurements of FI, BW, BF, and LMA are typically referred to as longitudinal data along the growth trajectory of pigs. Measurements across time for a single pig are inner-correlated and measurements of related pigs are also inter-correlated because of common genetic effects, permanent environmental effects (e.g. nutrition), and temporary environmental effects (e.g. measurement error) (Falconer and Mackay, 1996).

To deal with inner-correlations between longitudinal measurements for a given pig, one simple approach is to reduce the longitudinal measures to a single summary or a single measure at a single time point for each animal and then analyze each summary variable or single measure further. Diggle et al. (2002) referred to this as a two-stage analysis. For example, longitudinal FI records are often summarized as ADFI; BW records are either summarized as ADG or only the last measure of BW is used; for BF and LMA records, typically only the last measure is used. These single summaries or measures of ADFI, ADG, BF, and LMA for individual pigs are analyzed using the mixed linear animal model (Henderson, 1984) to estimate genetic parameters for these traits and to estimate the breeding value, i.e. the random animal genetic effect, for each animal. This simple two-stage method is effective and fits well into the strategies of classical index selection and RFI selection.

The other option for genetic analysis of these longitudinal measurements is by multi-trait mixed models (Henderson, 1984). In this case, the longitudinal data for animals must be measured at regular times and the measurements taken at different times are considered as different traits. If the data are measured at irregular times, times of measurement need to be clustered into categories in order to apply multi-trait mixed models.

Random regression (RR) or random coefficient models (Longford, 1993) are another suitable option for analysis of this type of longitudinal data. Schaeffer and Dekkers (1994), as one of the first applications in animal breeding, applied RR models to milk production data from dairy cattle. As one of the first applications to data other than milk production in cattle, Andersen and Pedersen (1996) applied RR models to analyze growth and feed intake curves for pigs. Schaeffer (2004) presented a thorough review of the applications of RR models in animal breeding. In general, the standard formulation of RR models for longitudinal data takes two-levels: the upper level models the population (or subpopulation) regression coefficients on time or age, which are the fixed effects in the model, and the low level models individual specific regression coefficients; these are the random effects in the model. In these models, inner-correlations among longitudinal measurements are modeled by allowing the regression coefficients to vary between individuals. The causes of the random effects can be further partitioned into additive genetic effects and permanent environment effects to deal with genetic relationships between individuals. Such RR models are particularly useful because they use data from all individuals simultaneously, handle longitudinal measurements at irregular times, and allow estimation of individual and population curves.

Random regression models using global polynomials or piecewise polynomials, i.e. splines (Hastie et al., 2009), are flexible and easy to fit because all parameters appear linearly in the model. These polynomial models may provide adequate descriptions of the longitudinal data if the data are collected across a limited range of the growth trajectory. However, the asymptotic behavior of growth-related processes such as growth and voluntary feed intake in pigs is difficult to model by linear RR models. In addition, RR models typically provide limited understanding of the biological data-generating mechanisms and are dangerous for data extrapolation (Lindsey, 2001). Nonlinear mixed models (Lindstrom and Bates, 1990) are an alternative option for analysis of the longitudinal data that addresses some of the limitations of the linear RR models. Nonlinear mixed models can be viewed as an extension of mixed models to nonlinear response functions. A nonlinear regression function means that at least one of the parameters appears nonlinearly, i.e. in formal definition, that at least one of the first derivatives of the response variable with respect to the

functional parameters depends on at least one of those parameters (Ratkowsky, 1990). The parameters of the nonlinear function of nonlinear mixed models are affected by fixed effects that are associated with population or subpopulation, and by random effects that are associated with individuals. Thus, nonlinear mixed models allow each individual to have an individual specific nonlinear curve. This is especially useful when inference on individual curves is necessary.

Ratkowsky (1990) presented a thorough review of commonly used nonlinear regression functions (e.g., the three-parameter Logistic and Gompertz functions) and their statistical properties. Generally, with respect to age, most organisms show a sigmoid growth process (West et al., 2001), i.e. a period of an increasing growth rate (the first derivative) is followed by a period with decreasing growth rate. The point of inflection of the growth curve is where the curve turns from concave to convex. Therefore, the point of inflection defines the age at which an organism shows its fastest growth. West et al. (2001) explained the reasons for the sigmoid growth based on fundamental principles of allocating metabolic energy between producing and maintaining biomass. Both Logistic and Gompertz nonlinear growth functions are characterized by sigmoid-shaped curves. The Logistic function is symmetric about its inflection point, but the Gompertz function is not. From this perspective, the Gompertz function typically represents growth related processes better (Vieira and Hoffmann, 1977; Emmans and Kyriazakis, 1999) and is often chosen for that purpose in animal breeding applications. A detailed description of the Logistic and Gompertz growth functions and the biological meanings of their parameters are introduced in chapters 3 and 5 of this dissertation. Whittemore et al. (1988) used the Gompertz function to model body weight of pigs over time on a pig-by-pig basis. Kyriazakis and Whittemore (2006) chose the Gompertz function to describe daily protein retention for the growing pigs. The parameters of the nonlinear models usually have biological interpretations. If such nonlinear models represent the biological data-generating mechanisms, they should allow better data extrapolation outside the data range (Lindsey, 2001).

As an alternative to the traditional selection approaches for multi-trait genetic improvement of pigs for lean growth based on a linear function of economically important traits such as ADG, BF, and LMA, Clutter and Brascamp (1998) illustrated another selection

strategy that is based on the linear plateau growth modeling of the relationship between daily lean growth rate and daily feed intake (Whittemore, 1986). The main points of the linear plateau model are: i) as the input trait of daily feed intake for a pig increases, the output trait of daily lean growth increases linearly until the plateau when the maximum rate of daily lean growth is reached; ii) the maximum rate of daily lean growth for a pig is relatively constant over the entire postweaning production period; iii) during the linear phase of lean growth, the genetic potential of the maximum rate of daily lean growth is not a limiting factor, but feed intake is limiting; iv) during the plateau phase of lean growth, feed intake is not limiting, but the maximum rate of daily lean growth is a limiting factor; v) the animal will partition its net energy for maintenance, lean growth, and a predetermined minimum level of fat deposition, and the extra energy beyond that is partitioned into extra fat deposition. The linear plateau relationship between lean growth rate and energy intake has been observed in the experiments with varied energy intake levels for different groups of pigs, such as different pig genotypes (Eissen, 2000). Figure 1.1 from Whittemore (1986) clearly shows that the same amount of feed supply (2 kg/d) results in nutritionally unlimited lean growth for animal (A), which has a lower maximum rate of daily lean growth than animal (B), but lean growth for animal (B) is nutritionally limited. Therefore, when trying to optimize feed intake capacity, the breakpoint of the linear plateau model, i.e., the maximum lean growth rate at the lowest feed supply, is the target for efficient swine production.

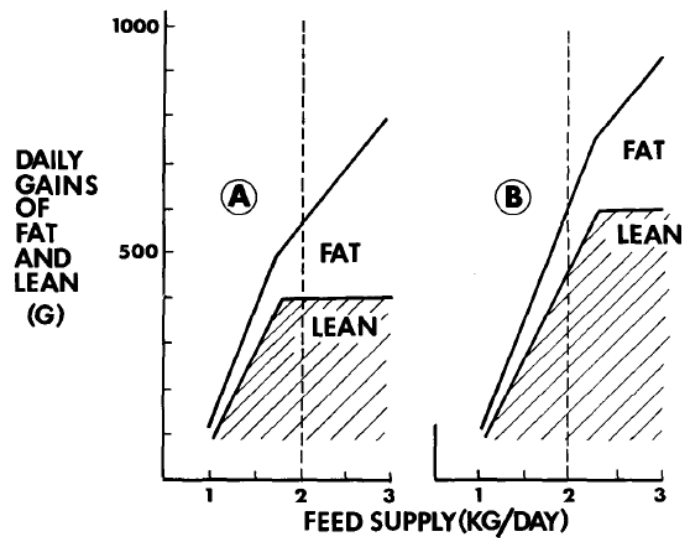


Figure 1.1 The linear plateau model hypothesis for the relationship between daily gains of lean and fat and the daily feed supply. (from Whittemore (1986))

Webb (1998) extended the linear plateau model idea for selection of pigs to the whole postweaning production period, i.e. from weaning to slaughter. Webb (1998) described that the feed intake capacity of modern pigs is not sufficient to achieve their genetic potential of maximum of lean growth rate at an early age, but their feed intake capacity is too high later in the growing period, which leads to extra fat deposition at a later age. Figure 1.2 from Webb (1998) is shown below to give a clear picture of the proposed idea. Webb (1998) suggested a direction for changing the shape of the feed intake curve, i.e. selection to increase feed intake at an early age but decrease it at a later age (see Figure 1.3 from Webb (1998)). Opportunities to directly select for the shape of feed intake, growth, and backfat curves are provided by longitudinal measurements of FI, BW, BF, and LMA along the growth trajectory of pigs by electronic feeders and sequential ultrasound scans.

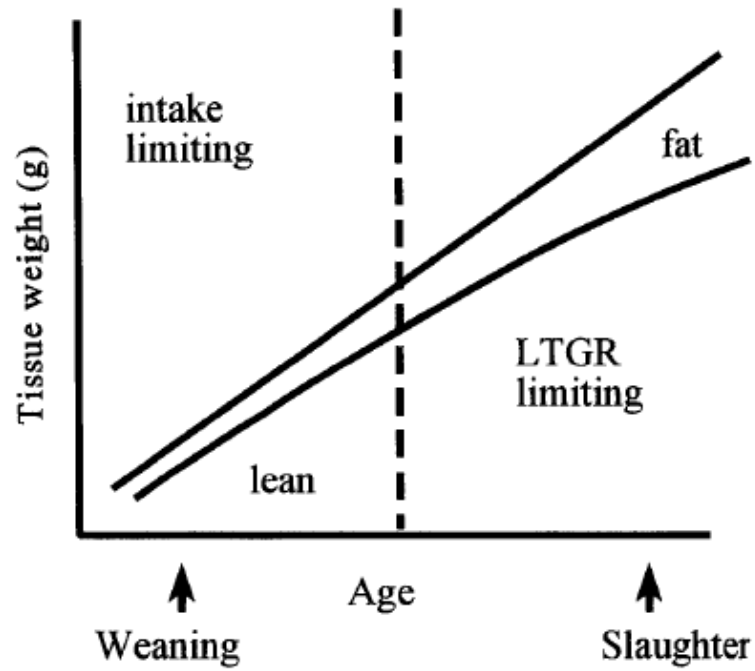


Figure 1.2 Representation of muscle and liveweight. LTGR = lean tissue growth rate. (from Webb (1998))

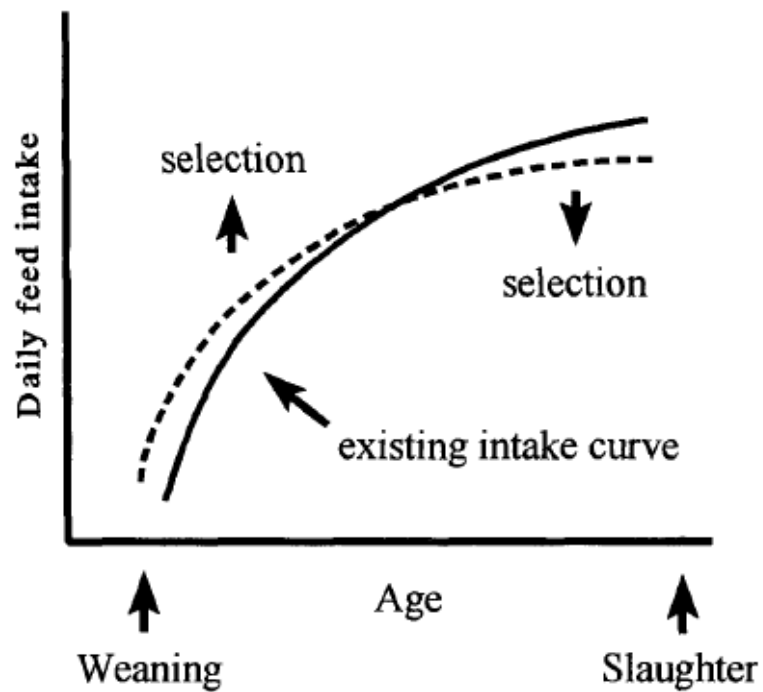


Figure 1.3 Representation of selection to increase early feed intake. (from Webb (1998))

The data used for the research presented in this dissertation were from a selection experiment for reduced RFI in Yorkshire pigs, which was initialized at Iowa State University in 2001. It consists of a line selected for lower RFI (LRFI) and a random selected control line (CTRL). Selection is on estimated breeding value (EBV) for RFI. The initial objective of this selection experiment was to create lines of Yorkshire pigs that have divergent feed intake but similar growth and backfat. The Yorkshire RFI selection lines have been kept as an important resource population to investigate the physiological differences, gene expression differences, single-nucleotide polymorphism (SNP) level differences between the two lines in order to understand the genetic, genomic, and physiological basis of feed efficiency. The ultimate goal of this selection experiment is to develop selection strategies to improve feed efficiency in pigs.

Within the scope of this selection experiment and against the background provided above, the overall objectives of this dissertation were to i) evaluate the effects of selection for reduced RFI, i.e. direct and correlated responses of production and carcass traits (cross-sectional measurements), and on changes in feed intake and growth curves (longitudinal measurements); ii) to estimate the genetic parameters of RFI and correlated traits; iii) to explore different statistical and genetic models to make most use of the longitudinal measurements of FI, BW, BF, and LMA along the growth trajectory of pigs to improve feed efficiency. To achieve these overall objectives, this dissertation addresses four specific objectives with four complementary research projects. The first objective of this dissertation was to evaluate direct response and correlated responses of production and carcass traits to selection on RFI and to estimate genetic parameters.

In practice, longitudinal measurements of FI and BW data are often missing for substantial parts of growth period, including at the beginning and end. Major missing data occur when pigs are switched between electronic and commercial feeders to enlarge the test capacity because of the high expense of electronic feeders (Casey 2003; Eissen et al. 1999; Schulze et al. 2001; Von Felde et al. 1996), and are caused by data errors and malfunction of electronic feeders (Casey et al. 2005; Eissen et al. 1998). Several studies have shown that missing FI information on different parts of the growth period has a limited effect on the

accuracy of evaluating ADFI (Casey 2003; Eissen et al. 1999). However, there have been few studies on the effect of missing data on evaluation of feed intake and body weight curves, which requires sophisticated statistical models to inter- and extrapolate FI and BW curves for individual pigs. Therefore, the second objective of this dissertation was to develop and compare RR models and non-linear mixed models for analysis of FI and BW in pigs with substantial missing data in order to identify the best model to predict FI and BW curves for individual pigs.

In order to further advance and investigate the possibilities of direct selection on individual curves, genetic parameters for FI, BW, BF, and LMA curves along the growth trajectory need to be estimated. Several studies have applied RR genetic analyses to longitudinal measurements of growth-related traits in pigs (Huisman et al. (2002) for weight data and Schnyder et al. (2001, 2002) for daily feed intake data), but there have been few studies on joint genetic analyses of longitudinal FI, BW, BF, and LMA data by RR models. Thus, the third objective of this dissertation was to apply RR genetic analyses to data from all generations of this selection experiment to estimate genetic parameters for FI, BW, BF, and LMA along the growth trajectory and to evaluate the effect of RFI selection on FI and BW curves.

As I indicated previously, the linear random regression models are easy to fit, but they provide limited understanding of the biological data-generating process and are dangerous for data extrapolation. In contrast, nonlinear mixed growth models are difficult to fit, but they could describe the entire growth-related process by a few of biologically meaningful parameters. Following the hierarchical Bayesian analysis scheme, Varona et al. (1998) analyzed the Wood lactation curve for dairy cows. Blasco et al. (2003) investigated the effect of selection for growth rate on growth curves in rabbits by the Gompertz growth function using similar methodology. Against this background, the fourth objective was to apply a hierarchical Bayesian method to investigate genetic variation in the parameters of the nonlinear mixed Gompertz growth model for longitudinal measurements of FI and BW, and to estimate the effect of selection for reduced RFI on growth and feed intake curves by the nonlinear Gompertz models.

Thesis Organization

Four journal papers (one published; two submitted; one to be submitted) were written to achieve the objectives of this dissertation. They are included as chapters in the dissertation. The general background introduction and the need for this research were addressed in the current Chapter 1. Direct and correlated responses to selection for reduced RFI in Yorkshire pigs and associated estimates of genetic parameters are included in Chapter 2. The identification of the best random regression models and non-linear mixed models to predict feed intake and body weight curves for individual pigs from longitudinal measurements of FI and BW with substantial missing data are included in Chapter 3. Estimation of genetic parameters for FI, BW, BF, and LMA along the growth trajectory and evaluation of the effect of RFI selection on FI and BW curves by random regression genetic analyses are in Chapter 4. The investigations of genetic variation and line differences of the parameters of the nonlinear Gompertz models for longitudinal measurements of FI and BW by the hierarchical Bayesian method are included in Chapter 5. General conclusions and discussion of the research are summarized in Chapter 6.

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CHAPTER 2. SELECTION RESPONSE AND GENETIC PARAMETERS FOR RESIDUAL FEED INTAKE IN YORKSHIRE SWINE

Modified from a paper published in Journal of Animal Science¹

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Abstract

Residual Feed Intake (RFI) is a measure of feed efficiency defined as the difference between observed feed intake and that predicted from average requirements for growth and maintenance. The objective of this study was to evaluate response in a selection experiment consisting of a line selected for low RFI and a random control line and to estimate genetic parameters for RFI and related production and carcass traits. Starting with random allocation of purebred Yorkshire littermates, in each generation, electronically measured average daily feed intake (ADFI), average daily gain (ADG), and ultrasound backfat (BF) were evaluated during a ~40 to ~115 kg test period on ~90 boars from first parity and ~90 gilts from second parity sows of the low RFI line. Following evaluation of first parity boars, ~12 boars and ~70 gilts from the select line were selected to produce ~50 litters for the next generation. About 30 control line litters were produced by random selection and mating. Selection was on EBV for RFI from an animal model analysis of ADFI, with on-test group and sex (fixed), pen within group and litter (random), and covariates for interactions of on- and off-test weight, on-test age, ADG, and BF with generations. RFI explained 34% of phenotypic variation in ADFI. After 4 generations of selection, estimates of heritability for RFI, ADFI, ADG, FE (=ADG/ADFI), and ultrasound-predicted BF, loin muscle area (LMA), and intramuscular fat (IMF) were 0.29, 0.51, 0.42, 0.17, 0.68, 0.57, and 0.28, respectively; predicted responses based on average EBV in the low RFI line were -114, -202, and -39 g/d for RFI (=0.9 phenotypic SD), ADFI (0.9 SD), and ADG (0.4 SD), 1.56 % for FE (0.5 SD), -0.37 mm for

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BF (0.1 SD), 0.35 cm² for LMA (0.1 SD), and -0.10 % for IMF (0.3 SD). Direct phenotypic comparison of the low RFI and control lines based on 92 low RFI and 76 control gilts from the 2nd parity of generation 4 showed that selection had significantly decreased RFI by 96 g/d ($P=0.002$) and ADFI by 165 g/d ($P<0.0001$). The low RFI line also had 33 g/d lower ADG ($P=0.022$), 1.36 % greater FE ($P=0.09$), and 1.99 mm less BF ($P=0.013$). There was not a significant difference in LMA and other carcass traits, including subjective marbling score, despite a large observed difference in ultrasound-predicted IMF (-1.05% with $P<0.0001$). In conclusion, RFI is a heritable trait and selection for low RFI has significantly decreased the feed required for a given rate of growth and backfat.

Key words: feed efficiency, pigs, residual feed intake, selection

Introduction

Feed for the growing phase is the largest variable cost in swine production. Therefore, feed intake (FI), as a vital component of feed efficiency (FE: kg product/kg feed), remains one of the most important considerations in pig breeding programs. Feed intake is genetically related to the economically important traits of growth and backfat (BF), but these relationships are not perfect; estimates of genetic correlations average 0.65 (0.32 to 0.89) with growth rate and 0.37 (0.08 to 0.59) with backfat thickness (Clutter and Brascamp, 1998). Thus, although a large proportion (36 to 64%) (Luiting, 1998) of variation in FI is related to production traits, there is considerable variation that is independent of growth and composition. This is referred to as residual FI (RFI: i.e., feed consumed over and above expected requirements for production and maintenance (Luiting, 1990)). Variation in RFI is not utilized in genetic selection for growth and composition, but is heritable; estimates in the pig range from 0.15 to 0.40 (Foster et al., 1983; Mrode and Kennedy, 1993; Von Felde et al., 1996; Johnson et al., 1999). Factors that contribute to genetic variation in RFI include feeding behavior, nutrient digestion, maintenance requirements, and energy homeostasis and partitioning (Luiting, 1998). Genetic differences in the ability to digest nutrients are small, but differences in maintenance requirements play a major role (Luiting, 1998). Although reduced maintenance requirements are desirable for improved FE, this may result in reduced fitness and increased susceptibility to stressors and diseases (Rauw et al., 1998). To enable

the study of the genetic and physiological basis of FE, we initiated a selection experiment for RFI in Yorkshire pigs, with the goal of creating lines that differ in RFI. The objective of this study was to evaluate direct and correlated responses to selection and to estimate genetic parameters based on the first 4 generations.

Materials and Methods

Selection Experiment

Experimental Design and Data Collection. Using purebred Yorkshire pigs, a selection line for reduced RFI (low RFI line) was started in 2001, along with a randomly selected control. An outline of the selection line protocol is in Figure 2.1. Starting with random allocation of littermates from generation 0 (the base population) to the low RFI and control lines, in each generation the following traits were evaluated on ~90 boars from first parity and ~90 gilts from second parity sows of the low RFI line: electronically measured FI, weekly body weight, and 10th rib backfat (BF), loin muscle area (LMA), and intramuscular fat (IMF, in generations 0 through 4 only) by ultrasound using an Aloka 500V SSD ultrasound machine fitted with a 3.5 MHz, 12.5-cm linear-array transducer (Corometrics Medical Systems, Inc., Wallingford, CT). Following evaluation of first parity boars based on EBV for RFI (see below), ~12 select line boars and 70 gilts were selected to produce ~50 litters for the next generation. Following selection, full- or half-sisters of the selected boars, produced in the second parity of their dams, were evaluated for RFI to provide additional data for the next generation (Figure 2.1). Each generation about 30 control line litters from approximately 10 boars and 40 gilts were produced by random selection and mating.

For feed intake recording, pigs were put in pens of 15 to 16 pigs, each of which had an electronic 1-space feeder (FIRE[®] (Osborne Industries, Inc., Osborne, KS)), at ~90 d of age and ~40 kg weight. Pigs were allowed to acclimate to the FIRE[®] feeders for about 1 wk before they were put on test in groups by on-test-date (typically in 2 or 3 age groups per generation) based on age and weight. In general, pigs were taken off test on an individual basis when they reached 115 kg, but were removed at a lighter weight if only 3 pigs were left in a pen, in which case they were all taken off test. All pigs with off-test weights greater than

102 kg were used for analysis. Because of limited capacity to measure FI, in general, only low RFI line pigs were evaluated for FI.

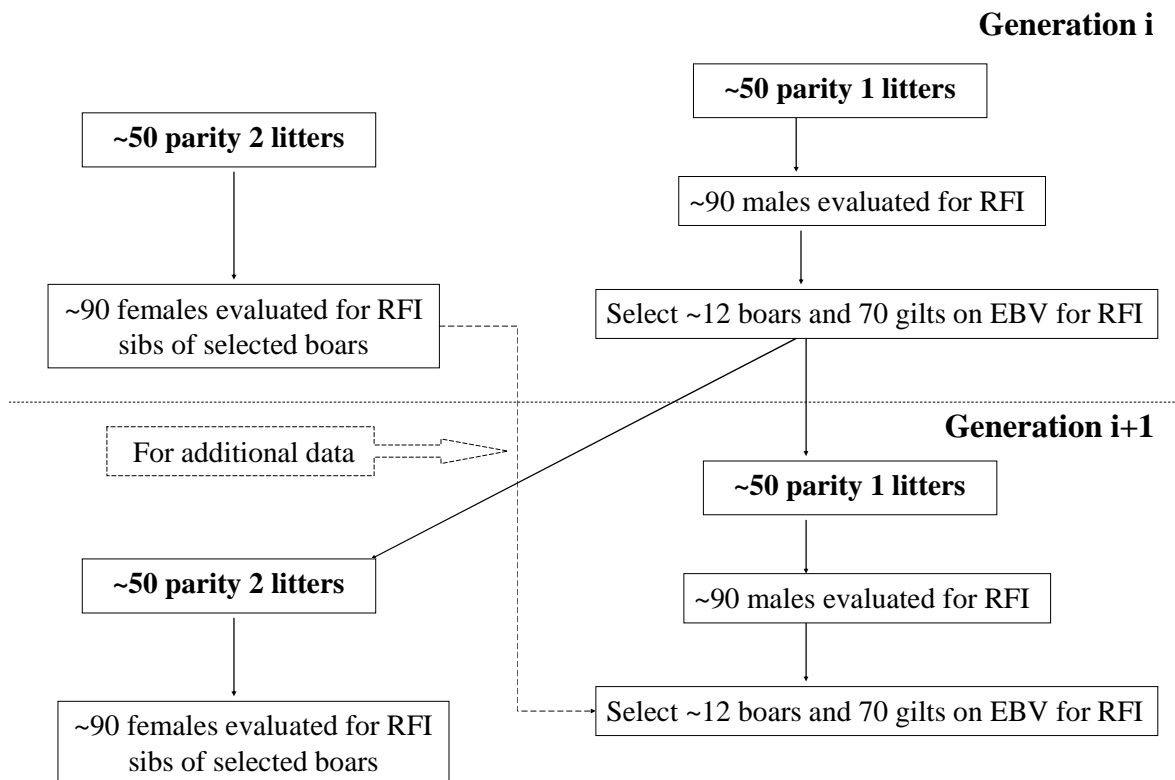


Figure 2.1 Design of the selection line for reduced residual feed intake (RFI)

Database and edit systems developed by Casey (2003) and Casey et al. (2005) to handle the large amount of FI data from the FIRE[®] feeders were used. The main steps in the edit procedures were to i) identify errors in each visit (a feeding event from a pig's entrance in the feeder to its exit) by 16 criteria (Casey et al., 2005) and count the number of errors of each type for each day (about 5% of visits contained at least 1 error); ii) compute error-free FI for each pig and day by summing feed consumed in visits without identified errors; iii) estimate the effect of error counts on error-free daily FI by fitting a linear mixed model to error-free daily FI observations with sex, generation by parity, and on-test weeks within generation by parity as fixed effects, variables created from the 16 error counts, body weight on that day and ADG as covariates, and pig as a random effect (Casey, 2003); iv) adjust error-free daily

FI for each pig and day for feed consumed in error visits by adding estimates of covariates from step iii); v) estimate daily FI for each pig for days with missing FI data (no records or too many error visits) by fitting a quadratic regression of daily FI against on-test day for each pig; vi) compute ADFI for each pig by averaging daily FI during the test period.

For each pig, ADG was estimated as the slope from simple linear regression of weekly body weight on number of days on test. The IMF content was predicted based on a longitudinal ultra-sound scan when pigs were taken off test using the model developed by Schwab and Baas (2006) on purebred Duroc barrows and gilts from the IMF selection project at Iowa State University. The R^2 and root mean square error for this prediction model were 0.36 and 1.31% (Schwab and Baas, 2006).

Genetic Evaluation. Each generation, selection of boars and gilts used to produce the next generation of the low RFI line was on EBV for RFI, with some consideration of avoiding selection of full-sib brothers. Using data from all generations up to that point, including data from the base population (generation 0) and the generation that created the base population (generation -1), EBV for RFI were obtained from a single-trait animal model analysis of ADFI, with fixed effects of on-test group and sex, random effects of litter and pen within on-test group, and linear covariates for interactions of on- and off-test weight, on-test age, ADG adjusted to an on-test age of 90 d (=ADGA) and BF adjusted to an off-test weight of 115 kg (=BFA) with generation. Adjusted values for ADG and BF were used as covariates rather than unadjusted ADG and BF because ADGA and BFA are expected to better reflect the impact of growth and BF on ADFI in a model that includes these same adjustments (i.e. for on-test age and off-test weight) for ADFI. Regression coefficients used for adjustment of ADG and BF to derive ADGA and BFA were obtained from models described in later. Inclusion of interactions of covariates with generation was based on significance ($P < 0.05$) using backward elimination. Inclusion of metabolic mid-weight as a covariate to account for average maintenance requirements, as suggested by Nguyen et al. (2005), was considered. However, the correlation between EBV of RFI with and without metabolic mid-weight was 0.98 in our data, indicating that maintenance requirements are accounted for by ADG and on- and off-test weights. The heritability used for genetic evaluation of RFI was re-estimated each generation using all available data and ranged from 0.27 to 0.36 for generations 0 to 4.

Estimation of Response to Selection and Genetic Parameters. After 4 generations of selection, genetic parameters and responses to selection for RFI, ADFI, ADG, FE (=ADG/ADFI), BF, LMA, and IMF were estimated by 2-trait animal model analyses using ASReml (Gilmour et al., 2002), using data from pigs evaluated for FI from generations -1 to 0 (the base population) and in the low RFI line from generations 1 up to and including generation 4 parity 1. The 2-trait animal models for all traits were the same as the single-trait genetic evaluation model for RFI, except covariates for the interaction of on-test age with generation were added for ADFI, ADG, and FE, and covariates for the interaction of off-test weight with generation were added for BF, LMA, and IMF. On- and off-test weights were not included as covariates for analysis of ADFI and ADG, because they included some biological variation related to feed intake and growth in view of the fact that high growing pigs tend to have higher on- and off-test weights. A summary of covariates included for each trait is in Table 2.1. Estimates of heritability, variance components, and selection response for all traits are reported from 2-trait animal models that always included RFI as one of the traits to account for the effect of selection on RFI.

Table 2.1 Covariates included in the model for different traits in the selection experiment and the direct line comparison experiment

Experiment	Trait ¹	Covariate by gen ²				
		on-age	on-weight	off-weight	ADG	BF
Selection line	RFI	√	√	√	√	√
	ADFI, ADG, FE	√				
	BF, LMA, IMF			√		
Direct line comparison	RFI	√	√	√	√	√
	ADFI, ADG, FE	√				
	BF, LMA, IMF			√		
	Carcass traits					
		Live-weight before slaughter				

¹RFI = residual feed intake, ADFI = average daily feed intake, ADG = average daily gain, FE=ADG/ADFI, BF = backfat, LMA = loin muscle area, IMF = intramuscular fat

²By gen: interaction with generation; this interaction was not included for the direct line comparison because it involved only 1 generation

Two-trait models, such as those that include ADFI to estimate RFI as one trait and ADG as the other trait result in a recursive system of equations with simultaneous feedback, because ADG is used as a trait and also as a covariate in the model that analyzes ADFI to obtain genetic parameters for RFI. As outlined by Gianola and Sorenson (2004), this results

in biased and inconsistent estimates of genetic parameters when solved by maximum likelihood. To avoid this, RFI was pre-adjusted for on- and off-test weight, and for ADGA and BFA before it was fitted in the 2-trait animal model analyses. Regression coefficients used for pre-adjustment were obtained from the single-trait RFI model.

Direct Line Comparison Experiment

Experimental Design and Data Collection. Since FI was not routinely recorded in the control line, a phenotypic comparison experiment was conducted to allow direct comparison of line differences for RFI, ADFI, ADG, FE, BF, LMA, IMF, and several carcass traits using gilts from the 2nd parity of generation 4. The same boars and sows that produced parity 1 of generation 4 were used to produce these gilts. This experiment was also used to evaluate the effects of a polymorphism in the calcitron receptor (*calcr*) as a candidate gene for bone strength (Hittmeier, 2005) on performance and bone strength. Because *calcr* genotype had limited effects on the traits considered here, results for bone strength will be reported elsewhere. As illustrated in Figure 2.2, the experiment was designed as a split-plot with 2 factors: line (low RFI vs. control) and *calcr* genotype (11, 12, and 22), with litter as the main experimental unit to test for line differences, and pig as the split-plot experimental unit to test for genotype differences. To increase power to detect genotype differences, pigs included in the comparison were selected to obtain adequate numbers within each genotype by line class. A total of 92 low RFI gilts from 27 litters and 76 control gilts from 17 litters were evaluated. They were grouped in 12 pens by weight and age, while balancing to the extent possible across line and genotype. Because only 6 pens were available for FI recording, pens were switched every 2 wk. Alternate pens were in the same room and had feeding equipment equivalent to the FIRE[®] feeders, so as not to induce an acclimation period. The FI data from the day of switching were not used.

Pigs were taken off-test in 3 groups (different off-test dates) and sent for harvest at a commercial abattoir (Hormel Foods, Austin, MN), at a minimum weight of 102 kg. In contrast to standard procedures in the selection experiment, where pigs were taken off-test individually at a target weight of 115 kg, taking pigs off-test in just 3 groups to allow for sufficient numbers per slaughter day resulted in substantial variation in off-test weights.

Carcass measurements were obtained 24 h postmortem using standard carcass collection procedures, as outlined in Pork Composition and Quality Assessment Procedures (NPPC, 2000) for carcass length, carcass weight, 10th rib BF, last rib BF, last lumbar BF, and 10th rib LMA. Ultimate pH was measured on the 10th-rib face of the loin using a pH star probe (SFK Ltd, Hvidovre, Denmark). Hunter L score and Minolta Y Reflectance (a measure of light reflectance, where lower values indicate darker and more desirable color) were measured on the 10th-rib face of the loin using a Minolta CR-310 (Minolta Camera Co., Ltd., Osaka, Japan) with a 50-mm-diameter aperture, D65 illuminant, and calibrated to the white calibration plate. Subjective scores for color (National Pork Board standards 6 point scale, 1 = pale pinkish gray to white; 6 = dark purplish red), firmness (National Pork Board standards 3 point scale, 1 = soft; 3 = very firm), and marbling (National Pork Board standards 10 point scale, 1 = 1.0% IMF; 10 = 10.0% IMF) were also recorded.

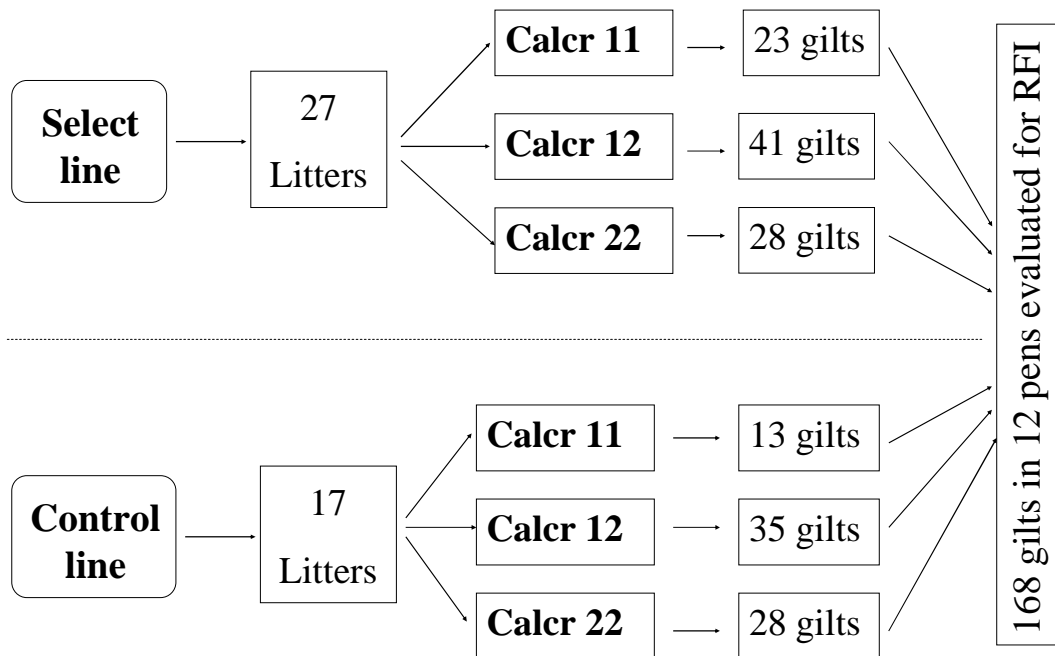


Figure 2.2 Design of direct phenotypic line comparison experiment

Statistical Analysis. Data from the production traits RFI, ADFI, ADG, FE, BF, LMA, and IMF were analyzed by a linear mixed model with on-test group (n=2), off-test group (n=3), line, *calcr*, and the interaction of line with *calcr* as fixed effects, litter and pen within on-test group as random effects, and covariates as specified in Table 2.1. Carcass traits were analyzed with a linear mixed model or a generalized linear mixed model (using a multinomial response distribution and cumulative logit link function for color, firmness, and marbling score), with liveweight before slaughter as the covariate, and the same fixed and random effects as for the production traits analysis, except on-test group and pen within on-test group were not included in the models. To enable the SAS GLIMMIX procedure (Statistical Analysis Systems Institute, 2007) to converge, class 5 of the color score, which had only 2 observations, was merged into class 4, and for marbling score, class 4 (2 observations) and class 3 (3 observations) were merged into class 2. The interaction of line with *calcr* was dropped after testing non significant ($P>0.20$), other than for ADG and ADFI. Also, interactions of all covariates with line were not significant ($P>0.05$) for all traits and were dropped from the models.

Results

Estimates of Genetic Parameters

Table 2.2 shows estimates of heritability and variance due to environmental components from the 2-trait animal model analyses. Estimates of genetic parameters and responses to selection for RFI were similar among 2-trait models of RFI with all other traits and are reported from the 2-trait animal model of RFI with ADFI. RFI had a substantial heritability (0.29), which is within the upper range of estimates (0.15 to 0.40) for RFI in pigs observed in the literature (Foster et al., 1983; Mrode and Kennedy, 1993; Von Felde et al., 1996; Johnson et al., 1999). About 34% of phenotypic variation in ADFI was contributed by RFI (= phenotypic variance ratio of RFI to ADFI), the rest being explained by variation in growth rate and backfat. The estimated heritability for ADFI (0.51) was in the upper range of literature estimates, with estimates averaging 0.29 and ranging from 0.13 to 0.62 (Clutter and Brascamp, 1998). Estimates of heritability for ADG and BF were 0.42 and 0.68, respectively, also in the upper range of literature estimates for ADG (0.03 to 0.49) and BF (0.12 to 0.74),

as specified by Clutter and Brascamp (1998). The estimated heritability for FE was 0.17, similar to the 0.16 heritability of feed conversion ratio (i.e. ADFI/ADG) from Large White boars estimated by Johnson et al. (1999). Table 2.2 also shows that the estimated common environmental effect of litter was close to zero for RFI, ADFI, ADG, and FE, but was not negligible for BF, LMA, and IMF. Pen accounted for 30%, 13%, and 16% of the phenotypic variation in RFI, ADFI, and FE, respectively, which is likely due to the operation and measurement errors associated with the FIRE[®] feeder located in each pen. Although the pen variance ratio was much greater for RFI (30%) than for ADFI (13%), the absolute value of the pen variance component was not much different between RFI and ADFI. Estimated pen within group common environmental effects were close to zero for ADG, BF, LMA, and IMF.

Table 2.2 Estimates (\pm SE) of heritability and of variance due to litter, pen (group), and residual, based on data from the low RFI line, expressed as a percentage of phenotypic variance¹

Trait ²	N	Mean	SD ¹	Heritability	Litter ³	Pen(group) ³	Residual
RFI, g/d	756	0	126	0.29 \pm 0.07	0.01 \pm 0.00	0.30 \pm 0.06	0.40 \pm 0.07
ADFI, g/d	756	1989	216	0.51 \pm 0.08	0.00 \pm 0.00	0.13 \pm 0.04	0.36 \pm 0.08
ADG, g/d	756	768	91	0.42 \pm 0.08	0.00 \pm 0.00	0.02 \pm 0.02	0.56 \pm 0.08
FE, %	756	38.76	3.30	0.17 \pm 0.07	0.05 \pm 0.00	0.16 \pm 0.04	0.62 \pm 0.07
BF, mm	756	15.88	3.48	0.68 \pm 0.09	0.08 \pm 0.01	0.00 \pm 0.00	0.24 \pm 0.09
LMA, cm ²	756	42.67	4.67	0.57 \pm 0.10	0.11 \pm 0.01	0.02 \pm 0.02	0.30 \pm 0.09
IMF, %	492	1.75	0.40	0.28 \pm 0.11	0.27 \pm 0.02	0.01 \pm 0.02	0.44 \pm 0.10

¹Phenotypic variance and standard deviation after adjustment for fixed effects and covariates

²RFI = residual feed intake, ADFI = average daily feed intake, ADG = average daily gain,

FE=ADG/ADFI, BF = backfat, LMA = loin muscle area, IMF = intramuscular fat

³0.00 denotes the number was smaller than 0.005

Estimates of phenotypic and genetic correlations are in Table 2.3. Genetic correlations of ADFI with ADG and BF were estimated at 0.88 and 0.57, in the upper range of literature estimates of ADFI with ADG (0.32 to 0.89) and of ADFI with BF (0.08 to 0.59) (Clutter and Brascamp, 1998). Estimated phenotypic correlations of RFI with ADG and BF were close to zero, as expected from adjusting for ADG and BF in the model for RFI. However, because adjustment for ADG and BF was at the phenotypic level, genetic correlations of RFI with ADG (0.17) and with BF (-0.14) were non-zero, although these estimates had large standard

errors and were not significantly different from zero. Johnson et al. (1999) obtained similar estimates of genetic correlations of RFI with ADG (0.17), but a slightly positive genetic correlation of RFI with BF (0.22) from Large White boars on individual pen testing, when RFI was adjusted for initial test age and weight, test ADG, and BF. However, Nguyen et al. (2005) reported a slightly negative genetic correlation of RFI (adjusted for test ADG and BF) with BF (-0.20) from Large White boars and gilts on individual pen feeding, similar to our result. Apart from sampling errors, differences in these estimates can result from population differences in phenotypic and genetic correlations among traits, as the genetic correlation of RFI with ADG and BF is a direct result of the phenotypic and genetic parameters of FI, ADG, and BF in the population (Kennedy et al., 1993). Genetic correlations of RFI with FE, LMA, and IMF were estimated as -0.74, -0.18, and 0.40, respectively. The estimated negative genetic correlation (-0.13) between BF and IMF is opposite to literature estimates (Lo et al., 1992; Suzuki et al., 2005), but the large standard error (0.26) of this estimate could explain this discrepancy.

Table 2.3 Estimates of phenotypic (above diagonal) and genetic correlations (below diagonal) based on bivariate analyses of the low RFI line data

Trait ¹	RFI ± SE	ADFI ± SE	ADG ± SE	FE ± SE	BF ± SE	LMA ± SE	IMF ± SE
RFI	-	0.61±0.03	0.06±0.05	-0.69±0.03	-0.01±0.04	-0.06±0.05	0.03±0.06
ADFI	0.52±0.12	-	0.73±0.02	-0.26±0.05	0.49±0.04	-0.01±0.05	0.08±0.06
ADG	0.17±0.18	0.88±0.05	-	0.46±0.04	0.36±0.04	0.11±0.05	0.16±0.05
FE	-0.74±0.13	-0.26±0.21	0.30±0.21	-	-0.09±0.04	0.14±0.05	0.11±0.05
BF	-0.14±0.16	0.57±0.10	0.45±0.13	-0.24±0.22	-	-0.10±0.05	-0.01±0.06
LMA	-0.18±0.18	-0.09±0.16	0.16±0.17	0.27±0.27	-0.10±0.17	-	0.03±0.06
IMF	0.40±0.28	0.37±0.24	0.38±0.23	-0.23±0.47	-0.13±0.26	0.22±0.28	-

¹RFI = residual feed intake, ADFI = average daily feed intake, ADG = average daily gain, FE=ADG/ADFI, BF = backfat, LMA = loin muscle area, IMF = intramuscular fat

Direct and Correlated Responses to Selection

Predicted from Average EBV in the Low RFI Line. Predicted selection responses for RFI and production traits are shown in Figure 2.3, in which the average EBV of boars with data in the low RFI line for each generation was plotted on a genetic SD scale and deviated from the average EBV of boars with data in the base population (generation 0). Single-trait selection for decreasing RFI resulted in the expected selection response (close to 2 genetic SD in generation 4). As expected, selection on RFI also led to a substantial reduction in

ADFI. Selection on RFI also resulted in small negative correlated responses in ADG, BF, and IMF, and a slight increase in LMA, consistent with the estimated genetic correlations of RFI with ADFI, ADG, IMF, and LMA of 0.52, 0.17, 0.40, and -0.18, respectively (Table 2.3). Selection on RFI also slightly reduced BF, which was opposite to the estimated genetic correlation of -0.14 between RFI and BF (Table 2.3), but which had a large standard error that could explain this discrepancy. Although there was a small reduction in ADG, selection for decreasing RFI, as expected resulted in substantial improvements in FE (about 1.2 genetic SD in generation 4) because of a substantial reduction in ADFI.

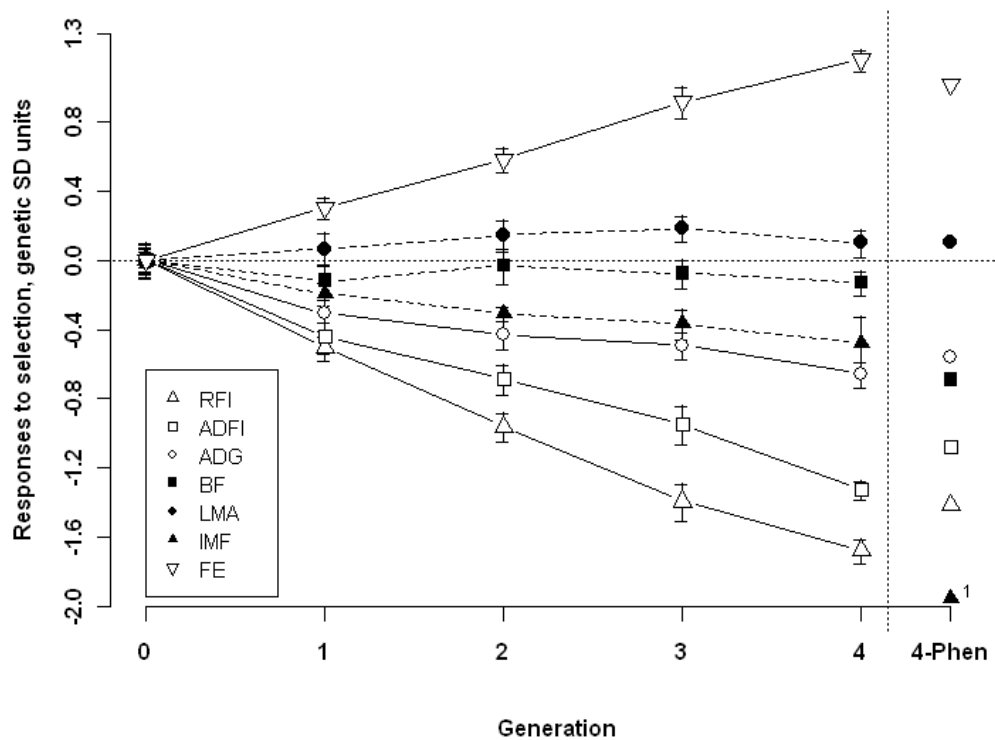


Figure 2.3 Direct and correlated responses to selection on residual feed intake (RFI) based on average EBV (connected symbols) and direct phenotypic line comparison in generation 4 (4-Phen). Average EBV and SE bars are based on only boars with data in the low RFI line. 4-Phen: Phenotypic line differences (low RFI-control) based on the direct line comparison in generation 4; ADFI = average daily feed intake; FE (feed efficiency) = ADG/ADFI; BF = backfat; LMA = loin muscle area; IMF = intramuscular fat. *The direct phenotypic line comparison for IMF in generation 4 was -5 genetic SD

Estimates from Direct Line Comparison. The 27 selection litters (92 gilts) and the 17 control litters (76 gilts) finished test with average on- and off-test weights (\pm SD) of approximately 60 (\pm 8) kg and 110 (\pm 6) kg and these were used to estimate line differences in performance. Results are shown in Table 2.4 and also in Figure 2.3. The low RFI line gilts had significantly lower RFI (96 g/d, $P=0.002$), lower ADFI (165 g/d, $P<0.0001$), and greater FE (1.36 %, $P=0.09$) than the control line gilts, although the select line gilts also had significantly lower growth (33 g/d, $P=0.022$), less BF (1.99 mm, $P=0.013$), less IMF (1.05%, $P<0.0001$), and tended to have greater LMA (0.35 cm^2 , $P=0.7$). The estimated line difference for IMF was 5 genetic SD, which may be due to the poor quality of the IMF prediction (see discussion section).

Table 2.4 Estimates of line differences (low RFI - control) in generation 4 based on average EBV from analysis of the low RFI line and based on direct line comparison of the low RFI and control lines, depending on the inclusion of additional covariates in the model

Trait ¹	Covariates included in model	Difference based on EBV \pm SEM ²	Difference based on direct line comparison \pm SED with inclusion of covariates in addition to on-age			
			none	on-weight	off-weight	on-weight off-weight
RFI, g/d	on-age, ADG, BF	-114 \pm 5	-89 ^{**} \pm 30	-100 ^{**} \pm 30	-97 ^{**} \pm 28	-96 ^{3**} \pm 28
ADFI, g/d	on-age	-202 \pm 8	-165 ^{3***} \pm 35	-171 ^{***} \pm 35	-164 ^{***} \pm 34	-139 ^{***} \pm 34
ADG, g/d	on-age	-39 \pm 4	-33 ^{3*} \pm 14	-26 [*] \pm 13	-30 [*] \pm 12	-4 ^{NS} \pm 5
FE, %	on-age	1.56 \pm 0.08	1.36 ^{3†} \pm 0.78	1.73 [*] \pm 0.73	1.39 [†] \pm 0.78	2.31 ^{**} \pm 0.69
BF, mm	off-weight	-0.37 \pm 0.20	-1.99 ^{3*} \pm 0.76	-	-	-
LMA, cm ²	off-weight	0.35 \pm 0.28	0.35 ^{3NS} \pm 0.93	-	-	-
IMF, %	off-weight	-0.10 \pm 0.03	-1.05 ^{3***} \pm 0.23	-	-	-

¹RFI = residual feed intake, ADFI = average daily feed intake, ADG = average daily gain,

FE=ADG/ADFI, BF = backfat, LMA = loin muscle area, IMF = intramuscular fat

²Average EBV and SEM are based on only boars with data in the low RFI line

³Indicates results for the preferred model

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; † $P < 0.10$; NS $P > 0.10$

Since the phenotypic comparison experiment had substantial on- and off-test weight variation, in contrast to standard procedures in the selection experiment, the impact of including these weights as covariates in the models for analysis of RFI, ADG, and ADFI was evaluated. Results in Table 2.4 show limited impact of including these covariates on estimates of line differences, except when both on- and off-test weights were included, in which case estimates of line differences were reduced for ADFI and in particular for ADG (-4 versus -33 g/d). The on- and off-testing procedures caused variation in on- and off-test weights to be correlated with true biological variation in ADG. Thus, including on- and off-test weights as covariates in the models for ADG and ADFI not only removes noise, but also removes some biological variation in ADG and ADFI, which is undesirable. Thus, for these traits, the model that included neither of these covariates was deemed the preferred model. Although the impact of including one or both of these covariates in the model for RFI was limited, for this trait all variation associated with ADG must be removed, such that the model that includes all covariates is the preferred model. This model resulted in an estimated line difference of -96 g/d in RFI (Table 2.4).

Phenotypic Comparison for Carcass Traits

Estimates of line differences for carcass traits are presented in Table 2.5, which also includes estimates for production traits for completeness. Line differences for the subjective scores of color, firmness, and marbling are expressed as logarithm odds ratios. A ratio close to zero means no difference between the lines and a positive ratio means a higher score for the low RFI line. Except for 10th rib BF, none of the carcass traits had a significant ($P > 0.10$) difference between the low RFI and control lines. The estimated line differences for 10th rib BF and LMA measured on the carcass were -2.62 mm and 0.73 cm², respectively, which are in the same direction and order of magnitude as the line difference of -1.99 mm ($P < 0.05$) for BF and 0.35 cm² ($P > 0.10$) for LMA measured in live pigs by real time ultrasound on the farm. The line difference for marbling score was -0.52 on the logarithm odds ratio scale, which is in the same direction as the line difference of IMF predicted by longitudinal ultrasound scan but was not significant ($P > 0.10$), in contrast to the high level of significance for IMF estimated by ultrasound. This result is probably because IMF data was of poor quality, which may have resulted in an overestimate of the line difference. The line

difference for color by subjective scores was positive, though not significant ($P>0.10$). Nevertheless, this estimate was in the same direction as estimates for objective reflectance measures by Minolta Y and Hunter L, in that the low RFI line tended to have greater color and less reflectance.

Table 2.5 Estimates of line differences for production and carcass traits based on the direct line comparison (N=168)

	Trait ¹	Mean	SD ²	Line difference (select-control) ± SED
Production traits	RFI, g/d	0	165	-96 ^{**} ± 28
	ADFI, g/d	1990	193	-165 ^{***} ± 35
	ADG, g/d	702	72	-33 [*] ± 14
	FE, %	38.76	3.30	1.36 [†] ± 0.78
	BF, mm	15.88	3.02	-1.99 [*] ± 0.76
	LMA, cm ²	45.02	4.08	0.35 ^{NS} ± 0.93
	IMF, %	3.60	0.95	-1.05 ^{***} ± 0.23
Carcass traits	Carcass length, cm	83.32	1.78	-0.35 ^{NS} ± 0.39
	Carcass weight ³ , kg	83.94	1.53	-0.03 ^{NS} ± 0.31
	10 th rib BF, mm	16.68	4.08	-2.62 [*] ± 1.01
	Last rib BF, mm	22.41	4.55	-1.28 ^{NS} ± 0.88
	Last lumbar BF, mm	27.12	4.65	-1.11 ^{NS} ± 0.89
	LMA, cm ²	46.73	6.18	0.73 ^{NS} ± 1.48
	Color ⁴	3.35	0.65	0.09 ^{NS} ± 0.37
	Firmness ⁴	2.30	0.61	-0.35 ^{NS} ± 0.31
	Marbling ⁴	1.38	0.59	-0.52 ^{NS} ± 0.39
	pH	5.62	0.11	-0.02 ^{NS} ± 0.02
	Minolta Y	23.14	2.55	-0.26 ^{NS} ± 0.48
	Hunter L	48.02	2.65	-0.25 ^{NS} ± 0.49

¹RFI = residual feed intake, ADFI = average daily feed intake, ADG = average daily gain,

FE=ADG/ADFI, BF = backfat, LMA = loin muscle area, IMF = intramuscular fat

²SD: Phenotypic standard deviation after adjustment for fixed effects and covariates

³Live weight was included as covariate such that results apply to dressing percentage

⁴Subjective score: SD without adjustment; Line difference in logarithm odds ratio scale

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; † $P < 0.10$; ^{NS} $P > 0.10$

Regression Coefficients for ADG and BF

Estimates of regression coefficients on ADGA and BFA when analyzing ADFI to obtain RFI, represent the average increase in feed intake per unit of change in ADG or BF and are shown in Table 2.6 for the different analyses. The mixed model used for analysis of the low RFI line data across generations included interactions of generation with ADGA and BFA to

allow for different regression coefficients as a result of selection or year effects. Both interactions were significant ($P < 0.05$).

The regression coefficient for ADGA was fairly stable up to generation 4, at which point it dropped dramatically (Table 2.6). A possible reason for this result was that the growth test in generation 4 was during a long hot period. The regression coefficient for BFA was fairly stable, except for generation 3, but this coefficient had a large standard error, because only 51 pigs from parity 1 in that generation had data. Estimates of the regression coefficients for ADGA and BFA from the direct phenotypic comparison were similar to those obtained from the genetic analysis (Table 2.6).

Table 2.6 Estimates of partial regression coefficients of average daily feed intake (ADFI, kg/d) on average daily gain (ADG, kg/d) and backfat (BF, mm), when analyzing ADFI to calculate residual feed intake, based on data from the low RFI line by generation and the direct line comparison

Experiment	Trait	Gen ¹	Estimate of regression coefficient \pm SE with inclusion of covariates in addition to on-age		
			none	on-weight	on-weight off-weight
Selection ²	ADG	-1	1.61 \pm 0.10	1.23 \pm 0.10	1.14 \pm 0.10
		0	1.46 \pm 0.12	1.33 \pm 0.11	1.24 \pm 0.11
		1	1.44 \pm 0.13	1.27 \pm 0.13	1.20 \pm 0.13
		2	1.37 \pm 0.12	1.33 \pm 0.11	1.18 \pm 0.12
		3	1.99 \pm 0.22	1.52 \pm 0.23	0.88 \pm 0.27
		4	0.80 \pm 0.17	0.76 \pm 0.16	0.58 \pm 0.16
	BF	-1	0.014 \pm 0.003	0.018 \pm 0.003	0.020 \pm 0.003
		0	0.016 \pm 0.003	0.015 \pm 0.003	0.015 \pm 0.003
		1	0.011 \pm 0.003	0.012 \pm 0.003	0.013 \pm 0.003
		2	0.019 \pm 0.003	0.019 \pm 0.003	0.019 \pm 0.003
		3	-0.007 \pm 0.007	-0.003 \pm 0.007	0.001 \pm 0.006
		4	0.018 \pm 0.006	0.019 \pm 0.006	0.019 \pm 0.006
Direct line comparison ³	ADG	4	1.51 \pm 0.17	1.69 \pm 0.17	0.78 \pm 0.40
	BF	4	0.023 \pm 0.004	0.023 \pm 0.004	0.023 \pm 0.004

¹Gen: generations

²Data were on both gilts and boars from the low RFI line

³Data were on gilts from both the low RFI and control lines

Estimates of regression coefficients on ADGA were affected by the inclusion of other covariates in the model (Table 2.6). When on-test or off-test weight were included as additional covariates, compared with only including on-test age, the regression coefficient on ADGA decreased, especially when on- or off-test weights had large variation (e.g., at generation 3 of the genetic analysis and in the direct phenotypic comparison), indicating that on- and off-test weights capture some biological variation in ADGA. The regression coefficients for BFA did not change much across generations. To obtain partial regression coefficients for ADGA and BFA when analyzing RFI, the model that includes on-test age is preferred, because it does not remove biological variation in ADGA.

Regression coefficients for ADGA ranged from 1.37 to 1.99 $\text{kg}\cdot\text{d}^{-1}\cdot\text{kg}^{-1}\cdot\text{d}$, which was similar to the 1.29 $\text{kg}\cdot\text{d}^{-1}\cdot\text{kg}^{-1}\cdot\text{d}$ reported by Nguyen et al. (2005), but the coefficients for BFA, which ranged from 0.011 to 0.023 $\text{kg}\cdot\text{d}^{-1}\cdot\text{mm}^{-1}$, were about 10 times larger than the 0.00185 $\text{kg}\cdot\text{d}^{-1}\cdot\text{mm}^{-1}$ reported by Nguyen et al. (2005). A possible reason for the latter difference is that, in Nguyen et al. (2005) RFI was evaluated on Large White pigs selected for body weight gain on restricted feeding when they were housed individually and fed *ad libitum*, vs. our group housed Yorkshire pigs selected for reduced RFI on *ad libitum* feeding.

Discussion

Comparison of Responses Based on Genetic Evaluation and Direct Line Comparison

The limited capacity to measure FI did not allow systematic measurement of RFI in the control line, which reduces the accuracy of the estimation of response to selection. This was addressed by evaluating RFI on both lines in the direct line comparison in the final generation. Estimated responses of RFI and ADFI in the fourth generation based on direct comparison of lines were -96 and -165 g/d, and were slightly smaller than the predicted response of -114 and -202 g/d based on average line EBV of boars from analysis of data observed in the low RFI line. In addition to sampling errors (SE of line differences from direct comparison were 28 and 35 g/d), this slightly lower response in the direct comparison may be because it was evaluated on gilts, while most selection was on RFI observed on

boars. Some differences also existed in on- and off-test weights: pigs were evaluated from ~60 kg to ~110 kg in the direct comparison and from ~40 kg to 115 kg in the selection line.

Selection slightly reduced ADG and BF in the low RFI line, probably because of non-zero genetic correlations of RFI with ADG and BF when using these traits to adjust ADFI to obtain RFI on a phenotypic level (Kennedy et al, 1993). Because of a large reduction in ADFI relative to the reduction in ADG, selection on RFI increased feed efficiency by 1.56 % kg of growth per kg of feed (Table 2.4) from generation 0 (base population) to generation 4 based on average EBV of boars with data in the low RFI line, which is close to the difference in feed efficiency (1.36% kg of growth per kg of feed) based on direct comparison of the 2 lines in generation 4.

Genetic analysis of the low RFI line resulted in a small line difference for ultrasound IMF (-0.10 %) but the direct phenotypic line comparison resulted in a large difference in ultrasound IMF (-1.05 %), although the difference in subjective marbling scores was not significant (Table 2.5). One explanation for the large difference in ultrasound IMF in the phenotypic comparison is that the variance for IMF was much higher in the phenotypic line comparison (based on gilts) than in the data used for the genetic evaluation, which was primarily on boars; the mean and phenotypic SD of IMF (after adjustment for fixed effects and covariates) were 3.60 and 0.95%, respectively, in the phenotypic line comparison vs. 1.75 and 0.40%, respectively, based on the genetic evaluation data. Another explanation is that these differences may be because the IMF ultrasound predictions had limited accuracy and may be biased in view of the fact that the prediction model was developed based on a Duroc population and had low R^2 and high root mean square error even for that population (Schwab and Baas, 2006).

Differences in body composition (fat to lean) can cause differences in RFI, because depositing fat requires more energy per gram than depositing lean. The model used for evaluating RFI corrects for differences in body composition to the extent they are related to ultrasound backfat. Thus, to evaluate differences in IMF as a potential contributor to observed line differences in RFI in the phenotypic comparison experiment, the impact of including IMF (pre adjusted for off-test weight) as an additional covariate in the model for RFI was evaluated. Results showed that this only slightly decreased the estimated line

difference in RFI, from -96 to -87 g/d. Thus, IMF was not a large factor associated with differences in RFI. This does, however, not preclude differences in other fat depots to contribute to the observed line differences in RFI. Also, LMA was not included in the model adjustment for RFI in this study because, as Johnson et al. (1999) indicated, LMA was not a large factor beyond ADG and BF associated with RFI. Johnson et al. (1999) compared RFI adjusted for ADG, and BF with RFI adjusted for ADG, BF, and LMA, and the results showed RFI heritability (0.11 vs. 0.10 respectively), litter variance, and error variance components were all very similar between these two adjustments.

Table 2.7 Frequencies of the *calcr* genotype for the low RFI and control line in generation 4 parity 2

Line	Calcr genotype	Frequency in all pigs genotyped	Frequency in pigs evaluated
Select	11	0.21	0.25
	12	0.58	0.45
	22	0.21	0.30
Control	11	0.15	0.17
	12	0.45	0.46
	22	0.40	0.37

There are a number of aspects of the design of the direct line comparison that could have affected results from this comparison, although none are expected to have a major effect that changes conclusions from this comparison, as explained in the following. The gilts that were evaluated in the direct line comparison were not a random sample of gilts produced in the second parity of the 4th generation, but were partially chosen based on their genotype for *calcr* to obtain sufficient numbers per genotype. But, as shown in Table 2.7, genotype frequencies for the *calcr* gene polymorphism among pigs that were included in the comparison for the low RFI and control lines (92 and 76 gilts) were very similar with the frequencies observed among all pigs that were genotyped (175 gilts in the low RFI line and 91 gilts in the control line). Therefore, including *calcr* genotypes in the experiment and evaluating a sample of pigs that was not completely random is expected to have very limited impact on observed line differences. Also, in the direct line comparison, pigs from the two lines were mixed, which may result in some bias by behavioral interactions between lines

because selection for low RFI may lead to changes in behavior. But this bias is not expected to be large. Moreover, the alternative design of separating pigs by pen would have substantially reduced power to detect any differences. Thirdly, the standard errors of differences on direct phenotypic line comparison include drift variance at least partially because the litter is included as a random effect in the model, which accounts for relationships due to sire and dam, and litter was used as the experimental unit to test for line differences. Including all the drift variance will increase standard errors of differences to some degree and, correspondingly, will increase P-values to some degree. These changes will, however, not change our conclusions because the line differences for RFI and ADFI were highly significant ($p=0.002$ and $p<0.0001$, respectively) and a larger SE will make difference in ADG, BF, and LMA even less significant.

In this selection experiment, selection was on RFI, derived using phenotypic regression of feed intake on ADG and BF. There are other ways of selection to improve feed efficiency, as Kennedy et al. (1993) suggested. One option is to use genetic rather than phenotypic regressions to adjust feed intake for ADG and BF. An equivalent strategy is to select on a restricted selection index, i.e. an index of ADFI, ADG, and BF, restricted to hold ADG and BF constant. These two selection strategies may have reduced correlated responses in ADG and BF but require accurate estimates of genetic correlations among ADG, BF, and ADFI, which were not available at the start of the selection experiment.

Comparison with Other Selection Experiments

Results of a similar selection experiment on RFI that is ongoing in France have been reported by Gilbert et al. (2006). In that study, divergent selection for RFI is practiced in a Large White population, with RFI measured on group-housed males between 35 and 95 kg body weight, selection of males based on their phenotype for RFI predicted from a selection index of ADFI, ADG, and BF that was derived from prior studies in the same population, and random selection of females. To evaluate response to selection, castrated males and females from second parity litters were slaughtered at an average body weight of 107 kg, and measured for carcass traits (Gilbert et al. 2006). Using data from the first 3 generations, Gilbert et al. (2006) estimated heritabilities for RFI, ADFI, ADG, and BF at 0.15, 0.17, 0.25,

and 0.62, respectively. The estimated difference between the high and low RFI lines after 3 generations was about 0.3 phenotypic SD for RFI and about 0.2 SD for ADFI. These responses are substantially lower than those we observed between the low RFI and control lines after 4 generations (about 0.9 phenotypic SD for RFI and 0.9 SD for ADFI), especially considering the uni- vs. bi-directional design of our experiment.

To get some understanding of potential causes for the differences in responses in RFI between the 2 studies (the study of Gilbert et al. (2006) and our own study), predicted asymptotic (based on the Bulmer effect) responses in RFI for these 2 studies given their respective estimated genetic parameters were calculated using the SelAction program (Rutten and Bijma, 2001). For the Gilbert et al. (2006) study, using a realized selection intensity of 1.6 (selected proportion of 6.7%) for males and 0 for females, and selection on own phenotype for a trait with a heritability of 0.15, predicted divergent response in RFI over 3 generations was $0.114\sigma_p \times 2 \times 3 \approx 0.7\sigma_p$, which is relatively higher than the observed response of 0.3 SD. In our study, response to selection on BLUP EBV was approximated by a pseudo BLUP index of own phenotype and phenotype on 1 full-brother for males and phenotype on 2 full-brothers for females, in addition to information from sire and dam BLUP EBV for both males and females. Using a heritability of 0.29, resulting asymptotic accuracies of selection were 0.54 for males and 0.31 for females, which using selection intensities of 1.63 for males (13% selected) and 1.06 for females (35% selected), resulted in a predicted response of $0.3\sigma_p \times 4 = 1.2\sigma_p$ after 4 generations, which is close to the 0.9 SD of response we observed based on EBV. These calculations show that there may be other potential reasons for the large difference in response for RFI between our study and that of Gilbert et al. (2006), besides use of different electronic feeders (ACEMA[®] vs. FIRE[®]), selection in a different breed population (Large White vs. Yorkshire), use of a different test period (35 to 95 kg vs. 40 to 115 kg body weight), and their selection only on the male side and based on own phenotype for RFI rather than EBV.

Gilbert et al. (2006) reported that the low RFI line tended to have less BF, similar to our result. In contrast to our results, Gilbert et al. (2006) reported significant correlated responses in several carcass traits; the low RFI line had significantly lower pH, lighter meat color, heavier carcass weight (increased dressing percent) and lean cuts (weight of loin). In

comparison, our data showed no significant differences ($P>0.10$) between the lines for pH, meat color, carcass weight, or LMA, although the low RFI line tended to have slightly lower pH, darker meat color, lighter carcass weights, and larger LMA. These differences in correlated responses between the 2 studies may be because of population and other differences; our study only evaluated gilts for carcass traits vs. castrated males and gilts in the Gilbert et al. (2006) study.

Gilbert et al. (2006) reported estimates of genetic correlations of RFI with ADFI, ADG, and BF of 0.38, -0.16, and -0.15, respectively, which are similar to the estimates of genetic correlations of RFI with ADFI (0.52) and BF (-0.14) in our results, but the estimate of the genetic correlation between RFI and ADG was of opposite sign than our estimate (0.17). Kennedy et al. (1993) showed that, although RFI is phenotypically independent of the component traits, it is not genetically independent, and the sign and magnitude of the genetic correlations are influenced by the genetic and environmental correlations with feed intake.

Out of interest, we also predicted correlated responses to selection on RFI in our study, using the estimated genetic correlations and the program SelAction. Correlated responses for ADFI and ADG from selection on RFI were predicted at -178 g/d and -22 g/d, respectively, in the fourth generation, similar to the observed values of -202 g/d and -39 g/d. The predicted correlated response for BF was 0.9 mm, which is of opposite sign from the observed -0.37 mm. The reason is that the estimated genetic correlation of -0.14 between RFI and BF with a large standard error is in opposite direction to the observed selection response.

Regression Coefficients for ADG and BF

The partial regression coefficients of ADFI on ADG and BF, when analyzing ADFI to calculate RFI, approximately can be interpreted as the average daily feed (kg) required for lean meat growth (kg) and for deposition of an additional 1 mm of BF, respectively. These coefficients can be compared with expected energy requirements for lean meat growth and for BF deposition. NRC (1998) showed that estimates for the energy costs of protein retention range from 6.8 to 14.0 Mcal of ME/kg, with a mean of 10.6 Mcal of ME/kg. Estimates for the energy costs of fat deposition range from 9.5 to 16.3 Mcal of ME/kg with a mean of 12.5 Mcal of ME/kg. Based on these estimates, the average energy required for 1 kg

of carcass fat-free lean tissue growth can be calculated as: $10.6/(2.55 \times 3.44) = 1.21$ kg of feed per kilogram of growth (range from 0.78 to 1.60), where 2.55 represents the kilograms of carcass fat-free lean tissue per kilogram of whole-body protein (NRC, 1998) and 3.44 is the energy density of feed used in the RFI selection project in Mcal/kg. This result is very close to the partial regression coefficients for ADG, while holding on-test age and BF constant, found in our analyses, which ranged from 1.37 to 1.99, excluding the apparent outlier result from parity 1 of generation 4 (Table 2.6). Feed required for a 1 mm increase in 10th rib BF was calculated as follows: a 1 mm increase in last rib BF was estimated to correspond to 1.12×0.78 kg of whole body lipid retention by Whittemore (2001); the estimated regression coefficient of last rib BF on 10th rib BF from our carcass data was 0.57; the test length was 105 d on average in our Yorkshire population; so, after ignoring on-test BF, which was small, this results in $0.57 \times 1.12 \times 0.78 \times 12.5 / (3.44 \times 105) = 0.017$ (range from 0.013 to 0.023) kg of extra feed required per day on average for a 1 mm increase in off-test 10th rib BF. This number is close to the partial regression coefficients for BF obtained while holding on-test age and ADG constant, which ranged from 0.011 to 0.023, excluding the apparent outlier result from parity 1 of generation 3 (Table 6).

Summary and Implications

The results of this study show that a substantial proportion of variation in feed consumption in growing pigs is unrelated to growth and backfat. RFI is a heritable trait and selection for RFI can significantly decrease the feed required for a given rate of growth and backfat. These results are important for developing strategies to select for feed efficiency in pigs. Feed efficiency has increased in importance in recent years and is expected to remain important, because of the increasing demand on feed crops and on land for bio-fuel production. Although intense selection for lean growth has significantly improved feed efficiency in pork production, further improvements require direct selection on feed intake and, specifically, on components of feed intake that are independent of lean growth. This is, however, prohibited by the difficulty and expense of recording feed intake on large numbers of animals, but possible if the genes responsible for differences in feed intake and efficiency are known. A thorough understanding of mechanisms that control feed intake and energy

metabolism will be needed to discover such genes and to utilize genetic information on feed intake in a manner that will enhance production efficiency. The Yorkshire selection lines described here can be an important resource for such research into the physiological and genetic (genomic) basis of feed efficiency.

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CHAPTER 3. LONGITUDINAL ANALYSIS OF BODY WEIGHT AND FEED INTAKE IN SELECTION LINES FOR RESIDUAL FEED INTAKE IN PIGS

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Abstract

A selection experiment for reduced residual feed intake (RFI) in Yorkshire pigs consists of a line selected for lower RFI (LRFI) and a random control line (CTRL). Longitudinal measurements of daily feed intake (DFI) and body weight (BW) from generation 5 of this experiment were used. The objectives of this study were to evaluate the use of random regression (RR) and non-linear mixed models to find the best RR models to predict DFI and BW for individual pigs, accounting for the substantial missing information that characterizes these data, and to evaluate the effect of selection for RFI on BW and DFI curves. Forty RR models with different-order polynomials of age as fixed and random effects, and with homogeneous or heterogeneous residual variance by month of age, were fitted for both DFI and BW. Based on predicted residual sum of squares (PRESS) and residual diagnostics, the quadratic polynomial RR model was identified to be best, but with heterogeneous residual variance for DFI and homogeneous residual variance for BW. Compared to the simple quadratic and linear regression models for individual pigs, these RR models decreased PRESS by 1% and 2% for DFI and by 42% and 36% for BW on boars and gilts, respectively. Given the same number of random effects as the polynomial RR models, i.e., two for BW and one for DFI, the non-linear Gompertz model predicted better than the polynomial RR models but not as good as higher order polynomial RR models. After five generations of

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selection for reduced RFI, the LRFI line had a lower population curve for DFI and BW than the CTRL line, especially towards the end of the growth period.

Key words: Longitudinal Analysis, Pigs, Residual Feed Intake, Selection

Introduction

Feed efficiency is a very important economic trait in swine production. For production purposes, feed efficiency is usually defined as the ratio of average daily body weight gain (ADG) to average daily feed intake (ADFI) or as its reciprocal, feed conversion ratio. In recent years, the swine industry has increasingly used electronic feeders in recording individual daily feed intake (DFI) and body weight (BW) on group-housed pigs to improve feed efficiency. Measurements of DFI and BW are typically longitudinal along the growth trajectory of pigs.

Longitudinal measurements of DFI and BW for a given pig tend to be correlated. One simple approach to deal with longitudinal measurements is to reduce the longitudinal measures to a single summary for each animal and then analyze each summary variable. For example, longitudinal DFI records are often summarized as ADFI for further analysis. Diggle et al. (2002) referred to this as two-stage analysis. Random regression models (Schaeffer and Dekkers, 1994) are other suitable option for analysis of longitudinal data on DFI and BW. Such models use data from all pigs simultaneously and allow estimation of individual and population curves. Schaeffer (2004) presented a thorough review on the application of random regression (RR) models in animal breeding. As one of the first applications to data other than milk production in cattle, Andersen and Pedersen (1996) applied RR models to analyze growth and food intake curves for pigs. Non-linear mixed models, e.g., the Logistic and Gompertz models, are another option for analysis of DFI and BW data. Whittemore et al. (1988) used the Gompertz function to model body weight of pigs over time on a pig-by-pig basis. Ratkowsky (1990) presented a thorough review of commonly used non-linear regression models (e.g., the Logistic and Gompertz models) and their statistical properties.

In practice, longitudinal measurements of DFI and BW data are often missing for substantial parts of growth period, including at the beginning and end. Major missing data come from switching of pigs between electronic and commercial feeders to enlarge the test

capacity because of high expense of electronic feeders (Von Felde et al. 1996; Eissen et al. 1999; Schulze et al. 2001; Casey 2003), and data errors and malfunction of electronic feeders (Eissen et al. 1998; Casey et al. 2005). Several studies have shown that missing DFI information on different parts of the growth period had a limited effect on the accuracy of evaluating ADFI (Eissen et al. 1999; Casey 2003). However, there have been few studies on the effect of missing data on evaluation of feed intake and body weight curves, which requires sophisticated statistical models to inter- and extrapolate DFI and BW curves for individual pigs. Thus, the first objective of this study was to develop and compare RR models and non-linear mixed models for analysis of DFI and BW in pigs with substantial missing data in order to identify the best model to predict DFI and BW curves for individual pigs. Data used for this study are from a selection experiment in Yorkshire pigs for reduced residual feed intake (RFI) at Iowa State University (Cai et al., 2008). The selection experiment consists of a line selected for lower residual feed intake (LRFI) for 5 generations and a randomly selected control line (CTRL). Thus, the second objective of this study was to evaluate the effect of selection for reduced RFI on DFI and BW population curves. These studies will bring opportunities for the swine industry to directly select growth and feed intake curves to improve feed efficiency.

Materials and Methods

Experiment Design and Data Collection

Pigs from the 5th generation of the LRFI and CTRL lines of the residual feed intake selection experiment conducted at Iowa State University were used in this study. All procedures with pigs were approved by the Iowa State University Institutional Animal Care and Use Committee. The protocol of the selection experiment was specified in detail by Cai et al. (2008). Selection was based on estimated breeding value (EBV) for RFI. The data used in this study follow a randomized complete block design with line (LRFI vs. CTRL) as the investigating factor and pen as the block factor. A total of 192 boars from the first parity of generation 5 were put into 12 pens at ~90 d of age and ~40 kg of body weight for evaluation of growth and feed intake. Sixteen boars from the LRFI and CTRL lines were assigned to each pen by body weight and age, balancing to the extent possible across line within pen.

Pigs that got sick or died were removed from their pens and pigs were taken off test on an individual basis when they reached 115 kg of body weight. When only three pigs were left in a pen, they were all taken off test, resulting in some lighter off-test body weights. A total of 151 pigs, 64 LRFI and 87 CTRL line boars with off-test body weight greater than 102 kg were used for analysis.

The experiment was replicated using 192 gilts from the second parity of generation 5. The same boars and sows that produced parity 1 of generation 5 were used to produce these gilts with the same mating design as parity 1. Besides gender, the only difference between the protocols from these two replicated experiments was that in order to get sufficient numbers of gilts for slaughter, gilts were off-tested in three groups instead of on an individual basis. A total of 162 pigs, 75 LRFI and 87 CTRL line gilts, with off-test body weight greater than 102 kg were used for analysis.

Six of the twelve pens were equipped with one single-space FIRE® feeder for FI recording. To allow all pigs to obtain feed intake data, pens were switched every 2 wk. Alternate pens were in the same room and had feeding equipment equivalent to the FIRE® feeders so as not to induce an acclimation period. The FI data from the day of switching were not used. Body weights were measured bi-weekly. Longitudinal measurements of DFI and BW data on these pigs were from ~3 to ~8 months of age. The average number of measurements of BW and DFI per pig is shown in Table 3.1.

Table 3.1 Frequency of measurements on daily feed intake and body weight per pig

	Body weight				Daily feed intake			
Number of measurements	7	8	9	10	25-50	51-60	61-70	71-85
Number of boars	36	50	36	29	21	52	55	23
Number of gilts	41	2	77	42	91	35	28	8

Model Selection and Statistical Analysis

Data from the two parities were analyzed separately using random regression and non-linear mixed model analyses. For comparison, data were also analyzed using simple linear

and quadratic models fitted on a pig-by-pig basis. The models used and the process of model selection will be described in the following.

Simple individual pig models. Cai et al. (2008) fitted simple quadratic and linear regressions of DFI and BW against days of age for each pig separately. For the purpose of comparison, these two simple regression models on a pig-by-pig basis were also fitted in this study by the MIXED procedure of SAS (SAS Institute, 2008).

Random regression models. Let Y_{hijk} denote either BW or DFI at k days of age (from 64 to 230 days for boars and from 80 to 253 days for gilts) for pig j ($j=1,2,\dots,151$ for boars and $j=1,2,\dots,162$ for gilts) of line i ($i=1,2$; 1 is LRFI and 2 is CTRL) raised in pen h ($h=1,2,\dots,12$). For numerical reasons, age was adjusted as $t_k = (age - 90)/100$, where 90 is the average on-test age (days). Random regression models with different-order polynomials of age as fixed and random effects, and with homogeneous residual variance, were fitted for both DFI and BW using the MIXED procedure of SAS (SAS Institute, 2008). Taking the model with quadratic polynomials of age as fixed and random effects as an example, the model can be denoted as: $y_{hijk} = Pen_h + \beta_{0i} + \beta_{1i}t_k + \beta_{2i}t_k^2 + b_{0j} + b_{1j}t_k + b_{2j}t_k^2 + \varepsilon_{jk}$, where $\beta_{0i} + \beta_{1i}t_k + \beta_{2i}t_k^2$ are the fixed effects representing the population curve; $b_{0j} + b_{1j}t_k + b_{2j}t_k^2$ are the random effects representing the individual pig curve; Pen is the fixed block effect to account for systematic difference between pens and feeding stations. The distribution assumptions for the random effects were multivariate normal:

$$b_j = \begin{pmatrix} b_{0j} \\ b_{1j} \\ b_{2j} \end{pmatrix} \sim N \left(\begin{pmatrix} 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_{11} & \sigma_{12} & \sigma_{13} \\ \sigma_{12} & \sigma_{22} & \sigma_{23} \\ \sigma_{13} & \sigma_{23} & \sigma_{33} \end{pmatrix} \right), \text{ which was independent of}$$

residuals $\varepsilon_{jk} \sim N(0, \sigma_e^2)$. The design vector of random coefficients for the k th observation on the j th pig was $Z_{jk} = (1, t_k, t_k^2)$. The method of residual maximum likelihood (REML) was used to estimate the variance components. Based on this model, the variance of the response variable Y changes with age as:

$$Var(Y_{hijk}) = \sigma_{11} + 2t_k\sigma_{12} + t_k^2(2\sigma_{13} + \sigma_{22}) + 2t_k^3\sigma_{23} + t_k^4\sigma_{33} + \sigma_e^2.$$

In matrix form, the model is written as $\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma} + \boldsymbol{\varepsilon}$ with $E(\mathbf{Y}) = \mathbf{X}\boldsymbol{\beta}$ and $Var(\mathbf{Y}) = \mathbf{V} = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R}$, where $\boldsymbol{\gamma} \sim N(\mathbf{0}, \mathbf{G})$ and $\boldsymbol{\varepsilon} \sim N(\mathbf{0}, \mathbf{R})$. Estimates of $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ can be written as $\hat{\boldsymbol{\beta}} = (\mathbf{X}'\hat{\mathbf{V}}^{-1}\mathbf{X})^{-1}\mathbf{X}'\hat{\mathbf{V}}^{-1}\mathbf{y}$ and $\hat{\boldsymbol{\gamma}} = \hat{\mathbf{G}}\mathbf{Z}'\hat{\mathbf{V}}^{-1}(\mathbf{y} - \mathbf{X}\hat{\boldsymbol{\beta}})$, respectively. The variance of the response at different ages based on the RR model can be estimated by substituting the estimated variance components for \mathbf{G} and \mathbf{R} in the above equation.

A total of 20 different RR models were fitted by varying the order of fixed and random polynomials. Fixed-effect polynomials of age were fitted up to the 5th order, while random-effect polynomials of age were fitted up to the highest order polynomials of the fixed effects in the model. That is, if the fixed effect in the model was a quadratic polynomial, three different random-effect polynomials were fitted: 1) intercept only; 2) intercept and linear term of age; 3) intercept, linear and quadratic term of age. The same set of 20 linear mixed models were also fitted with heterogeneous residual variances by month of age, allowing for a different residual variance for each of 6 months of age in view of possible different variation in different periods of growth. Six different periods (each of 6 months of age) were chosen to balance between the numbers of residual variance parameters to estimate and the numbers of available observations within each period for estimating them. Residual variances in different periods were assumed independent of each other. This is the same specification as models with homogeneous residual variances because the covariance between the observations had already been accounted by the covariance between random coefficients.

Non-linear mixed models. Logistic and Gompertz non-linear mixed models were fitted to the DFI and BW data using the NLMIXED procedure of SAS (SAS Institute, 2008). The random effects were estimated by the empirical Bayes method. Using the adaptive Gaussian quadrature method to do integral approximations, the NLMIXED procedure maximized the approximate likelihood integrated over the random effects. The number of quadrature points was set to 50 and the dual quasi-Newton algorithm was used as the optimization technique. Model details are described below.

To avoid convergence problems, the DFI and BW data were pre-adjusted for the effect of pen (12 pens in this study) before non-linear-model analysis, using the estimates from the selected RR models for DFI and BW, which were those with quadratic polynomials of age as both fixed and random effects. Then, for BW, the Logistic and Gompertz non-linear mixed

models were fitted using the following non-linear mixed model equations:
 $Y_{ijk} = \alpha_{1ij} / (1 + \exp(-(age_k - \alpha_{2i}) / \alpha_{3ij})) + \varepsilon_{ijk}$ for the Logistic model and
 $Y_{ijk} = \alpha_{1ij} \times \exp(-\exp(-(age_k - \alpha_{2i}) / \alpha_{3ij})) + \varepsilon_{ijk}$ for the Gompertz model. For both models, α_{1ij} represents the mature body weight for pig j in line i ; α_{2i} represents the fixed inflection point (number of days) for line i ; α_{3ij} represents the decay parameter for pig j in line i . Only two random effects α_{1ij} and α_{3ij} were fitted because of convergence problems when more random effects were fitted. Distribution assumptions for the random effects were multivariate normal:

$$\alpha = \begin{pmatrix} \alpha_{1ij} \\ \alpha_{3ij} \end{pmatrix} \sim iid N \left(\begin{pmatrix} \alpha_{1i} \\ \alpha_{3i} \end{pmatrix}, \begin{pmatrix} \sigma_{11} & \sigma_{12} \\ \sigma_{12} & \sigma_{22} \end{pmatrix} \right), \text{ which were independent of } \varepsilon_{ijk} \sim N(0, \sigma_e^2) .$$

Because the random effects enter both the Logistic and Gompertz mixed models non-linearly, the variance of the response for the k th observation on the j th pig at different ages was derived by the delta method (Casella and Berger, 2002).

For DFI, the same Logistic and Gompertz non-linear mixed models were fitted as for BW, except that only one random effect α_{1ij} was fitted for DFI because of convergence problems. Therefore, for both the Logistic and Gompertz non-linear models of DFI, α_{3i} represents the fixed decay parameter across pigs for line i , in contrast to α_{3ij} for BW, which represented the decay parameter for pig j in line i . The distribution assumption for the random effect was $\alpha_{1ij} \sim N(\alpha_{1i}, \sigma_{11})$, independent of $\varepsilon_{ijk} \sim N(0, \sigma_e^2)$.

Model selection. Model comparison and selection was based on statistics of predicted residual sum of squares (PRESS) because prediction is the most important focus here. The basic concept of the PRESS statistic is to fit the model to a subset of the data, use the resulting estimates to predict observations in the rest of the data, and compute the sum of squares of predicted residuals. A smaller PRESS indicates a model with better predictive ability. The PRESS residuals given by the MIXED procedure of SAS (SAS Institute, 2008) are marginal PRESS residuals, i.e., they are not conditional on random effects but calculated as $\hat{\mathbf{e}}_{m(-m)} = \mathbf{y}_m - \mathbf{X}_m \hat{\boldsymbol{\beta}}_{(-m)}$, with notations explained below. However, to evaluate the

predictability of the model reasonably, PRESS residuals should be conditional on random effects. Therefore, a macro was written to compute conditional PRESS residuals as described in the following.

The data from each pig (observed feed intake on each day for DFI data and observed bi-weekly body weight for BW data) were randomly divided into 9 parts. To compute the PRESS, each time one part of the data (\mathbf{y}_m , with $m = 1$ to 9) was set aside and the model was built based on the other 8 parts of the data ($\mathbf{y}_{(-m)}$). The estimate of $\boldsymbol{\beta}$ obtained from data $\mathbf{y}_{(-m)}$ will be denoted by $\hat{\boldsymbol{\beta}}_{(-m)}$. Prediction of the part of data \mathbf{y}_m based on data $\mathbf{y}_{(-m)}$ was $\hat{\mathbf{y}}_{m(-m)} = \mathbf{X}_m \hat{\boldsymbol{\beta}}_{(-m)} + \hat{\mathbf{C}}_{m(-m)} \hat{\mathbf{V}}_{(-m)}^{-1} (\mathbf{y}_{(-m)} - \mathbf{X}_{(-m)} \hat{\boldsymbol{\beta}}_{(-m)})$, where $\hat{\mathbf{C}}_{m(-m)}$ is the estimates of the model-based covariance matrix between \mathbf{y}_m and $\mathbf{y}_{(-m)}$, and $\hat{\mathbf{V}}_{(-m)}$ is the estimates of the model-based variance matrix of $\mathbf{y}_{(-m)}$. The conditional PRESS residual was computed as $\hat{\boldsymbol{\epsilon}}_{m(-m)} = \mathbf{y}_m - \hat{\mathbf{y}}_{m(-m)}$. This procedure was used for prediction of each of the 9 subsets and the PRESS statistic was computed as $\text{PRESS} = \sum_{m=1}^9 \hat{\boldsymbol{\epsilon}}_{m(-m)}' \hat{\boldsymbol{\epsilon}}_{m(-m)}$. A similar procedure was used to compute the PRESS statistic for the non-linear mixed models.

The forecast ability of the models to account for missing data at the beginning (90 to 120 days old) and end (181 to 210 days old) of the test period was also evaluated. For this evaluation, data from ages younger than 121 days for one pig were set aside each time and the model was built based on the remaining data for that pig and all data for all other pigs. The conditional PRESS residuals were then calculated for the data from 90 to 120 days of age for that pig by the above method. After repeating this one-pig-at-a-time for all pigs, the PRESS statistics were summarized for all pigs from 90 to 120 days old. Similarly, the forecast ability of the model at the end was evaluated by setting aside data with age older than 180 days for one pig at a time. Because these approaches are computationally intensive, only quadratic and cubic polynomial RR models and the Gompertz non-linear mixed model were evaluated, along with the simple quadratic and linear regression on age on a pig-by-pig basis for DFI and BW.

Results

Model Selection on Random Regression Models

Figure 3.1 shows the PRESS statistics for DFI and BW on gilts and boars from 40 different RR models with different-order polynomials of age as fixed and random effects, and with homogeneous or heterogeneous residual variance by month of age. The PRESS statistics are expressed as a percentage of the PRESS statistics from using simple quadratic and linear regression on age on a pig-by-pig basis. For both boars and gilts, RR models with at least quadratic-order polynomials for random effects for DFI and at least linear order for BW had smaller PRESS statistics than the individual pig models. Heterogeneous residual variance models had PRESS statistics that were similar to those from homogeneous residual variance models for both sexes and both traits.

Table 3.2 shows that the quadratic and cubic polynomial RR models decreased PRESS statistics dramatically for DFI and BW at the beginning (90 to 120 days old) and end (181 to 210 days old) of the test period compared with the individual pig models. This indicates that RR models have a much better forecast ability than the individual pig models at the beginning and end of the test period. Table 3.2 also shows that, in most cases, cubic polynomial RR models had smaller PRESS statistics than quadratic polynomial RR models for both DFI and BW. However, for DFI at the end of the test period for boars, quadratic RR models had smaller PRESS than cubic RR models.

For all models and both traits, the PRESS statistics decreased with increasing order of polynomials of age as random effects but at a decreasing rate (Figure 3.1). With quadratic polynomials for both fixed and random effects, residuals checking showed no clear trend of residuals along fitted values but obvious unequal residual variance for DFI. When models with heterogeneous residual variance by month of age were fitted for DFI, the unequal residual variance was much improved. This indicates that the heterogeneous residual variance models behaved better for DFI. Based on these results, quadratic polynomial random regression models were identified to be “best” for both DFI and BW, but with heterogeneous residual variance for DFI and homogeneous residual variance for BW. These models had the smallest possible order based on both PRESS and residual diagnostics, although they did not have the smallest PRESS among all evaluated polynomials.

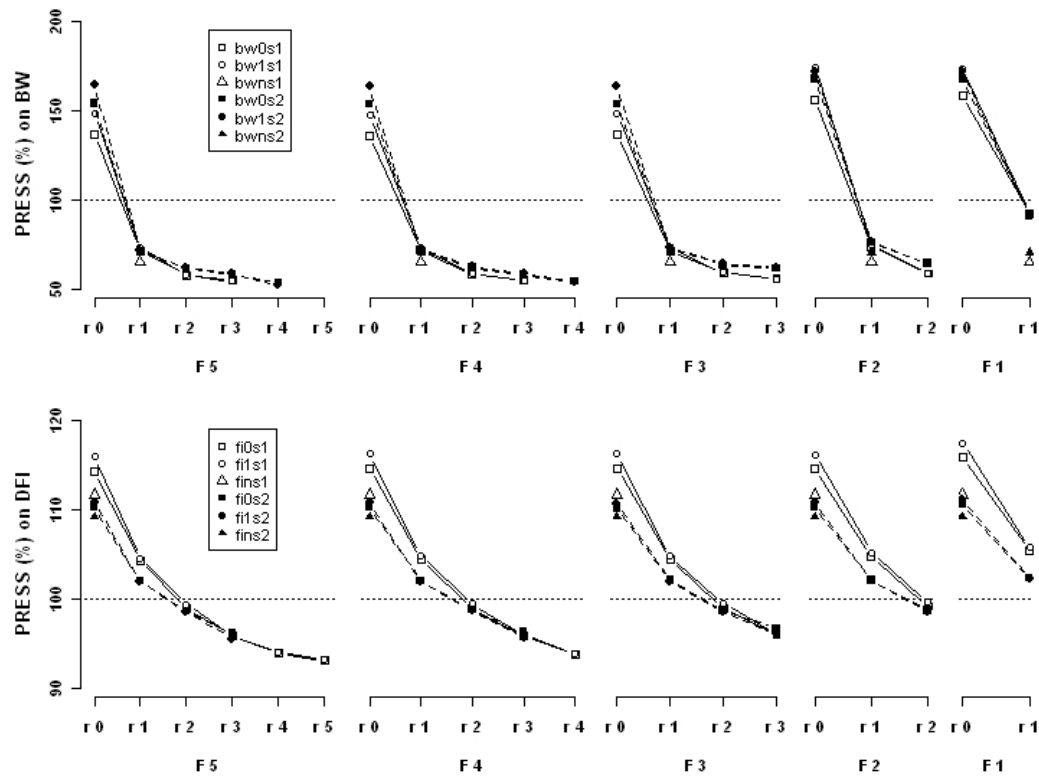


Figure 3.1 PRESS statistics for random regression models. DFI: daily feed intake; BW: body weight. F: the fixed effects of polynomials of age for linear mixed models, e.g., F2 representing intercept, linear and quadratic term of age as the fixed effect. r: the random effects of polynomials of age for linear mixed models, e.g., r2 representing intercept, linear and quadratic term of age as the random effect. bw0s1 and bw0s2: linear mixed models with homogeneous residual variance for BW for boars and gilts, respectively. bw1s1 and bw1s2: linear mixed models with heterogeneous residual variance for BW for boars and gilts, respectively. bwns1 and bwns2: Gompertz non-linear mixed models for BW for boars and gilts, respectively. fi0s1 and fi0s2: linear mixed models with homogeneous residual variance for DFI for boars and gilts, respectively. fi1s1 and fi1s2: linear mixed models with heterogeneous residual variance for DFI for boars and gilts, respectively. fins1 and fins2: Gompertz non-linear mixed models for DFI for boars and gilts, respectively. The PRESS statistics are relative percent of PRESS statistics from the models using simple quadratic and linear regression on age on a pig-by-pig basis for DFI and BW

Compared to the individual pig models of simple quadratic and linear regression on age, for predictability over the whole test period, the selected quadratic polynomial RR models decreased PRESS by 1% and 2% for DFI for boars and gilts and by 42% and 36% for BW

for boars and gilts. For forecast ability at the beginning and end of the test period, the selected quadratic polynomial RR models decreased PRESS from 41% to 87% for DFI and from 26% to 75% for BW compared to the individual pig models. Thus, compared to the individual pig models, the RR models made prediction of an individual pig's DFI and BW curves more robust and accurate, especially at the beginning and end of the growth period.

Table 3.2 Predicted residual sum of squares for both daily feed intake and body weight from growth period of 90 to 120 days old and 181 to 210 days old

Sex	Model			PRESS (%) on BW ⁶		PRESS (%) on DFI ⁶	
	Fixed ¹	Random ²	Residual ³	90-120 d	181-210 d	90-120 d	181-210 d
boars	quadratic	quadratic	homo	25	74	13	59
	cubic	cubic	homo	23	64	13	67
	quadratic	quadratic	hetero	24	78	14	59
	cubic	cubic	hetero	23	65	13	68
	Gompertz with unadjusted pen ⁴			30	76	14	47
	Gompertz with adjusted pen ⁵			29	76	14	46
gilts	quadratic	quadratic	homo	40	67	26	29
	cubic	cubic	homo	35	63	23	28
	quadratic	quadratic	hetero	41	70	27	29
	cubic	cubic	hetero	35	65	23	28
	Gompertz with unadjusted pen			44	69	28	29
	Gompertz with adjusted pen			43	68	27	29

¹Fixed: fixed effect in the model with quadratic representing quadratic polynomials of age and cubic representing cubic polynomials of age

²Random: random effect in the model with quadratic representing quadratic polynomials of age and cubic representing cubic polynomials of age

³Residual: the type of residual variance with homo representing homogeneous residual variance and hetero representing heterogeneous residual variance

⁴Gompertz with unadjusted pen: Gompertz nonlinear mixed model without pen effect pre-adjusted out for daily feed intake and body weight

⁵Gompertz with adjusted pen: Gompertz nonlinear mixed model with pen effect pre-adjusted out for daily feed intake and body weight based on the selected quadratic random regression models

⁶The Predicted residual sum of squares (PRESS) statistics are relative percent of PRESS statistics from the models using simple quadratic and linear regression on age on a pig-by-pig basis for daily feed intake (DFI) and body weight (BW)

Comparison of Random Regression Models and Non-linear Mixed Models

The Gompertz model forecasted better than individual pig models at the beginning (90 to 120 d) and end (181 to 210 d) of the test period for both traits (Table 3.2). The Gompertz model also predicted better than RR models with the same number of random effects, but not as good as RR models with higher order polynomials (Figure 3.1). Compared with the selected quadratic polynomial RR models, the Gompertz model had slightly poorer forecast ability at the beginning and end of the test period for BW (Table 3.2). However, the Gompertz model had comparable forecast ability to the selected RR models for DFI, especially for boars at the end of the test period (Table 3.2). Table 3.2 also shows that the forecast abilities of the Gompertz model with or without pre-adjustment for pen effect were very similar. The predictive ability of the Logistic model was similar to that of the Gompertz model (results not shown).

Estimated Standard Deviations

Estimated phenotypic standard deviations for DFI based on the Gompertz model increased slowly along the growth period for both sexes (Figure 3.2). Estimated standard deviations for DFI from the quadratic polynomial RR model were close to those for the Gompertz model from ~ 90 to ~ 180 days but increased sharply outside that range (Figure 3.2). Estimated standard deviations for BW from the quadratic polynomial RR and the Gompertz models had a similar increasing trend (Figure 3.3).

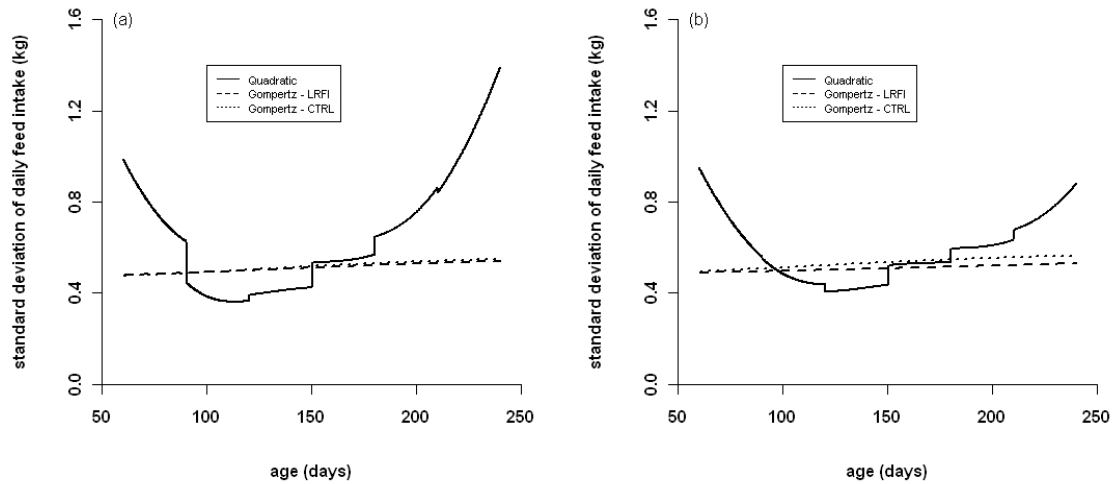


Figure 3.2 Estimated standard deviations of daily feed intake for (a) boars and (b) gilts. Quadratic: quadratic polynomial random regression model. Gompertz – LRFI: Gompertz non-linear mixed model for lower residual feed intake line. Gompertz – CTRL: Gompertz non-linear mixed model for control line

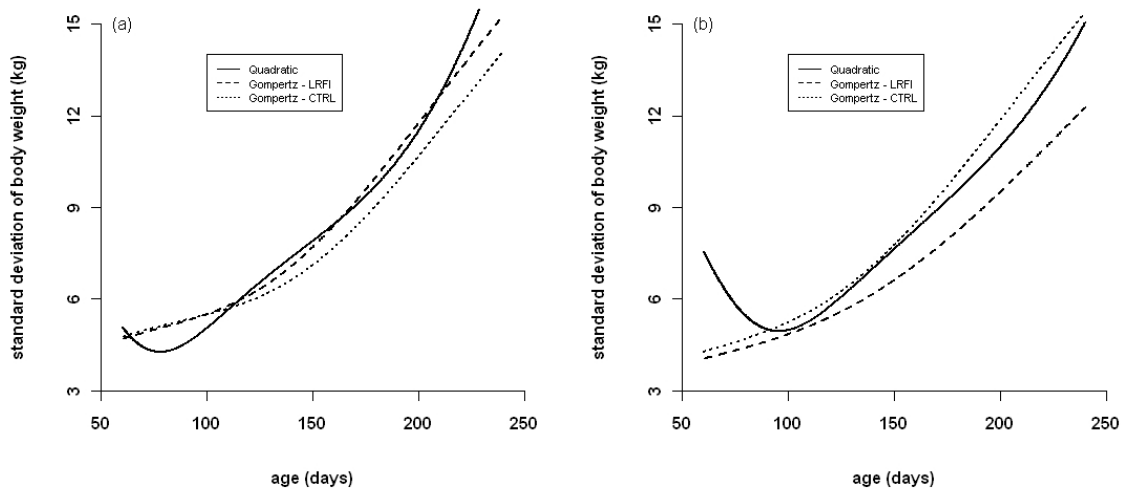


Figure 3.3 Estimated standard deviations of body weight for (a) boars and (b) gilts. Quadratic: quadratic polynomial random regression model. Gompertz – LRFI: Gompertz non-linear mixed model for lower residual feed intake line. Gompertz – CTRL: Gompertz non-linear mixed model for control line

Estimated Biological Parameters of the Gompertz Model

Based on the Gompertz model, LRFI boars had slightly lower mature feed intake (2.93 vs. 2.97 kg) and an earlier inflection point (80 vs. 84 d) for DFI than CTRL boars but

differences were not significant ($p > 0.1$) (Table 3.3). Boars from the LRFI line, however, had a significantly ($p = 0.06$) greater decay parameter (87 vs. 66 d) for DFI. Boars from the LRFI line had a significantly ($p = 0.03$) lower mature body weight (263 vs. 296 kg) and a significantly ($p = 0.08$) earlier inflection point (180 vs. 192 d) for BW than CTRL boars (Table 3.3). The decay parameter for BW was lower for LRFI boars (127 vs. 134 d) but not significant ($p > 0.1$). However, compared with CTRL gilts, LRFI gilts had a very significantly greater decay parameter for DFI (163 vs. 84 d with $p < 0.001$), a greater mature feed intake (3.31 vs. 2.66 kg with $p = 0.02$) and a later inflection point (86 vs. 57 d with $p = 0.04$) (Table 3.3). Gilts from the LRFI line also had a significantly ($p = 0.046$) higher mature body weight (296 vs. 266 kg), a significantly ($p < 0.001$) later inflection point (215 vs. 185 d), and a significantly ($p < 0.001$) greater decay parameter (168 vs. 136 d) for BW than CTRL gilts. Knap (2000) summarized previous estimates of mature body weights and the associated Gompertz growth rate parameters (equal to $1/\text{decay parameter}$ in this study) for growing pigs of eight genotypes. Estimates obtained from the current study are within the range summarized in Figure 3 of Knap (2000), which were ~180 to ~320 kg for mature body weight and ~0.005 to ~0.016 d^{-1} for the Gompertz growth rate parameter (corresponding to ~200 to ~63 days for the decay parameter in this study).

Table 3.3 Estimated parameters in the Gompertz non-linear mixed model for daily feed intake and body weight

Trait ¹	Sex	$\alpha_1 (\text{kg})^2$		$\alpha_2 (\text{days})^2$		$\alpha_3 (\text{days})^2$	
		LRFI ³	CTRL ³	LRFI ³	CTRL ³	LRFI ³	CTRL ³
DFI	Boars	2.93±0.17 ^{NS}	2.97±0.09 ^{NS}	80±4 ^{NS}	84±1 ^{NS}	87±11 [†]	66±5 [†]
	Gilts	3.31±0.29 [*]	2.66±0.16 [*]	86±13 [*]	57±3 [*]	163±23 ^{***}	84±15 ^{***}
BW	Boars	263±11 [*]	296±12 [*]	180±5 [†]	192±5 [†]	127±4 ^{NS}	134±4 ^{NS}
	Gilts	296±14 [*]	266±10 [*]	215±7 ^{***}	185±5 ^{***}	168±6 ^{***}	136±4 ^{***}

¹DFI: daily feed intake; BW: body weight

² α_1 : mature body weight or mature daily feed intake; α_2 : inflection point for both DFI and BW; α_3 : decay parameter for both DFI and BW

³LRFI: the line selected for lower residual feed intake; CTRL: the randomly selected control line

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; † $P < 0.10$; ^{NS} $P > 0.10$

Estimated Population Curves

Population curves for DFI (Figure 3.4) and BW (Figure 3.5) were based on estimated coefficients from the quadratic polynomial RR model and the Gompertz model. Selection for reduced RFI has led to a lower population curve for DFI for the LRFI than the CTRL line (Figure 3.4). Line differences (CTRL-LRFI) for DFI were small at the beginning (~90 d) and became larger later in the growing period. Population curves for DFI for boars from the quadratic polynomial RR were similar to those from the Gompertz model, except that curves from the RR model bended faster in the later parts of the growth period (Figure 3.4(a)). Population curves for DFI for gilts from the quadratic polynomial RR were higher than those from the Gompertz model (Figure 3.4(b)). Population curves for BW from the quadratic polynomial RR and the Gompertz model were similar (Figure 3.5). Selection for reduced RFI tended to lead to lower body weight for the LRFI than the CTRL line, especially during the later stages of the growth period.

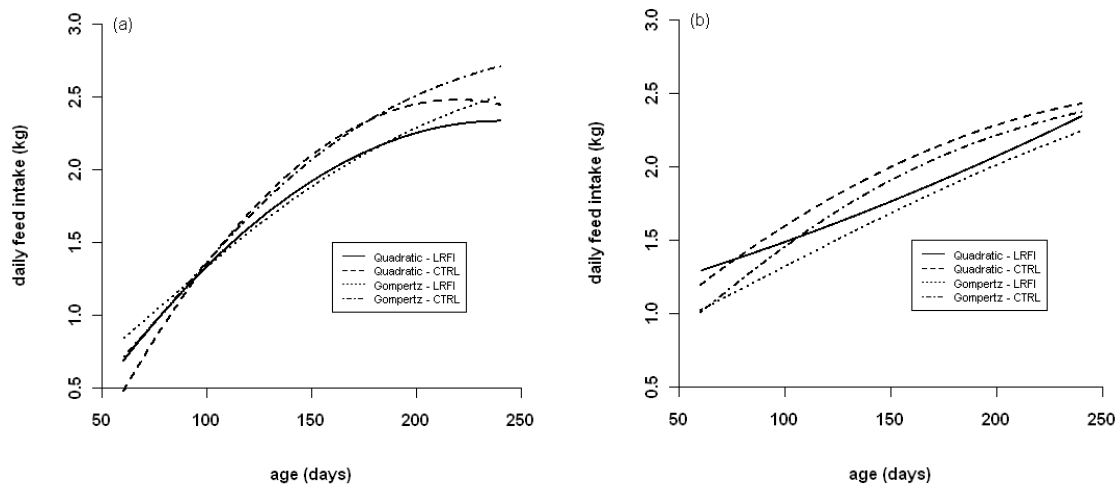


Figure 3.4 Estimated population curves of daily feed intake for (a) boars and (b) gilts. Quadratic – LRFI: quadratic polynomial random regression model for lower residual feed intake line. Quadratic – CTRL: quadratic polynomial random regression model for control line. Gompertz – LRFI: Gompertz non-linear mixed model for lower residual feed intake line. Gompertz – CTRL: Gompertz non-linear mixed model for control line

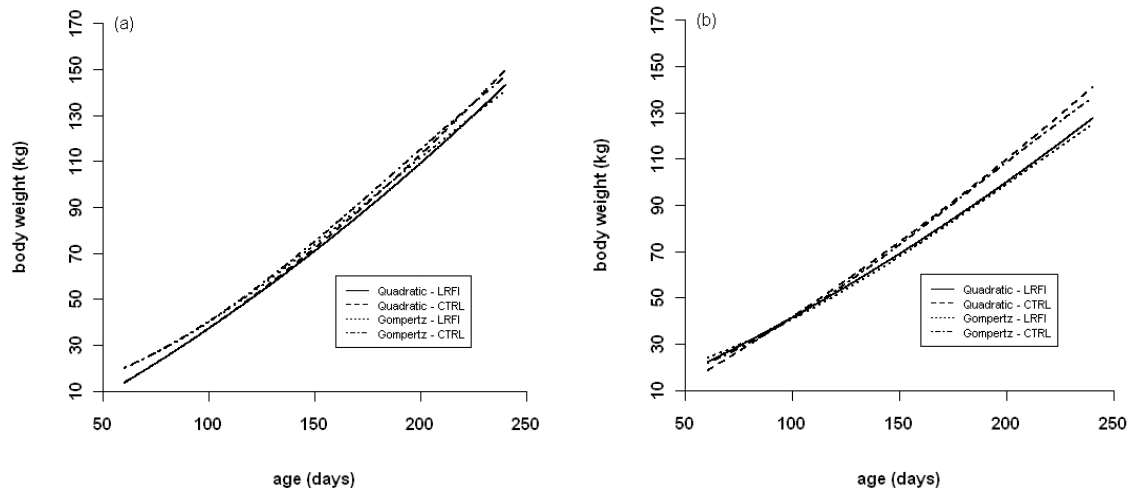


Figure 3.5 Estimated population curves of body weight for (a) boars and (b) gilts. Quadratic – LRFI: quadratic polynomial random regression model for lower residual feed intake line. Quadratic – CTRL: quadratic polynomial random regression model for control line. Gompertz – LRFI: Gompertz non-linear mixed model for lower residual feed intake line. Gompertz – CTRL: Gompertz non-linear mixed model for control line

Discussion

Random Regression Models

Polynomial RR models resulted in more robust and accurate predictions of an individual pig's DFI and BW curves than individual pig models. Random regression models are a compromise between estimates based only on individual pig's data and an overall estimate across all pigs. If a pig has outlier DFI and BW data, RR models will pull predictions toward the population curve. In addition, RR models allow estimation of population curves for different lines.

Care must be taken when using polynomial RR for data extrapolation because estimated variances for DFI from the RR model became erratic outside the range of the majority of data points (Figure 3.2). In addition, Lindsey (2001) warned “Care should be taken not to use polynomials of too high an order, usually not more than quadratic, because otherwise the model will be inherently unstable in replications of the data”. Typically, the higher the order of polynomials, the more dangerous data extrapolation becomes.

Based on decreases in PRESS, gains in accuracy from RR models were much greater for BW than for DFI. Compared to the individual pig models, the selected quadratic polynomial RR models only decreased PRESS by 1% and 2% for DFI for boars and gilts but decreased PRESS by 42% and 36% for BW for boars and gilts. One possible reason for the smaller gain in PRESS for DFI than BW is that DFI data are much noisier than BW data. The signal-to-noise ratio, i.e. the ratio of the mean to the standard deviation of a measurement, was ~ 3 for DFI and ~ 8 for BW on average over the test period. Thus, RR models may improve predictive accuracy more for data with a higher signal-to-noise ratio. The other possible reason was that BW is a cumulative trait but DFI is not. Typically, longitudinal measurements for a cumulative trait are more inter-correlated than for a non-cumulative trait. This stronger inter-correlation can be used by RR models to improve data prediction.

In this study, pen was included as a fixed effect, whereas in previous work (Cai et al. 2008), we fitted pen as a random effect. Cai et al. (2008) implemented a two-stage analysis method (Diggle et al., 2002) for longitudinal measurements of DFI and BW in the previous generations of this experiment. In the first stage, simple quadratic and linear regressions of DFI and BW were fitted for each pig to get a single summary of ADFI and ADG for that pig. Then, these summary variables were analyzed in the second stage. Pen was treated as the random effect when analyzing the summary variables of ADFI and ADG in the second stage because investigation of the variation of pens or feeding stations was one of interest in that study. The RR models of this study can be viewed as an extension of simple regression models of DFI and BW for individual pigs in the first stage. This hierarchical setting of RR models allows each pig within a pen to have its own regression coefficients, which are randomly deviated from their line (LRFI and CTRL) means. In this setting, it makes more sense to fit pen as the fixed block effect to account for systematic difference between pens and feeding stations.

Non-linear Mixed Models

Sandland and McGilchrist (1979) mentioned that polynomials may provide adequate descriptions of the observed data, but they provide little understanding of the biological data-generating mechanisms. In this study, it is hard to interpret the biological meaning of the

regression coefficients from the RR models. In contrast, non-linear models could represent biological data-generating mechanisms and their parameters usually have biological interpretations. As a result, non-linear models are more suitable for data extrapolation. In addition, non-linear models usually need fewer parameters than corresponding linear models for an equal fit to the data (Lindsey, 2001). In this study, the Gompertz non-linear model predicted better than RR models with the same number of random effects.

However, it is difficult for non-linear mixed models to handle complex experimental designs. In this study, both DFI and BW were pre-adjusted for pen effects before analyses by Gompertz and Logistic models to avoid convergence problems. Second, it is difficult to optimize non-linear models with multiple random effects. For example, when Gompertz and Logistic models were fitted to BW with three random effects or to DFI with two random effects, convergence problems occurred. This is the main reason why Andersen and Pedersen (1996) chose simpler linear models instead of non-linear models such as Gompertz and Logistic models.

Generally speaking, if the purpose of the model is data interpolation, and not about understanding the biological data-generating mechanism, polynomial RR models should be used because they are computationally simpler, more flexible, and easier to optimize than non-linear models. However, if the purposes of the model are to explore the biological data-generating mechanism and to do data extrapolation, the non-linear model would be a better option.

Pigs, as food animals, are usually slaughtered below the attainment of half of mature size (Kyriazakis and Whittemore, 2006). Correspondingly, pig breeding programs rarely collect growth performance and feed intake data through the whole growth period until maturity. In this study, pigs were measured repeatedly until they reached about 115 kg BW, which is far below maturity. Many pigs may not even arrive at the decelerating growth period. As a result, the three parameters of the Gompertz model were estimated with limited precision. This may also be one of possible reasons that high-order polynomial RR models predicted better than the Gompertz model.

In this study, we also found that differences between the LRFI and CTRL lines in estimates of coefficients from the Gompertz model for DFI and BW were not consistent

between boars and gilts. In addition to data from boars and gilts being obtained at different times and seasons, one possible reason for this inconsistency may be that the experimental protocol for off-testing differed between boars and gilts. Gilts were off-tested in three groups but boars were off-tested on an individual basis, which induced a shorter test period for most gilts. This may lead to less accuracy for estimation of parameters of the Gompertz model for gilts. For DFI, standard errors of estimated coefficients from the Gompertz model for gilts were larger than for boars.

Effect of Selection for Reduced RFI on DFI and BW Curves

In the lines used in this study, selection was based on estimated breeding value for RFI, with component traits of feed intake and growth averaged over the test period. Cai et al. (2008) reported that after four generations of selection, boars of the LRFI line consumed 202 g/d less feed and gained 39 g/d less weight than the CTRL line on average over the test period. This study showed that after five generations of selection for reduced RFI, the LRFI line had a lower population curve for DFI and BW than the CTRL line, especially towards the end of the growth period (Figure 3.4 and 3.5). This demonstrated that the difference in feed intake and growth between the LRFI and CTRL lines mostly comes from the late growth period. Lorenzo Bermejo et al. (2003) found that selection on average feed intake over the whole test period led to an increase of feed intake mainly in the second half of the test, which is similar with this study. The lower feed intake and body weight curves because of selection for reduced RFI also indicate that it is possible for the pig breeding industry to optimize growth and feed intake curves by selection.

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CHAPTER 4. GENETIC ANALYSIS OF LONGITUDINAL MEASUREMENTS OF PERFORMANCE TRAITS IN SELECTION LINES FOR RESIDUAL FEED INTAKE IN YORKSHIRE SWINE

A paper submitted to Journal of Animal Science

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Abstract

A 5-generation selection experiment in Yorkshire pigs for feed efficiency consists of a line selected for lower residual feed intake (LRFI) and a random control line (CTRL). The objectives of this study were to use random regression models to estimate genetic parameters for daily feed intake (DFI), body weight (BW), backfat (BF), and loin muscle area (LMA) along the growth trajectory and to evaluate the effect of LRFI selection on genetic curves for DFI and BW. An additional objective was to compare random regression models using polynomials (RRP) and spline functions (RRS). Data from ~3 to ~8 months of age on 586 boars and 495 gilts across 5 generations were used. The average number of measurements was 85, 14, 5, and 5 for DFI, BW, BF, and LMA, respectively. The RRP models for these four traits were fitted with pen by on-test group as fixed effects and second-order Legendre polynomials of age as fixed curves for each generation and random curves for additive genetic and permanent environment effects. Different residual variances were used for the first and second half of the test period. The RRS models were fitted with the same fixed effects and residual variance structure as the RRP models and included genetic and permanent environment random effects for both splines and linear Legendre polynomials of age. The RRP model was used for further analysis because the RRS model had erratic estimates of phenotypic variance and heritability, despite having a lower Bayesian information criterion than the RRP model. From 91 to 210 d of age, estimates of heritability

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from the RRP model ranged from 0.10 to 0.37 for boars and 0.14 to 0.26 for gilts for DFI, from 0.39 to 0.58 for boars and 0.55 to 0.61 for gilts for BW, from 0.48 to 0.61 for boars and 0.61 to 0.79 for gilts for BF, and from 0.46 to 0.55 for boars and 0.63 to 0.81 for gilts for LMA. In generation 5, LRFI pigs had lower average genetic curves than CTRL pigs for DFI and BW, especially towards the end of the test period; estimated line differences (CTRL-LRFI) for DFI were 0.04 kg/d for boars and 0.12 kg/d for gilts at 105 d and 0.20 kg/d for boars and 0.24 kg/d for gilts at 195 d. Line differences for BW were 0.17 kg for boars and 0.69 kg for gilts at 105 d and 3.49 kg for boars and 8.96 kg for gilts at 195 d. In conclusion, selection for reduced RFI has resulted in a lower feed intake curve and a lower body weight curve toward maturity.

Key words: Longitudinal Analysis, Pigs, Residual Feed Intake, Random Regression, Selection

Introduction

Random regression (RR) analyses have been widely used in animal breeding to model longitudinal measurements at different ages for animals, in particular for analysis of milk production traits in dairy cattle (Schaeffer and Dekkers, 1994; Jamrozik et al., 1997; Veerkamp et al., 2001; Guo et al., 2002). In recent years, applications of RR genetic analyses to longitudinal measurements of growth-related traits in pigs has increased, e.g. Huisman et al. (2002) for weight data and Schnyder et al. (2001, 2002) for daily feed intake data.

Most literature on RR analysis has used polynomials of age, especially Legendre polynomials. As an alternative, RR analysis using regression splines has received increasing attention. Regression splines are piecewise polynomials joined at knots, with the number of knots and their placement selected by the user (Hastie et al. 2009). Meyer (2005) applied RR analysis with splines to model growth of Australian Angus cattle. Huisman et al. (2002) investigated RR models with polynomials and splines for weight data of pigs.

The selection experiment for lower residual feed intake (RFI) in Yorkshire pigs at Iowa State University has resulted in a substantial reduction in average daily feed intake and a slight decrease in average daily gain over the growth period (Cai et al., 2008). Cai et al. (2010b) investigated RR models for phenotypic analysis of longitudinal measurements of

daily feed intake (DFI) and body weight (BW) in the 5th generation of this selection experiment. In the present study, RR genetic analyses were applied to data from all generations of this selection experiment. The first objective was to estimate genetic parameters for DFI, BW, backfat (BF), and loin muscle area (LMA) along the growth trajectory and to evaluate the effect of RFI selection on DFI and BW curves. The second objective was to investigate which RR model, i.e. using polynomials or splines, provided a better fit to the data for these four traits.

Materials and Methods

Experimental protocols for this study were approved by the Iowa State University Institutional Animal Care and Use Committee.

Experimental Design and Data Collection

Data were from a selection experiment for RFI in Yorkshire pigs. Cai et al. (2008) described the design of the selection experiment before generation 5 in detail. In brief, the selection experiment has two parallel lines: a line selected for lower RFI (LRFI) and a randomly selected control (CTRL) line. Selection was on estimated breeding value (EBV) for residual feed intake (RFI). Because of the limited number of electronic FIRE® feeders that were available to measure feed intake, only pigs from the LRFI line were evaluated for FI before generation 5. Pigs' 10th rib BF and LMA were measured by ultrasound scan (Cai et al., 2008). For the present analysis, data from ~3 to ~8 months of age on a total of 1081 pigs, 586 boars and 495 gilts, were used. This included data from generations -1 and 0, along with data from generations 1 to 5 of the LRFI line and generation 5 of the CTRL line. As shown in table 4.1, the average number of measurements per pig in generations -1 to 4 was 85-119 for DFI, 14-20 for BW, and 3-10 for BF and LMA. Gilts from the second parity of generations 3 and 4 were used for other research projects and were not included in the present analyses. In generation 5, feed intake was also recorded in the CTRL line. In this generation, the selection experiment was a randomized complete block design with line (LRFI vs. CTRL) as the investigating factor and pen as the block factor for boars from the first parity and gilts from the second parity (see Cai et al. 2010 for details). The average number of measurements of

DFI and BW per pig in generation 5 was 9 for BW and from 49 to 63 for DFI (Table 4.1). In generation 5, BF and LMA were only measured once, when the pig was taken off-test.

Table 4.1 The number of pigs and measurements for each line on boars and gilts by generation

Generation	Sex	Line ¹	Number of pigs	Averaged number of measurements		
				DFI ²	BW ³	BF and LMA ⁴
-1	Boars	LRFI	93	86	14	8
	Gilts	LRFI	100	91	15	8
0	Boars	LRFI	76	107	17	10
	Gilts	LRFI	77	119	19	10
1	Boars	LRFI	69	103	16	9
	Gilts	LRFI	70	102	16	9
2	Boars	LRFI	68	91	15	3
	Gilts	LRFI	86	91	15	3
3	Boars	LRFI	51	111	18	3
4	Boars	LRFI	78	85	20	3
	Boars	LRFI	64	63	9	1
5		CTRL	87	61	9	1
		LRFI	75	53	9	1
	Gilts	CTRL	87	49	9	1

¹Line: LRFI is low RFI line; CTRL is control line

²DFI = daily feed intake; the number of measurements range from 48 to 152 for generation -1 to 4 and from 25 to 84 for generation 5

³BW = body weight; the number of measurements range from 9 to 23 for generation -1 to 4 and from 6 to 10 for generation 5

⁴BF = backfat; LMA = loin muscle area; the number of measurements range from 4 to 12 for generation -1 to 1; 3 measurements for generation 2 to 4; 1 measurement for generation 5

Random Regression using Legendre Polynomials

Cai et al. (2010b) chose the quadratic polynomial RR model for phenotypic analyses of the 5th generation of the selection experiment, after comparing results from different orders of polynomials. For numerical reasons, Legendre polynomials of age were used in the present study. Following Kirkpatrick et al. (1990), to construct Legendre polynomials, age

(t) was first standardized as $t_p = -1 + \frac{2(t - \min(t))}{\max(t) - \min(t)}$, where $\min(t)$ and $\max(t)$ are the

minimum and maximum of age in the data across all animals. The first three orders (0, 1, and 2) of Legendre polynomials using t_p are $\sqrt{0.5}$, $\sqrt{1.5}t_p$, and $\sqrt{2.5}(1.5t_p^2 - 0.5)$, respectively.

For convenience of notation, LP1 and LP2 will represent the first two (0 and 1) and the first three (0, 1, and 2) orders of Legendre polynomials, respectively.

Random regression animal models using Legendre polynomials (RRP) were fitted for DFI, BW, BF, and LMA using ASREML (Gilmour et al., 2006). Fixed effects included pen within on-test group (typically 2 or 3 age groups for boars and gilts each generation) and LP2 by generation. Random effects included LP2 as both genetic and permanent environment effects. The complete relationship matrix, with pedigree going back to generation -1, was included for the genetic effects. For convenience, separate independent residual variances were fitted for the first (before 150 days of age) and second (after 150 days of age) half of the growth period for all four traits. Likelihood ratio tests were used to decide whether data from boars and gilts could be analyzed jointly, with equal variances and covariances by gender, or required separate analyses, with boars and gilts having their own variances and covariances. Likelihood ratio tests had $P < 0.001$ for DFI and BW, $P = 0.69$ for BF, and $P = 0.07$ for LMA, suggesting the need to analyze data from boars and gilts as separate traits. Results from these analyses will be reported.

Because of convergence problems with the four-trait analysis of DFI, BW, BF, and LMA, results will be reported from the three-trait analyses of DFI, BW, and BF, and from the single-trait analysis of LMA for boars and gilts separately. To estimate genetic correlations between boars and gilts, bivariate analyses were conducted separately for each of the four traits. Standard errors of estimates of genetic parameters were derived using the method of Fischer et al. (2004).

Random Regression using Splines

Random regression animal models using regression splines (RRS) were also used in this study. One popular choice of spline is the natural cubic spline, which is implemented in ASREML (Gilmour et al., 2006). The same fixed effects and residual variance structure were used as for the RRP animal models. Random effects of RRS contained genetic and permanent environment effects for LP1 and the cubic spline. As suggested by Verbyla et al. (1999) and Gilmour et al. (2006), the LP1 terms (intercept and slope) for each animal were included as random coefficients for RR models using splines. Models with different numbers

of knots were tried to determine the best number of knots and their placement: model RRS3 had three knots, at 75, 150, 210 days of age; RRS6 had six knots, at 75, 90, 120, 150, 180, 210 days of age; RRS10 had ten knots, at 75, 90, 105, 120, 135, 150, 165, 180, 195, 210 days of age; RRS3_END had three knots, at 60, 150, 253 days of age; and RRS5_END had five knots, at 60, 75, 150, 210, 253 days of age. The results from the RRS3_END and RRS5_END models were included to show the effect of putting the boundary knots at the minimum and maximum of age in the data across all animals, where the number of data points is very small.

Model Selection

The Bayesian information criterion (BIC) was used to compare RRS and RRP models. The BIC is defined as $BIC = -2I + d \log n$, where I denotes the maximum value of the residual log likelihood, d denotes the effective number of estimated covariance parameters, and n equals the number of effective subjects (586 boars and 495 gilts in this study) (SAS Institute, 2008). A smaller BIC criterion indicates a better model fit. Huisman et al. (2002) used n equal to the number of records, however, it is more appropriate to use n equal to the number of subjects for these longitudinal data (SAS Institute, 2008).

For the purposes of validation of estimates of genetic parameters from the RRS and RRP models, data for a given trait at different ages were also analyzed using multi-trait models (MT). For this purpose, data were separated into four traits based on age intervals: 91-120 days of age, 121-150 days, 151-180 days, and 181-210 days. Bivariate models were used to estimate correlations between each pair of age intervals. The model for each trait had fixed effects of pen within on-test group, a linear covariate of age by generation, and random genetic and permanent environment effects.

Results and Discussion

Model Selection

Placement of boundary knots for spline models. When analyzing longitudinal data by random regression using splines, one important question is how to select the number of knots and their placement. Specifically, for the natural cubic spline, the function is assumed linear

beyond the boundary knots. This assumption is usually reasonable because there is less information near the boundaries of the longitudinal range of the data (Hastie et al., 2009). However, placement of boundary knots can also affect behavior of the model in the middle part of the longitudinal range, despite an abundance of data in that range. In this study, the RRS3_END model with three knots at 60, 150, and 253 days of age had very inflated estimates of phenotypic standard deviation (SD) and heritability for DFI for boars in the middle of the growth trajectory compared with estimates from MT models (Figure 4.1). The boundary knots of the RRS3_END model were placed on the minimum and maximum days of age (60 and 253 d) in the data across all animals, where DFI records are very sparse; only 0.7% of the data fell between 60 and 74 d and 1.3% between 210 and 253 d (Table 4.2). By moving boundary knots inward, to 75 and 210 days of age, the estimates of phenotypic SD and heritability for DFI from the RRS3 model with three knots were much closer to estimates from the MT models than the RRS3_END model (Figure 4.1). The RRS5_END model with five knots at 60, 75, 150, 210, and 253 days of age, i.e. two additional boundary knots at 60 and 253 days of age beyond the RRS3 model, also had inflated estimates of phenotypic SD and heritability for DFI (Figure 4.1).

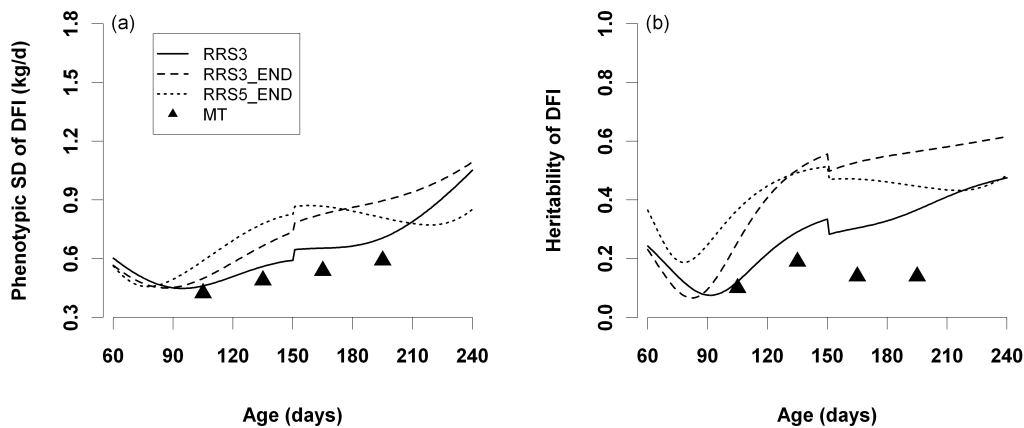


Figure 4.1 Estimates of the phenotypic standard deviation (a) and heritability (b) of daily feed intake for boars from random regression spline models with different boundary knots and from a multi-trait model. RRS3: random regression model using splines with 3 knots at 75, 150, and 210 days of age. RRS3_END: random regression model using splines with 3 knots at 60, 150, and 253 days of age. RRS5_END: random regression model using splines with 5 knots at 60, 75, 150, 210, and 253 days of age. MT: multi-trait model

This influence of the placement of boundary knots on the behavior of the model existed for all four traits and for both boars and gilts, although the impact was small for BF and LMA. One possible reason for the small impact for BF and LMA is that the cubic spline random term of the spline model (RRS3) explained a smaller percent of total phenotypic variation (sum of variance from all random terms, i.e. splines, intercept and slope for Legendre polynomials, and residuals) for BF (8%) and LMA (9%), compared to DFI (14%) and BW (12%). Another possible reason is that the proportion of records near the boundary knots of 60 and 253 days of age was greater for BF and LMA than for DFI and BW (Table 4.2). By moving boundary knots inside to where still a good proportion of data exist, sparse records beyond the boundary knots had less influence on the model fit between the boundary knots. Thus, when using random regression animal model analysis with regression splines, caution should be taken not to put the boundary knots at the minimum and maximum of time points in the data if limited data exist at those time points. Models RRS3_END and RRS5_END were not considered further in the analyses.

Table 4.2 The percent of records in each age interval in the data across all animals

Age interval (d)	Boars (% records)			Gilts (% records)		
	DFI ¹	BW ²	BF and LMA ³	DFI ¹	BW ²	BF and LMA ³
60-74	0.7	1.1	2.2	0.5	0.8	1.4
75-89	6.1	7.5	10.7	3.9	5.2	7.7
90-104	12.0	11.4	10.0	10.3	11.6	10.4
105-119	13.6	13.1	10.5	13.4	12.5	11.6
120-134	14.4	12.6	11.5	14.8	13.6	12.9
135-149	13.9	12.9	12.4	13.4	13.3	9.9
150-164	13.7	12.7	11.6	13.7	13.2	10.5
165-179	11.5	11.8	9.2	11.8	12.1	11.3
180-194	9.0	9.3	9.8	10.8	8.6	10.4
195-209	4.0	5.7	8.1	5.0	6.0	8.2
210-224	1.2	1.7	3.4	2.0	2.3	3.5
225-239	0.1	0.3	0.7	0.4	0.8	1.7
240-253	0.0	0.0	0.0	0.1	0.2	0.4
Total records	50841	8183	2703	41247	6569	2544

¹DFI = daily feed intake

²BW = body weight

³BF = backfat; LMA = loin muscle area

Spline versus Legendre polynomial models. Table 4.3 shows BIC values for the RRP model and the RRS models with 3, 6, and 10 knots. For DFI and BW, BIC values of the RRS models decreased as the number of knots increased. The RRS model with 10 knots had the smallest BIC values among all RRS models for both DFI and BW. For BF and LMA, BIC values of the RRS models decreased as the number of knots increased from 3 to 6, but increased as the number of knots increased from 6 to 10. The RRS model with 6 knots had the smallest BIC values among all RRS models for both BF and LMA. For DFI, the RRS models with 6 and 10 knots had smaller BIC values than the RRP model. For BW, all RRS models had smaller BIC values than the RRP model. For BF and LMA, the best RRS model, with 6 knots, also had a smaller BIC value than the RRP model.

Table 4.3 Bayesian information criteria of random regression models for boars and gilts

Model ¹	DFI ²		BW ²		BF ²		LMA ²	
	Boars	Gilts	Boars	Gilts	Boars	Gilts	Boars	Gilts
RRP	-33447	-30793	24615	19024	4759	4403	7090	7078
RRS3	-33329	-30750	24257	18864	4810	4393	7110	7070
RRS6	-35189	-32376	23230	18007	4758	4358	7038	6955
RRS10	-36025	-33270	23172	17867	4791	4373	7066	6982

¹Model: RRP represents random regression using polynomials; RRS3, RRS6, and RRS10 represent random regression using splines with 3, 6, and 10 knots, respectively

²DFI = daily feed intake; BW = body weight; BF = backfat; LMA = loin muscle area

Estimates of phenotypic SD of DFI, BW, BF, and LMA for boars and gilts from the MT model showed an increasing trend from 91 to 210 days of age (Figure 4.2). To provide additional information, raw phenotypic standard deviations were calculated for intervals of 15 days from 60 to 224 days of age and these are also shown in Figure 4.2. Raw phenotypic SD increased from about 90 d of age and then leveled off or decreased at about 180 d of age for DFI, BW, BF, and LMA. Estimates of phenotypic SD from the MT model matched the raw phenotypic SD well. However, close to the boundaries, estimates of the phenotypic SD from the RRP and RRS models increased fast and deviated substantially from estimates from the MT model and the raw phenotypic SD. This indicates that the RRP and RRS models behave poorly close to the boundaries of the data, which is a well-known property of polynomial and spline models (Hastie et al., 2009). Thus, the RRP and RRS models should not be used for data extrapolation.

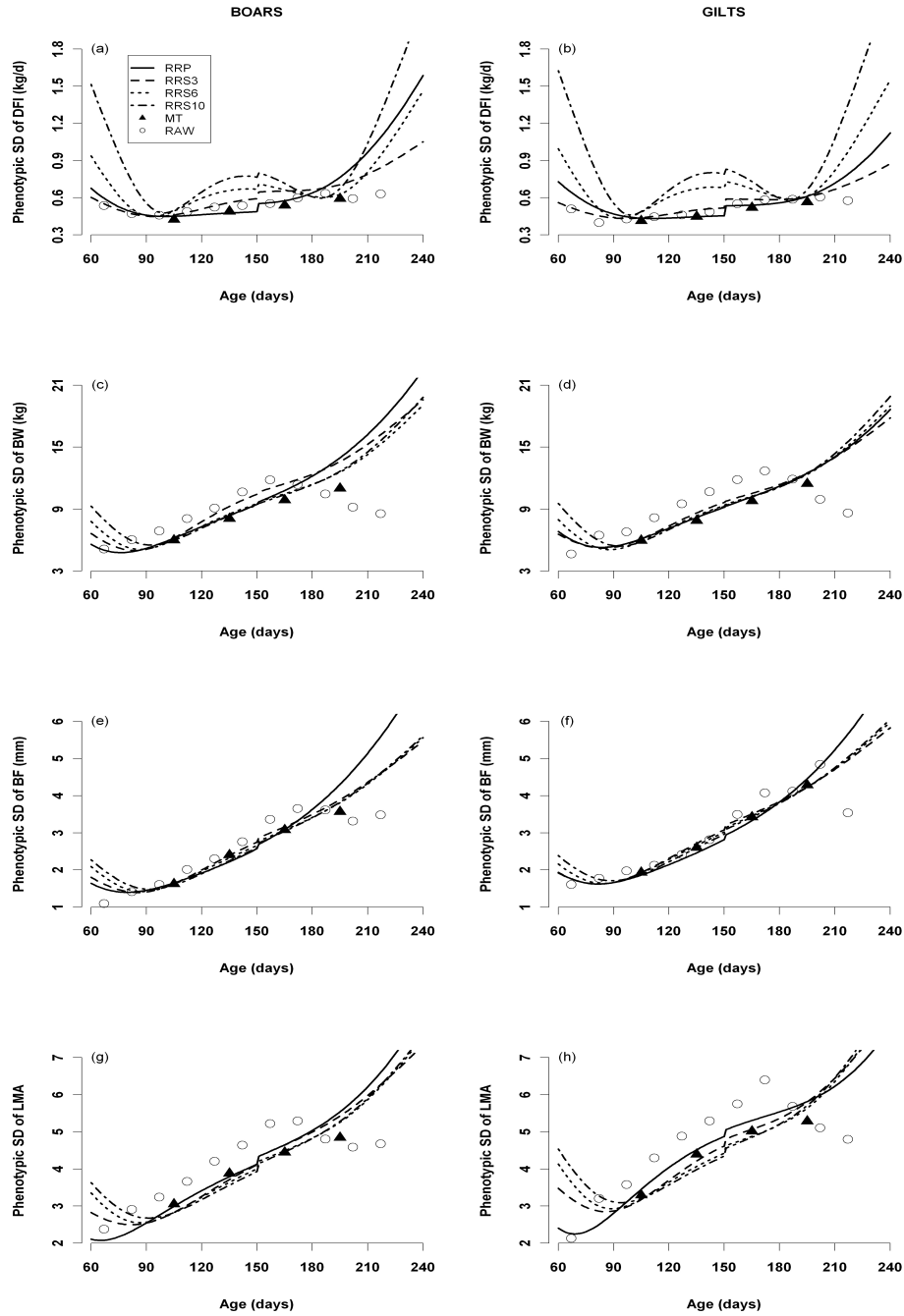


Figure 4.2 Estimates of the phenotypic standard deviation of daily feed intake (DFI), body weight (BW), backfat (BF), loin muscle area (LMA, cm²) from random regression models using polynomials and splines, and from a multi-trait model. The left panels refer to boars and the right panels refer to gilts. RRP: random regression model using quadratic Legendre polynomials. RRS3, RRS6, and RRS10: random regression models using splines with 3, 6, and 10 knots. MT: multi-trait model. RAW: raw phenotypic standard deviation on intervals of 15 days of age

For DFI, BW, BF, and LMA, the RRP model had similar estimates of phenotypic SD as the MT model for 91 to 210 days of age (Figure 4.2). As the number of knots increased, estimates of phenotypic SD for DFI, BW, BF, and LMA from RRS models increased faster when close to the boundaries of the data (Figure 4.2). For DFI, the RRS3 model had estimates of phenotypic SD that were close to those of the RRP and MT models (Figure 4.2 (a) and (b)). As the number of knots increased from 3 to 10, estimates of the phenotypic SD for DFI from RRS models increased and deviated more and more from the estimates from the RRP and MT models for 91 to 210 days of age (Figure 4.2 (a) and (b)). In contrast, estimates of the phenotypic SD for BW, BF, and LMA from RRS models with 3, 6, and 10 knots were very close and similar to those from the RRP and MT models for both boars and gilts (Figure 4.2 (c), (d), (e), (f), (g), and (h)).

For DFI and BW, the RRP model had estimates of heritability that were close to those from the MT model (Figure 4.3 (a), (b), (c), and (d)). For DFI, the RRS3 model had estimates of heritability close to estimates from the RRP and MT models. For the RRS models, inflation of estimates of heritability for DFI compared to the RRP and MT models increased with the number of knots. In contrast, estimates of heritability for BW from RRS models decreased as the number of knots increased from 3 to 6, but were similar for RRS models with 6 and 10 knots. For BW, the RRS models had greater estimates of heritability than the RRP and MT models (Figure 4.3 (c) and (d)). For BF and LMA, the RRS models with 3, 6, and 10 knots had similar estimates of heritability (Figure 4.3 (e), (f), (g), and (h)). For BF, the RRP model had estimates of heritability that were closer to those from the MT model than the RRS models for boars (Figure 4.3 (e)), while RRS models had closer estimates than the RRP model for gilts (Figure 4.3 (f)). For LMA, the RRP model and the RRS models with different number of knots had similar estimates of heritability (Figure 4.3 (g) and (h)). Estimates of heritability from these models were close to those from the MT model for boars (Figure 4.3 (g)) but greater for gilts (Figure 4.3 (h)).

The RRS models with 6 or 10 knots for DFI and LMA, 3, 6, or 10 knots for BW, and 6 knots for BF had smaller BIC values than the RRP model (Table 4.3). They fitted better than the RRP model based on the BIC criterion. However, compared with the MT model, the RRS models had, in most of cases, more erratic estimates of phenotypic variance and heritability

than the RRP model, especially for DFI and BW. Therefore, the RRP model was selected and only results from this model will be reported in the remainder.

Estimates of Phenotypic Standard Deviation along Age

Estimates of the phenotypic SD for DFI, BW, BF, and LMA from the RRP model had an increasing trend from 91 to 210 d of age for both boars and gilts (Figure 4.2). Estimates of the phenotypic SD for DFI ranged from 0.45 to 0.97 kg/d for boars and from 0.43 to 0.72 kg/d for gilts from 91 to 210 d of age. For BW, estimates of the phenotypic SD ranged from 5.3 to 16.2 kg for boars and from 5.4 to 14.1 kg for gilts. Consistent with our results, Huisman et al. (2002) also observed an increasing trend for estimates of the phenotypic SD for BW, ranging from 2.9 to 11.3 kg for 70 to 190 d of age for boars by a polynomial random regression model. For BF and LMA (Figure 4.2 (e), (f), (g), and (h)), estimates of the phenotypic SD ranged from 1.5 to 5.1 mm and from 2.6 to 6.2 cm² for boars, and from 1.7 and 5.2 mm and from 2.8 to 6.2 cm² for gilts, respectively.

Estimates of Heritability along Age

For boars from 91 to 210 d of age, estimates of heritability for DFI and BW from the RRP model had increasing trends, ranging from 0.10 to 0.37 for DFI and from 0.39 to 0.58 for BW (Figure 4.3 (a) and (c)). For the RRP model for gilts, estimates of heritability for BW were fairly consistent across age, with a range from 0.55 to 0.61 (Figure 4.3 (d)), but initially increased and then remained constant for DFI, with a range from 0.14 to 0.26 (Figure 4.3 (b)). Schnyder et al. (2001) used a quadratic polynomial random regression model on weekly means of DFI for French Landrace and Large White growing pigs. In that study, estimates of heritability for DFI ranged from 0.09 to 0.25, which is similar to this study. Estimates of heritability for BW in this study were greater than the estimates ranging from 0.13 to 0.20 for 70 to 190 d of age in the study of Huisman et al. (2002). In addition to the population difference, the difference between our study and the study of Huisman et al. (2002) is that we used an animal model for BW with second-order Legendre polynomials of age for both animal and permanent environment effects, compared with their sire model with fourth-order Legendre polynomials of age for the sire effect and second-order Legendre polynomials of age for the permanent environment effect.

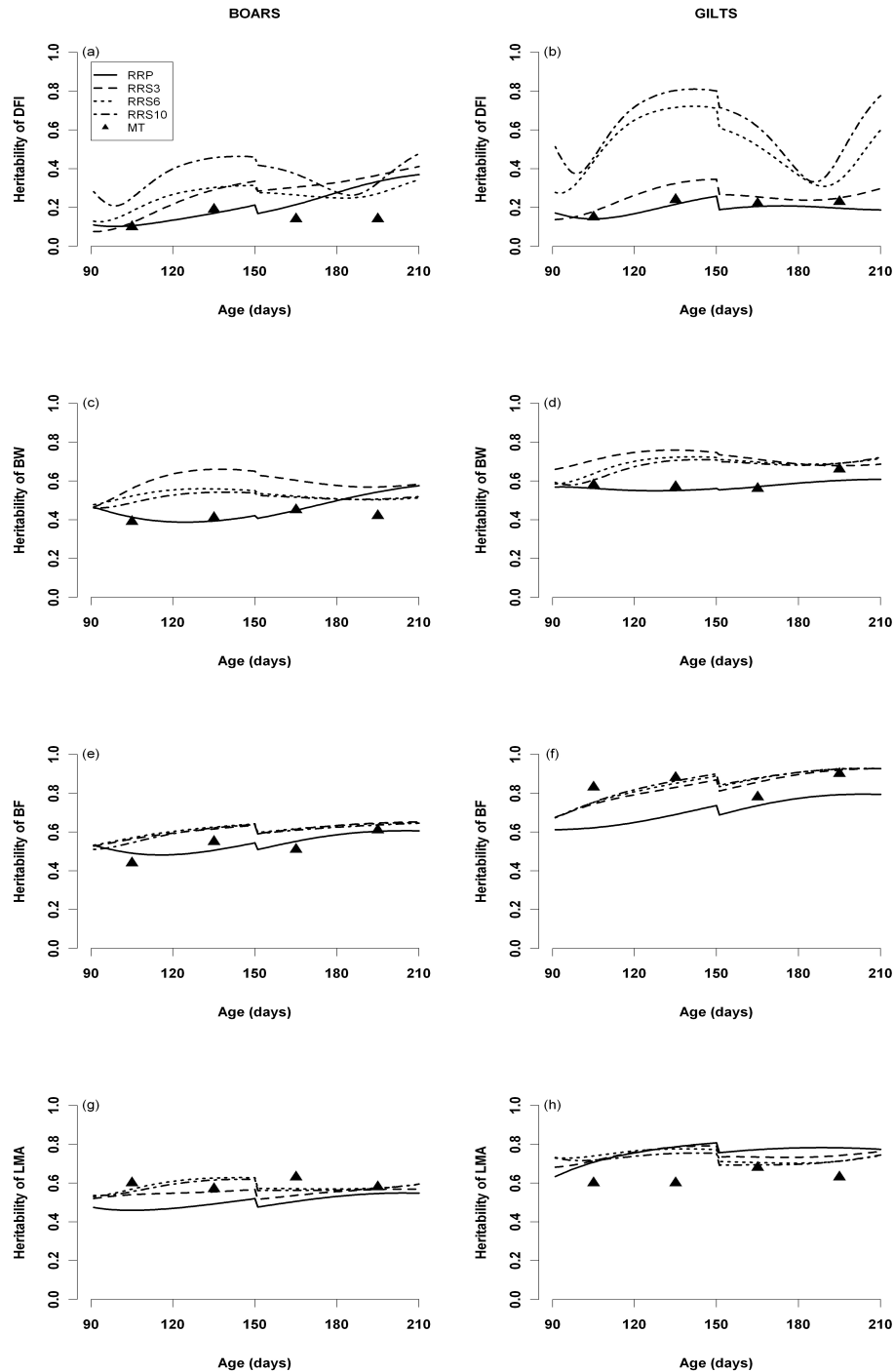


Figure 4.3 Estimates of heritability of daily feed intake (DFI), body weight (BW), backfat (BF), loin muscle area (LMA) from random regression models using polynomials and splines, and from a multi-trait model. The left panels refer to boars and the right panels refer to gilts. RRP: random regression model using quadratic Legendre polynomials. RRS3, RRS6, and RRS10: random regression models using splines with 3, 6, and 10 knots. MT: multi-trait model

The RRP model resulted in a slightly increasing trend of estimates of heritability for BF for boars and gilts from 91 to 210 d of age (Figure 4.3 (e) and (f)). Estimates ranged from 0.48 to 0.61 for boars and from 0.61 to 0.79 for gilts. Estimates of heritability for LMA from the RRP model were fairly consistent from 91 to 210 d of age, with a range from 0.46 to 0.55 for boars, but initially increased and then remained relatively constant for gilts, with a range from 0.63 to 0.81 (Figure 4.3 (g) and (h)).

Estimates of Genetic Correlations along Age

Genetic and phenotypic correlations between ages. Table 4.4 shows estimates of genetic and phenotypic correlations between 105, 135, 165, and 195 d of age for DFI, BW, BF, and LMA from the RRP model. Generally, estimates of genetic and phenotypic correlations for these four traits decreased with increasing age intervals. Correspondingly, standard errors increased as the magnitude of estimates of correlations decreased. Decreasing patterns with length of the age interval for both genetic and phenotypic correlations were consistent between boars and gilts for BW, BF, and LMA. However, for DFI, estimates of genetic correlations for boars decreased much faster with length of the age interval than for gilts, although decreasing patterns of phenotypic correlations were similar between boars and gilts. Schnyder et al. (2001) found that, although the phenotypic correlations of intercept, linear, and quadratic regression coefficients for daily feed intake from a quadratic polynomial random regression model were very similar between breeds of French Landrace and Large White, genetic correlations were very different between the breeds. This study, in companion with their study, may indicate that the development of feed intake capacity genetically differs between genders and breeds.

Table 4.4 Estimates of heritability (on diagonal) and of phenotypic (above diagonal) and genetic (below diagonal) correlations for boars and gilts at different ages based on random regression models using Legendre polynomials, with SE in brackets

Trait ¹	Age (d)	Boars				Gilts			
		105	135	165	195	105	135	165	195
DFI	105	0.11 (0.02)	0.23 (0.01)	0.11 (0.01)	-0.02 (0.02)	0.14 (0.02)	0.24 (0.02)	0.13 (0.02)	0.04 (0.02)
	135	0.77 (0.05)	0.17 (0.02)	0.26 (0.02)	0.09 (0.02)	0.76 (0.05)	0.22 (0.02)	0.27 (0.02)	0.12 (0.02)
	165	0.41 (0.09)	0.82 (0.04)	0.21 (0.02)	0.36 (0.02)	0.63 (0.08)	0.96 (0.02)	0.21 (0.02)	0.26 (0.02)
	195	0.04 (0.12)	0.41 (0.10)	0.85 (0.03)	0.33 (0.03)	0.57 (0.12)	0.76 (0.09)	0.89 (0.04)	0.20 (0.03)
BW	105	0.41 (0.04)	0.91 (0.01)	0.82 (0.01)	0.68 (0.02)	0.56 (0.03)	0.89 (0.01)	0.83 (0.01)	0.72 (0.02)
	135	0.96 (0.01)	0.39 (0.04)	0.92 (0.01)	0.80 (0.02)	0.95 (0.01)	0.55 (0.03)	0.93 (0.01)	0.84 (0.01)
	165	0.87 (0.03)	0.96 (0.01)	0.45 (0.03)	0.91 (0.01)	0.88 (0.02)	0.97 (0.01)	0.57 (0.03)	0.93 (0.01)
	195	0.75 (0.05)	0.87 (0.03)	0.97 (0.01)	0.54 (0.03)	0.78 (0.04)	0.89 (0.02)	0.97 (0.01)	0.60 (0.03)
BF	105	0.49 (0.03)	0.79 (0.02)	0.68 (0.02)	0.54 (0.03)	0.62 (0.03)	0.83 (0.01)	0.74 (0.02)	0.63 (0.03)
	135	0.93 (0.01)	0.51 (0.03)	0.84 (0.01)	0.74 (0.02)	0.95 (0.01)	0.69 (0.02)	0.87 (0.01)	0.78 (0.02)
	165	0.81 (0.03)	0.96 (0.01)	0.55 (0.03)	0.87 (0.01)	0.88 (0.02)	0.97 (0.01)	0.74 (0.02)	0.88 (0.01)
	195	0.69 (0.05)	0.89 (0.03)	0.98 (0.01)	0.60 (0.03)	0.79 (0.04)	0.91 (0.02)	0.98 (0.01)	0.79 (0.02)
LMA	105	0.46 (0.04)	0.85 (0.01)	0.76 (0.02)	0.63 (0.03)	0.71 (0.02)	0.84 (0.01)	0.77 (0.02)	0.63 (0.03)
	135	0.97 (0.01)	0.49 (0.04)	0.85 (0.01)	0.75 (0.02)	0.98 (0.01)	0.79 (0.02)	0.86 (0.01)	0.76 (0.02)
	165	0.91 (0.02)	0.98 (0.01)	0.51 (0.03)	0.83 (0.01)	0.92 (0.02)	0.98 (0.00)	0.77 (0.02)	0.83 (0.01)
	195	0.81 (0.05)	0.90 (0.03)	0.97 (0.01)	0.55 (0.03)	0.79 (0.04)	0.88 (0.02)	0.96 (0.01)	0.78 (0.02)

¹DFI = daily feed intake; BW = body weight; BF = backfat; LMA = loin muscle area

Genetic correlations between DFI, BW, and BF. Figure 4.4(a) shows estimates of genetic correlations between DFI, BW, and BF from three-trait analyses, separately for boars and gilts. Estimates of genetic correlations between DFI and BW were similar for boars and gilts before 150 d of age. After that, estimates of genetic correlations between DFI and BW

decreased sharply from 0.78 to 0.39 for boars but only from 0.79 to 0.58 for gilts. Estimates of genetic correlations between DFI and BF had different trends with age for boars and gilts; correlations increased from 0.35 to 0.74 for gilts but decreased from 0.56 to 0.31 for boars. This demonstrated that DFI was genetically more correlated with BF for gilts than for boars during the growing period. Estimates of genetic correlations between BW and BF increased with age from 0.35 to 0.63 for boars and from 0.40 to 0.55 for gilts. Zhang et al. (2000) estimated genetic correlations between BW and BF at 22 weeks of age in a Chinese \times European *Tiameslan* composite pig line to be 0.10 for boars and -0.38 for gilts, which differs from our results. In addition to population differences, another possible reason is that backfat thickness in that study was adjusted to a BW of 100 kg.

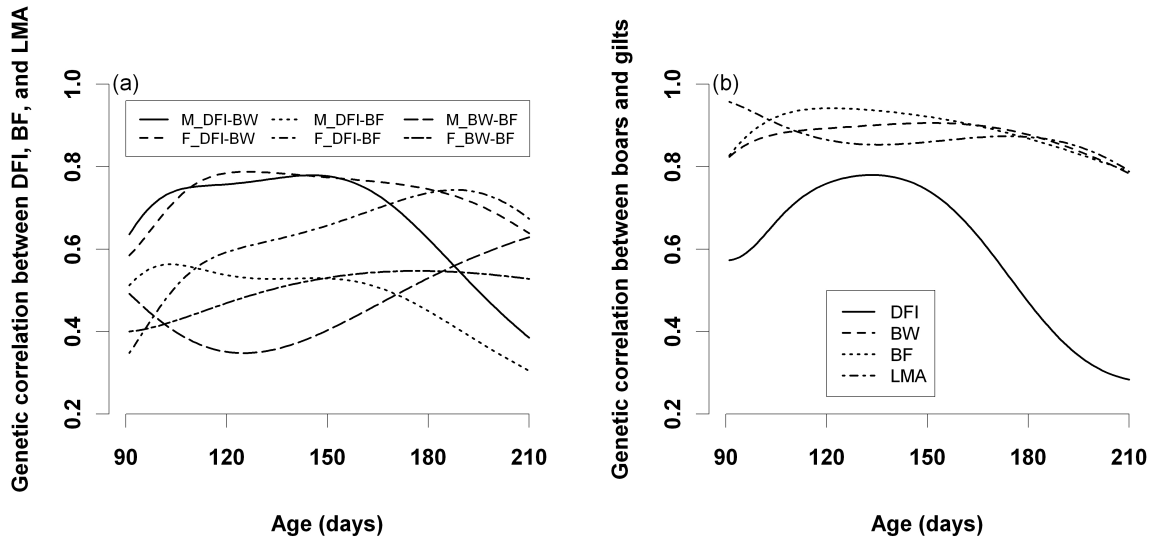


Figure 4.4 Estimates of genetic correlations (a) between daily feed intake (DFI), body weight (BW), and backfat (BF), and (b) between boars and gilts for DFI, BW, BF, and loin muscle area (LMA) from random regression models using Legendre polynomials. M_DFI-BW: genetic correlation between DFI and BW for boars; F_DFI-BW: genetic correlation between DFI and BW for gilts; M_DFI-BF: genetic correlation between DFI and BF for boars; F_DFI-BF: genetic correlation between DFI and BF for gilts; M_BW-BF: genetic correlation between BW and BF for boars; F_BW-BF: genetic correlation between BW and BF for gilts

Genetic correlations between boars and gilts for DFI, BW, BF, and LMA. Estimates of genetic correlations between boars and gilts differed little by age for BW (0.78 to 0.91), BF

(0.79 to 0.94), and LMA (0.79 to 0.96) (Figure 4.4 (b)). In contrast, estimates of genetic correlations between boars and gilts for DFI first increased with age to a maximum of 0.78 at 133 d of age and then sharply decreased to 0.28 at the end of test period (210 d of age) (Figure 4.4 (b)). One possible reason is that DFI is not a cumulative trait, in contrast to BW, BF, and LMA. Zhang et al. (2000) reported estimates of genetic correlations between boars and gilts ranging from 0.79 to 0.95 for BW at 4, 8, and 22 weeks of age, and 0.82 for BF at 22 weeks of age, which are consistent with our results.

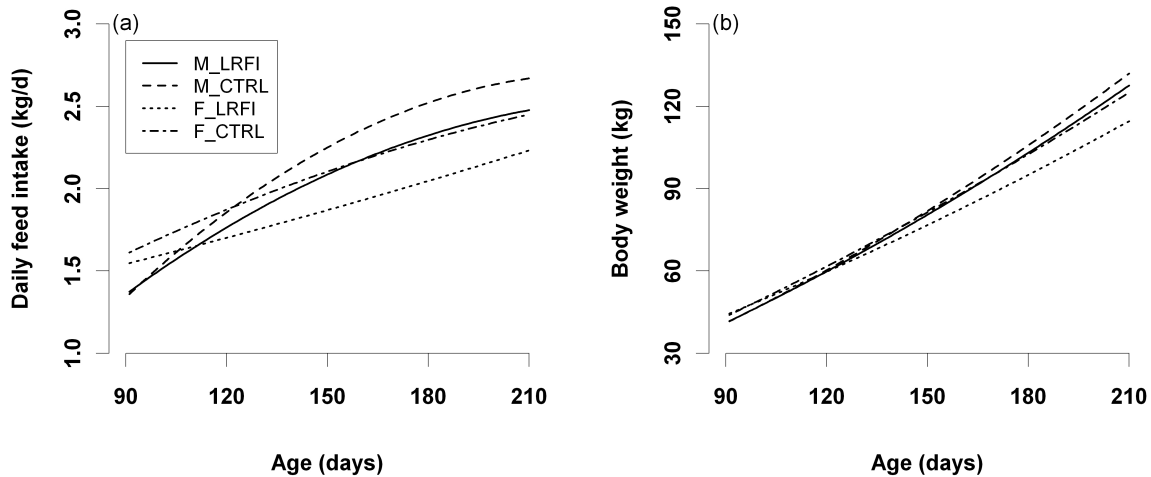


Figure 4.5 Estimated genetic population curves of daily feed intake (a) and body weight (b) for boars and gilts of low RFI and control lines at 5th generation from the random regression model using Legendre polynomials. M_LRFI: boars at low RFI line; M_CTRL: boars at control line; F_LRFI: gilts at low RFI line; F_CTRL: gilts at control line

Estimates of Population Curves with Age

Estimates of genetic population curves for DFI and BW are shown in Figure 4.5. They were derived from results of the RRP model for boars and gilts of the LRFI and CTRL lines at generation 5 of the selection experiment based on the sum of estimates of fixed curves and average EBV by line. Since fixed curves were common to both lines, differences in curves between the two lines were entirely determined by differences in average EBV. Thus, Figure 4.5 visualize the effect of selection for reduced RFI on genetic population curves of growth and feed intake along the growth trajectory from 91 to 210 d of age. Compared with the

CTRL line, the LRFI line had a lower DFI curve for both boars and gilts. Line differences for DFI (CTRL-LRFI) at 105, 135, 165, and 195 d of age were 0.04, 0.13, 0.19, and 0.20 kg/d for boars and 0.12, 0.21, 0.25, and 0.24 kg/d for gilts. Line differences were small at the beginning of the growth period from ~90 days of age and became larger later in the growing period (Figure 4.5 (a)). The LRFI line also tended to have a lower body weight curve than the CTRL line for both boars and gilts later in the growing period (Figure 4.5 (b)). The line differences for BW (CTRL-LRFI) at 105, 135, 165, and 195 d of age were 0.17, 0.93, 2.04, and 3.49 kg for boars and 0.69, 3.26, 6.02, and 8.96 kg for gilts. In summary, selection for reduced RFI has resulted in a lower feed intake curve and a lower body weight curve, especially later in the growing period.

Conclusion

This study clearly shows that random regression using Legendre polynomials is better than using splines for the longitudinal performance data in pigs because the random regression spline model had erratic estimates of phenotypic variance and heritability, although it had a lower Bayesian information criterion than the random regression polynomial model. This study also shows that, when using random regression with splines, the boundary knots should not be placed at the minimum and maximum of time points in the data if limited data exist at those time points. Selection for reduced RFI has resulted in a lower feed intake curve and a lower body weight curve, which indicates that it is possible to change both growth and feed intake curves by selection to improve feed efficiency in pigs. Estimates of genetic parameters of the performance traits in this study provide valuable information for swine industry to move one-step further toward direct selection on performance curves. Further research is needed to investigate how to optimally change the performance curves.

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CHAPTER 5. BAYESIAN ANALYSIS OF THE EFFECT OF SELECTION FOR RESIDUAL FEED INTAKE ON GROWTH AND FEED INTAKE CURVES IN YORKSHIRE SWINE

A paper to be submitted to the Journal of Animal Science

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Abstract

Gompertz growth functions were fitted to longitudinal measurements of daily feed intake (DFI) and body weight (BW) of 586 boars and 495 gilts from a selection experiment in Yorkshire pigs for residual feed intake (RFI). The selection experiment consists of a line selected for lower residual feed intake (LRFI) for 5 generations and a randomly selected control line (CTRL). The objectives of this study were to use Bayesian methods to estimate genetic parameters of the Gompertz growth curve parameters for DFI and BW and to evaluate the effect of selection for reduced RFI on the parameters and shape of curves for DFI and BW. The average number of measurements was 85 and 14 for DFI and BW for pigs from ~3 to ~8 months of age. Separate analyses were done for boars and gilts and for BW and DFI. A hierarchical model was specified in two levels: in the first level, the Gompertz function was fitted for each pig and a 3-trait linear mixed model was fitted to the three Gompertz parameters (asymptotic value, inflection point, and decay parameter) as the second level, with fixed effects of generation and random effects of additive genetic and environmental effects. Bayesian methods were used to combine the two levels of modeling. A total of 30,000 random samples of the posterior distributions after convergence of Markov chains were used for inference. Posterior means of heritability for the asymptotic value, inflection point, and decay parameter for DFI were 0.74, 0.68, and 0.81 for boars and 0.75, 0.64, and 0.53 for gilts; corresponding estimates for BW were 0.61, 0.56, and 0.57 for boars

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and 0.42, 0.32, and 0.32 for gilts. Compared with the CTRL line in generation 5, the LRFI line had a significantly lower mature daily feed intake, with line differences (LRFI-CTRL) of -0.13 kg/d ($p = 0.08$) for boars and -0.21 kg/d ($p = 0.04$) for gilts. The LRFI line had an earlier inflection point for DFI than the CTRL line: -4 d ($p = 0.03$) for boars and -5 d ($p = 0.11$) for gilts. The LRFI line also had a lower mature body weight than the CTRL line: -11 kg ($p = 0.11$) for boars and -15 kg ($p = 0.12$) for gilts. The other parameters of the Gompertz curves for DFI and BW were not significantly affected by selection for reduced RFI with $p > 0.15$ for line differences (LRFI-CTRL) of these parameters. Graphs of Gompertz curves for the LRFI and CTRL lines from the posterior samples of curve parameters showed that selection for reduced RFI has resulted in pigs that have a lower feed intake curve and a lower body weight curve towards maturity.

Key words: Bayesian Analysis, Growth Curves, Pigs, Residual Feed Intake, Selection

Introduction

In view of the economic importance of feed efficiency, electronic feeders have been widely used in swine breeding programs for measuring individual feed intake for group housed pigs. Measurements of daily feed intake (DFI) and body weight (BW) from electronic feeders are longitudinal along the growth trajectory. How to make best use of these data in pig breeding programs needs to be investigated further (Hermesch, 2004).

The data for this study were from a selection experiment for reduced residual feed intake (RFI) in Yorkshire pigs. It consists of a line selected for lower residual feed intake (LRFI) for 5 generations and a randomly selected control line (CTRL) (see Cai et al. (2008) for details on selection protocols). (Cai et al., 2008) showed that selection for reduced RFI has significantly decreased average feed consumption over the growth trajectory but has also reduced average growth rate.

As one attempt to investigate use of these longitudinal growth and feed intake data in pig breeding programs, random regression models were implemented for genetic analyses of this selection experiment (Cai et al., 2010a). Linear random regression models could adequately describe the observed data and are easy to implement in existing software such as ASREML (Gilmour et al., 2006). However, the parameters of linear models don't have a biological

meaning and give limited insight in the biological data-generating process. In contrast, nonlinear growth models attempt to describe the growth-related process by a few of biologically meaningful parameters. Several studies (Barbato, 1991 in chickens; Kachman et al., 1988 in mice; Koivula et al., 2008 in pigs) have investigated genetic variation of growth curve parameters by a two-stage method, in which parameters of the growth curve were first estimated for each individual and then genetic analyses were implemented on these estimated growth parameters. Varona et al. (1997) specified Bayesian analysis methodology which combines these two stages of analyses. Varona et al. (1998) used this hierarchical Bayesian analysis scheme to analyze the Wood's lactation curve in dairy cows. Blasco et al. (2003) investigated the effect of selection for growth rate on growth curves in rabbits by the Gompertz growth function using similar methods.

Among nonlinear growth functions, the Gompertz function is one of the most popular choices for modeling processes related to animal growth (Whittemore et al., 1988; Emmans and Kyriazakis, 1999). The Gompertz function has three parameters with biological interpretations (Ratkowsky, 1990), i.e. asymptotic value, inflection point, and decay parameter. Against this background, the objectives of this study were to apply the hierarchical Bayesian method to analysis of data from the RFI selection experiment. Specific objectives were to investigate genetic variation of the parameters of the Gompertz growth curves for DFI and BW, and to evaluate the effect of selection for reduced RFI on curves for DFI and BW.

Materials and Methods

Experimental protocols for this study were approved by the Iowa State University Institutional Animal Care and Use Committee.

Data

A total of 1030 Yorkshire pigs (both boars and gilts) from 7 generations (-1, 0, up to 5) of the selection experiment for reduced RFI described by Cai et al. (2008) were used in this study. A summary of the longitudinally measured DFI and BW data are in Table 4.1.

Model Specification

The hierarchical model that was used in this study is specified in two levels. For the first level of the model, the Gompertz non-linear function was chosen to model individual feed intake and growth curves. The second level of the model describes variation among pigs for the Gompertz curve parameters by a linear mixed model with the fixed effect of generation and random genetic and environmental effects. The analyses were done separately for boars and gilts and separately for BW and DFI. All programs were written using the R program (R, 2010).

Notations are as follows.

n = total number of pigs;

r_i = number of repeated measurements for pig i ($i=1,2,...,n$);

N = total number of observations;

y_{ij} = BW or DFI for pig i measured at t_{ij} days of age ($j=1,2,...,r_i$);

\mathbf{y}_i = vector of BW or DFI observations taken on pig i ;

$\mathbf{y} = (\mathbf{y}'_1, \mathbf{y}'_2, ..., \mathbf{y}'_n)'$ = whole data vector of BW or DFI;

$\boldsymbol{\theta}_i = (a_i, b_i, c_i)'$ = parameters of the Gompertz function for pig i ;

a_i = asymptotic value (mature BW or DFI) for pig i ;

b_i = inflection point (number of days) for pig i ;

c_i = decay parameter (number of days) for pig i ; i.e. $c_i = \frac{\text{response}}{d(\text{response})/dt}$ at the

curve's inflection point for pig i ;

$\boldsymbol{\theta} = (\boldsymbol{\theta}'_1, \boldsymbol{\theta}'_2, ..., \boldsymbol{\theta}'_n)'$ = vector of parameters of the Gompertz function for all pigs.

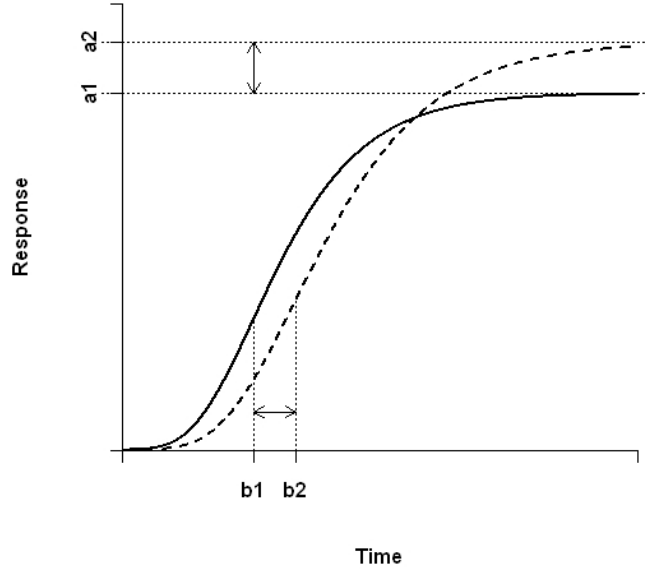


Figure 5.1 Prototype of two Gompertz curves with parameters (a_1, b_1, c_1) and (a_2, b_2, c_2)

Gompertz non-linear function. Each pig's BW or DFI data were modeled as $y_{ij} = a_i \times \exp(-\exp(-(t_{ij} - b_i)/c_i)) + \varepsilon_{ij}$, for $i=1,2,\dots,n$ and $j=1,2,\dots,r_i$. Two prototype Gompertz curves with different parameters are shown in Figure 5.1. Random residuals ε_{ij} were assumed normally distributed and independent of each other, i.e. $\varepsilon \sim N(\mathbf{0}, \sigma_e^2 \mathbf{I}_{N \times N})$, where ε is the vector of residuals for the data vector \mathbf{y} and \mathbf{I} is an $N \times N$ identity matrix. The likelihood of \mathbf{y} is

$$\begin{aligned}
 f(\mathbf{y} | \boldsymbol{\theta}, \sigma_e^2) &= \prod_{i=1}^n \prod_{j=1}^{r_i} f(y_{ij} | \boldsymbol{\theta}_i, \sigma_e^2) \\
 &= \prod_{i=1}^n \prod_{j=1}^{r_i} (2\pi\sigma_e^2)^{-\frac{1}{2}} \exp\left(-\frac{(y_{ij} - a_i \times \exp(-\exp(-(t_{ij} - b_i)/c_i)))^2}{2\sigma_e^2}\right) \\
 &= (2\pi\sigma_e^2)^{-N/2} \exp\left(-\frac{1}{2\sigma_e^2} \sum_{i=1}^n \sum_{j=1}^{r_i} (y_{ij} - a_i \times \exp(-\exp(-(t_{ij} - b_i)/c_i)))^2\right).
 \end{aligned}$$

Model for parameters of the Gompertz non-linear function. Linear mixed models were used in the second level of the hierarchical model, i.e. for modeling parameters of the Gompertz function. A multivariate animal model was fitted to the three Gompertz parameters

with the fixed effect of generation (-1, 0, 1, 2, 3, 4, and 5) to account for systematic environmental differences between generations, and random animal genetic and environmental effects. The model for parameter θ_i for pig i was specified as $\theta_i = \beta_{k(i)} + \mathbf{u}_i + \mathbf{e}_i$, where $\beta_{k(i)}$ represents the mean vector for generation $k(i) = -1, 0, \dots, 5$ for pig i ; \mathbf{u}_i and \mathbf{e}_i represent random animal genetic and environmental effects for pig i . The covariance matrixes for the random effects are denoted as:

$$\mathbf{G} = \text{var}(\mathbf{u}_i) = \begin{pmatrix} G_{aa} & G_{ab} & G_{ac} \\ G_{ab} & G_{bb} & G_{bc} \\ G_{ac} & G_{bc} & G_{cc} \end{pmatrix}, \text{ and } \mathbf{G}^{-1} = \begin{pmatrix} G^{aa} & G^{ab} & G^{ac} \\ G^{ab} & G^{bb} & G^{bc} \\ G^{ac} & G^{bc} & G^{cc} \end{pmatrix};$$

$$\mathbf{R} = \text{var}(\mathbf{e}_i) = \begin{pmatrix} R_{aa} & R_{ab} & R_{ac} \\ R_{ab} & R_{bb} & R_{bc} \\ R_{ac} & R_{bc} & R_{cc} \end{pmatrix}, \text{ and } \mathbf{R}^{-1} = \begin{pmatrix} R^{aa} & R^{ab} & R^{ac} \\ R^{ab} & R^{bb} & R^{bc} \\ R^{ac} & R^{bc} & R^{cc} \end{pmatrix}.$$

Notations of vectors of parameters for all pigs are as follows: $\boldsymbol{\beta} = (\boldsymbol{\beta}'_{-1(1)}, \boldsymbol{\beta}'_{-1(2)}, \dots, \boldsymbol{\beta}'_{5(n)})'$ = vector of fixed effects of generation; $\mathbf{u} = (\mathbf{u}'_1, \mathbf{u}'_2, \dots, \mathbf{u}'_n)'$ = vector of random animal genetic effects; $\mathbf{e} = (\mathbf{e}'_1, \mathbf{e}'_2, \dots, \mathbf{e}'_n)'$ = vector of random environmental effects. The distributional assumption for random environmental effects is $\mathbf{e} \sim N(\mathbf{0}, \mathbf{I}_{n \times n} \otimes \mathbf{R})$. In matrix form, the model for the three parameters of the Gompertz function is denoted as $(\boldsymbol{\theta} | \boldsymbol{\beta}, \mathbf{u}, \mathbf{R}) \sim N(\boldsymbol{\beta} + \mathbf{u}, \mathbf{I} \otimes \mathbf{R})$. The likelihood of this model is,

$$f(\boldsymbol{\theta} | \boldsymbol{\beta}, \mathbf{u}, \mathbf{R}) = (2\pi)^{-n/2} |\mathbf{R}|^{-n/2} \exp\left(-\frac{1}{2}(\boldsymbol{\theta} - \boldsymbol{\beta} - \mathbf{u})'(\mathbf{I} \otimes \mathbf{R})^{-1}(\boldsymbol{\theta} - \boldsymbol{\beta} - \mathbf{u})\right)$$

$$= (2\pi)^{-n/2} |\mathbf{R}|^{-n/2} \exp\left(-\frac{1}{2} \sum_{i=1}^n (\theta_i - \beta_{k(i)} - \mathbf{u}_i)' \mathbf{R}^{-1} (\theta_i - \beta_{k(i)} - \mathbf{u}_i)\right).$$

The distributional assumption for random animal genetic effects is $(\mathbf{u} | \mathbf{G}) \sim N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G})$, where \mathbf{A} is the numerator relationship matrix between animals with entries denoted as A_{ij} for i and $j = 1, \dots, n$. The likelihood of the model for random animal genetic effects is

$f(\mathbf{u} | \mathbf{G}) = (2\pi)^{-n/2} |\mathbf{G}|^{-n/2} \exp\left(-\frac{1}{2} \mathbf{u}' (\mathbf{A} \otimes \mathbf{G})^{-1} \mathbf{u}\right)$, where n is the number of animals ($n = 586$ for boars and $n = 495$ for gilts) with data in the pedigree. The \mathbf{A} relationship matrix was formulated based on all 9327 pigs in the pedigree, and then \mathbf{A}^{-1} (the inverse of the relationship matrix \mathbf{A}) was calculated using ASREML (Gilmour et al., 2006). Only n rows and n columns corresponding to the pigs with phenotypic data were kept in the \mathbf{A}^{-1} matrix for later analyses, with entries denoted as A^{ij} for i and $j = 1, \dots, n$.

Bayesian Analysis

Prior distributions. The prior distribution for the residual variance σ_e^2 was the inverse Chi-square distribution $\sigma_e^2 \sim \text{Inv} - \chi^2(\nu_e, \sigma_0^2)$ with probability density function $g(\sigma_e^2 | \nu_e, \sigma_0^2) = (\nu_e / 2)^{\nu_e/2} (\Gamma(\nu_e / 2))^{-1} (\sigma_0^2)^{\nu_e} (\sigma_e^2)^{-(\nu_e/2+1)} \exp(-\nu_e \sigma_0^2 / (2\sigma_e^2))$. The prior distribution for parameter $\boldsymbol{\beta}$ was $g(\boldsymbol{\beta}) = g(\boldsymbol{\beta}_k; k = -1, 0, \dots, 5) \propto \text{constant}$. The prior distributions of covariance matrix \mathbf{G} and \mathbf{R} were both inverse Wishart distributions with $\mathbf{G} \sim IW(\nu_g, \mathbf{G}_0^{-1})$ and $\mathbf{R} \sim IW(\nu_r, \mathbf{R}_0^{-1})$. The probability density functions for these matrices are

$$g(\mathbf{G} | \nu_g, \mathbf{G}_0^{-1}) = \left(2^{3\nu_g/2} \pi^{3(3-1)/4} \prod_{i=1}^3 \Gamma\left(\frac{\nu_g+1-i}{2}\right)\right)^{-1} |\mathbf{G}_0|^{\nu_g/2} |\mathbf{G}|^{-\frac{\nu_g+3+1}{2}} \exp\left(-\frac{1}{2} \text{tr}(\mathbf{G}_0 \mathbf{G}^{-1})\right), \text{ and}$$

$$g(\mathbf{R} | \nu_r, \mathbf{R}_0^{-1}) = \left(2^{3\nu_r/2} \pi^{3(3-1)/4} \prod_{i=1}^3 \Gamma\left(\frac{\nu_r+1-i}{2}\right)\right)^{-1} |\mathbf{R}_0|^{\nu_r/2} |\mathbf{R}|^{-\frac{\nu_r+3+1}{2}} \exp\left(-\frac{1}{2} \text{tr}(\mathbf{R}_0 \mathbf{R}^{-1})\right).$$

Degrees of freedoms of prior distributions were set equal to $\nu_e = \nu_g = \nu_r = 4$ in order to have vague prior information. Parameter σ_0^2 was set equal to 0.25 (kg/d)^2 for DFI and to 7 (kg)^2 for BW for boars and gilts based on the results of phenotypic analyses from chapter 3. The scale matrices \mathbf{G}_0 and \mathbf{R}_0 for DFI and BW for boars and gilts were obtained from the 3-trait analyses of the Gompertz curve parameters of the 353 boars and 240 gilts, where Gompertz parameters were estimated based on each individual pig's own data from the two-

stage analysis. A detailed description of the two-stage analysis is given later in this chapter.

For DFI, \mathbf{G}_0 and \mathbf{R}_0 were set equal to:

$$\mathbf{G}_0 = \begin{pmatrix} 0.1037 & 0.5649 & 1.105 \\ 0.5649 & 45.00 & -35.58 \\ 1.105 & -35.58 & 58.79 \end{pmatrix}, \text{ and } \mathbf{R}_0 = \begin{pmatrix} 0.5544 & 9.765 & 26.42 \\ 9.765 & 498.1 & 386.8 \\ 26.42 & 386.8 & 1838 \end{pmatrix} \text{ for boars,}$$

$$\mathbf{G}_0 = \begin{pmatrix} 0.2347 & 1.475 & 9.110 \\ 1.475 & 138.7 & 28.30 \\ 9.110 & 28.30 & 683.9 \end{pmatrix}, \text{ and } \mathbf{R}_0 = \begin{pmatrix} 0.4279 & 9.534 & 23.42 \\ 9.534 & 489.0 & 308.1 \\ 23.42 & 308.1 & 1849 \end{pmatrix} \text{ for gilts.}$$

For BW, \mathbf{G}_0 and \mathbf{R}_0 were set equal to:

$$\mathbf{G}_0 = \begin{pmatrix} 1097 & 243 & 54 \\ 243 & 139 & 40 \\ 54 & 40 & 14 \end{pmatrix}, \text{ and } \mathbf{R}_0 = \begin{pmatrix} 8576 & 3520 & 2613 \\ 3520 & 1539 & 1158 \\ 2613 & 1158 & 909 \end{pmatrix} \text{ for boars,}$$

$$\mathbf{G}_0 = \begin{pmatrix} 3621 & 1387 & 1171 \\ 1387 & 620 & 518 \\ 1171 & 518 & 522 \end{pmatrix}, \text{ and } \mathbf{R}_0 = \begin{pmatrix} 3031 & 1527 & 1101 \\ 1527 & 827 & 609 \\ 1101 & 609 & 452 \end{pmatrix} \text{ for gilts.}$$

Conditional posterior distributions. The joint posterior distribution is

$p(\boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{R}, \sigma_e^2 | \mathbf{y}) = f(\mathbf{y} | \boldsymbol{\theta}, \sigma_e^2) \times f(\boldsymbol{\theta} | \boldsymbol{\beta}, \mathbf{u}, \mathbf{R}) \times f(\mathbf{u} | \mathbf{G}) \times g(\mathbf{G}) \times g(\mathbf{R}) \times g(\boldsymbol{\beta}) \times g(\sigma_e^2) / f(\mathbf{y})$.
To simplify notation, denote $d(\boldsymbol{\theta}_i, t_{ij}) = a_i \times \exp(-\exp(-(t_{ij} - b_i)/c_i))$. The full conditional posterior distributions for parameters are then as follows.

$$p(\sigma_e^2 | \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{R}, \mathbf{y}) \propto f(\mathbf{y} | \boldsymbol{\theta}, \sigma_e^2) \times g(\sigma_e^2)$$

$$\propto (\sigma_e^2)^{-N/2} \exp\left(\frac{-1}{2\sigma_e^2} \sum_{i=1}^n \sum_{j=1}^{r_i} (y_{ij} - d(\boldsymbol{\theta}_i, t_{ij}))^2\right) (\sigma_e^2)^{-(\nu_e/2+1)} \exp(-\nu_e \sigma_0^2 / (2\sigma_e^2))$$

$$\propto (\sigma_e^2)^{-((\nu_e+N)/2+1)} \exp\left(\frac{-1}{2\sigma_e^2} (\nu_e \sigma_0^2 + \sum_{i=1}^n \sum_{j=1}^{r_i} (y_{ij} - d(\boldsymbol{\theta}_i, t_{ij}))^2)\right)$$

i.e. $\sigma_e^2 | \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \mathbf{R}, \mathbf{y} \sim \text{Inv-}\chi^2\left(\nu_e + N, (\nu_e \sigma_0^2 + \sum_{i=1}^n \sum_{j=1}^{r_i} (y_{ij} - d(\boldsymbol{\theta}_i, t_{ij}))^2) / (\nu_e + N)\right)$;

$$\begin{aligned}
p(\mathbf{R} \mid \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \sigma_e^2, \mathbf{y}) &= p(\mathbf{R} \mid \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}) \propto f(\boldsymbol{\theta} \mid \boldsymbol{\beta}, \mathbf{u}, \mathbf{R}) \times g(\mathbf{R}) \\
&\propto |\mathbf{R}|^{-n/2} \exp\left(-\frac{1}{2}(\boldsymbol{\theta} - \boldsymbol{\beta} - \mathbf{u})'(\mathbf{I} \otimes \mathbf{R})^{-1}(\boldsymbol{\theta} - \boldsymbol{\beta} - \mathbf{u})\right) |\mathbf{R}|^{-\frac{\nu_r+3+1}{2}} \exp\left(-\frac{1}{2}\text{tr}(\mathbf{R}_0 \mathbf{R}^{-1})\right) \\
&\propto |\mathbf{R}|^{-\frac{\nu_r+n+3+1}{2}} \exp\left(-\frac{1}{2}\text{tr}\left(\left(\sum_{i=1}^n (\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)(\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)' + \mathbf{R}_0\right) \mathbf{R}^{-1}\right)\right)
\end{aligned}$$

i.e. $\mathbf{R} \mid \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}, \mathbf{G}, \sigma_e^2, \mathbf{y} \sim \text{Inv-W}(\nu_r + n, (\sum_{i=1}^n (\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)(\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)' + \mathbf{R}_0)^{-1})$;

$$\begin{aligned}
p(\mathbf{G} \mid \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{u}, \mathbf{R}, \sigma_e^2, \mathbf{y}) &= p(\mathbf{G} \mid \mathbf{u}) \propto f(\mathbf{u} \mid \mathbf{G}) \times g(\mathbf{G}) \\
&\propto |\mathbf{G}|^{-n/2} \exp\left(-\frac{1}{2}\mathbf{u}'(\mathbf{A} \otimes \mathbf{G})^{-1}\mathbf{u}\right) |\mathbf{G}|^{-\frac{\nu_g+3+1}{2}} \exp\left(-\frac{1}{2}\text{tr}(\mathbf{G}_0 \mathbf{G}^{-1})\right) \\
&\propto |\mathbf{G}|^{-\frac{\nu_g+n+3+1}{2}} \exp\left(-\frac{1}{2}\text{tr}((\mathbf{U}'\mathbf{A}^{-1}\mathbf{U} + \mathbf{G}_0)\mathbf{G}^{-1})\right)
\end{aligned}$$

i.e. $\mathbf{G} \sim IW(\nu_g + n, (\mathbf{U}'\mathbf{A}^{-1}\mathbf{U} + \mathbf{G}_0)^{-1})$, where $\mathbf{U}_{n \times 3}$ is a matrix with the i th row representing the animal genetic effect \mathbf{u}_i for pig i .

Conditional posterior distributions for fixed effects $\boldsymbol{\beta}$ are:

$$\begin{aligned}
p(\boldsymbol{\beta}_{k(i)} \mid \boldsymbol{\theta}, \mathbf{u}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}) &\propto \prod_{i \text{ s.t. } k(i)=k}^{n_k} f(\boldsymbol{\theta}_i \mid \boldsymbol{\beta}_{k(i)}, \mathbf{u}_i, \mathbf{R}) \\
&\propto \exp\left(-\frac{1}{2} \sum_{i \text{ s.t. } k(i)=k}^{n_k} [(\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)' \mathbf{R}^{-1} (\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)]\right) \\
&\propto \exp\left(-\frac{1}{2} \left[\boldsymbol{\beta}_{k(i)} - \sum_{i \text{ s.t. } k(i)=k}^{n_k} (\boldsymbol{\theta}_i - \mathbf{u}_i) / n_k \right]' \left(\frac{\mathbf{R}}{n_k} \right)^{-1} \left[\boldsymbol{\beta}_{k(i)} - \sum_{i \text{ s.t. } k(i)=k}^{n_k} (\boldsymbol{\theta}_i - \mathbf{u}_i) / n_k \right] \right)
\end{aligned}$$

i.e. $(\boldsymbol{\beta}_{k(i)} \mid \boldsymbol{\theta}, \mathbf{u}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}) \sim N\left[\sum_{i \text{ s.t. } k(i)=k}^{n_k} (\boldsymbol{\theta}_i - \mathbf{u}_i) / n_k, \mathbf{R} / n_k\right]$, where n_k is the number of pigs

in generation k .

$$\begin{aligned}
p(\mathbf{u} | \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}) &\propto f(\boldsymbol{\theta} | \boldsymbol{\beta}, \mathbf{u}, \mathbf{R}) \times f(\mathbf{u} | \mathbf{G}) \\
&\propto \exp\left(-\frac{1}{2}\left[(\boldsymbol{\theta} - \boldsymbol{\beta} - \mathbf{u})'(\mathbf{I} \otimes \mathbf{R})^{-1}(\boldsymbol{\theta} - \boldsymbol{\beta} - \mathbf{u}) + \mathbf{u}'(\mathbf{A} \otimes \mathbf{G})^{-1}\mathbf{u}\right]\right)
\end{aligned}$$

Let $\boldsymbol{\delta} = \boldsymbol{\theta} - \boldsymbol{\beta}$ with $\boldsymbol{\delta}_i$ representing elements for pig i , $\boldsymbol{\Sigma}^{-1} = \mathbf{A}^{-1} \otimes \mathbf{G}^{-1}$, and $\mathbf{S}^{-1} = \mathbf{I} \otimes \mathbf{R}^{-1}$ to simplify the notations.

$$\begin{aligned}
p(\mathbf{u} | \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}) \\
&\propto \exp\left(-\frac{1}{2}\left[\mathbf{u}'\mathbf{S}^{-1}\mathbf{u} - 2\mathbf{u}'\mathbf{S}^{-1}\boldsymbol{\delta} + \mathbf{u}'\boldsymbol{\Sigma}^{-1}\mathbf{u}\right]\right) \\
&\propto \exp\left(-\frac{1}{2}\left[(\mathbf{u} - \hat{\mathbf{u}})'(\mathbf{S}^{-1} + \boldsymbol{\Sigma}^{-1})(\mathbf{u} - \hat{\mathbf{u}}) + 2\mathbf{u}'(\mathbf{S}^{-1} + \boldsymbol{\Sigma}^{-1})\hat{\mathbf{u}} - 2\mathbf{u}'\mathbf{S}^{-1}\boldsymbol{\delta}\right]\right)
\end{aligned}$$

Therefore, $(\mathbf{u} | \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}) \sim N[\hat{\mathbf{u}}, (\mathbf{S}^{-1} + \boldsymbol{\Sigma}^{-1})^{-1}]$, if and only if, for every \mathbf{u} , $2\mathbf{u}'(\mathbf{S}^{-1} + \boldsymbol{\Sigma}^{-1})\hat{\mathbf{u}} = 2\mathbf{u}'\mathbf{S}^{-1}\boldsymbol{\delta}$, i.e. $(\mathbf{S}^{-1} + \boldsymbol{\Sigma}^{-1})\hat{\mathbf{u}} = \mathbf{S}^{-1}\boldsymbol{\delta}$, i.e. $\hat{\mathbf{u}} = (\mathbf{S}^{-1} + \boldsymbol{\Sigma}^{-1})^{-1}\mathbf{S}^{-1}\boldsymbol{\delta}$.

To sample the whole vector \mathbf{u} from a multivariate normal distribution, the dimension is too big. We could sample $\mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_n$ individually conditional on all others, i.e. sample $(\mathbf{u}_i | \mathbf{u}_{-i}, \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y})$, where \mathbf{u}_i represents the animal genetic effects for the three Gompertz parameters for pig i and \mathbf{u}_{-i} represent vector \mathbf{u} with the three elements for pig i removed. Wright et al. (2000) showed that sampling either the whole vector \mathbf{u} or $\mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_n$ individually conditional on all others both result in a Gibbs sampler with stationary distribution for the posterior distribution. Each iteration of the Gibbs sampler for the whole vector \mathbf{u} is very slow if the dimension of \mathbf{u} is large, while each iteration is much faster for sampling $\mathbf{u}_1, \mathbf{u}_2, \dots, \mathbf{u}_n$ individually conditional on all others (Wright et al., 2000).

$$\begin{aligned}
p(\mathbf{u}_i | \mathbf{u}_{-i}, \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}) \\
&\propto \exp\left(-\frac{1}{2}\left[\mathbf{u}_i'\mathbf{R}^{-1}\mathbf{u}_i - 2\mathbf{u}_i'\mathbf{R}^{-1}\boldsymbol{\delta}_i + \mathbf{u}_i'A^{ii}\mathbf{G}^{-1}\mathbf{u}_i + 2\sum_{i \neq j}^n \mathbf{u}_i'A^{ij}\mathbf{G}^{-1}\mathbf{u}_j\right]\right) \\
&\propto \exp\left(-\frac{1}{2}\left[(\mathbf{u}_i - \hat{\mathbf{u}}_i)'(\mathbf{R}^{-1} + A^{ii}\mathbf{G}^{-1})(\mathbf{u}_i - \hat{\mathbf{u}}_i) + 2\mathbf{u}_i'(\mathbf{R}^{-1} + A^{ii}\mathbf{G}^{-1})\hat{\mathbf{u}}_i - 2\mathbf{u}_i'\mathbf{R}^{-1}\boldsymbol{\delta}_i + 2\sum_{i \neq j}^n \mathbf{u}_i'A^{ij}\mathbf{G}^{-1}\mathbf{u}_j\right]\right)
\end{aligned}$$

Therefore, $(\mathbf{u}_i | \mathbf{u}_{-i}, \boldsymbol{\theta}, \boldsymbol{\beta}, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}) \sim N(\hat{\mathbf{u}}_i, (\mathbf{R}^{-1} + A^{ii}\mathbf{G}^{-1})^{-1})$, if and only if, for every \mathbf{u}_i ,

$$2\mathbf{u}_i'(\mathbf{R}^{-1} + A^{ii}\mathbf{G}^{-1})\hat{\mathbf{u}}_i = 2\mathbf{u}_i'(\mathbf{R}^{-1}\boldsymbol{\delta}_i + \sum_{i \neq j}^n A^{ij}\mathbf{G}^{-1}\mathbf{u}_j),$$

$$\text{i.e. } (\mathbf{R}^{-1} + \mathbf{A}^{ii} \mathbf{G}^{-1}) \hat{\mathbf{u}}_i = \mathbf{R}^{-1} \boldsymbol{\delta}_i + \sum_{i \neq j}^n \mathbf{A}^{ij} \mathbf{G}^{-1} \mathbf{u}_j ,$$

i.e. $\hat{\mathbf{u}}_i = (\mathbf{R}^{-1} + \mathbf{A}^{ii} \mathbf{G}^{-1})^{-1} (\mathbf{R}^{-1} \boldsymbol{\delta}_i + \sum_{i \neq j}^n \mathbf{A}^{ij} \mathbf{G}^{-1} \mathbf{u}_j)$, where \mathbf{A}^{ii} and \mathbf{A}^{ij} are entries of the inverse relationship matrix \mathbf{A}^{-1} for i and $j = 1, \dots, n$.

The conditional posterior distribution of $\boldsymbol{\theta}_i$ was set as below,

$$\begin{aligned} p(\boldsymbol{\theta}_i | \boldsymbol{\beta}_i, \mathbf{u}_i, \mathbf{G}, \mathbf{R}, \sigma_e^2, \mathbf{y}_i) &\propto f(\mathbf{y}_i | \boldsymbol{\theta}_i, \sigma_e^2) \times f(\boldsymbol{\theta}_i | \boldsymbol{\beta}_{k(i)}, \mathbf{u}_i, \mathbf{R}) \\ &\propto \exp\left(\frac{-1}{2\sigma_e^2} \sum_{j=1}^{r_i} (y_{ij} - d(\boldsymbol{\theta}_i, t_{ij}))^2\right) \exp\left(-\frac{1}{2} (\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)' \mathbf{R}^{-1} (\boldsymbol{\theta}_i - \boldsymbol{\beta}_{k(i)} - \mathbf{u}_i)\right). \end{aligned}$$

Additional notations are introduced as follows.

$\boldsymbol{\theta}_i^c$: the current value of $\boldsymbol{\theta}_i$ at an iteration of the Markov chain;

$\boldsymbol{\theta}_i^{MLE}$: the maximum likelihood estimate for $\boldsymbol{\theta}_i$ using the data from pig i only;

$J(\boldsymbol{\theta}_i | \boldsymbol{\theta}_i^c)$: a jumping distribution given the current value for $\boldsymbol{\theta}_i$;

$\boldsymbol{\theta}_i^*$: a candidate value for $\boldsymbol{\theta}_i$ sampled from the jumping distribution;

$$A_{ij} = \frac{\partial d(\boldsymbol{\theta}_i, t_{ij})}{\partial a_i} = \exp(-\exp(-(t_{ij} - b_i)/c_i)) ;$$

$$B_{ij} = \frac{\partial d(\boldsymbol{\theta}_i, t_{ij})}{\partial b_i} = -\frac{1}{c_i} d(\boldsymbol{\theta}_i, t_{ij}) \exp(-(t_{ij} - b_i)/c_i) ;$$

$$C_{ij} = \frac{\partial d(\boldsymbol{\theta}_i, t_{ij})}{\partial c_i} = -\frac{t_{ij} - b_i}{c_i^2} d(\boldsymbol{\theta}_i, t_{ij}) \exp(-(t_{ij} - b_i)/c_i) ;$$

$$l_i: \text{the log-likelihood for the } i\text{th pig} = \frac{-1}{2\sigma_e^2} \sum_{j=1}^{r_i} (y_{ij} - d(\boldsymbol{\theta}_i, t_{ij}))^2 ;$$

$$\mathbf{F}_i: \text{the gradient of the log-likelihood for the } i\text{th pig} = \begin{pmatrix} \frac{\partial l_i}{\partial a_i} & \frac{\partial l_i}{\partial b_i} & \frac{\partial l_i}{\partial c_i} \end{pmatrix}, \text{ where}$$

$$\frac{\partial l_i}{\partial a_i} = \frac{1}{\sigma_e^2} \sum_{j=1}^{r_i} \varepsilon_{ij} A_{ij} , \quad \frac{\partial l_i}{\partial b_i} = \frac{1}{\sigma_e^2} \sum_{j=1}^{r_i} \varepsilon_{ij} B_{ij} , \quad \frac{\partial l_i}{\partial c_i} = \frac{1}{\sigma_e^2} \sum_{j=1}^{r_i} \varepsilon_{ij} C_{ij} ;$$

\mathbf{H}_i : Hessian matrix, the second derivative matrix of the log-likelihood for the i th pig

$$= \begin{pmatrix} \frac{\partial^2 l_i}{\partial a_i^2} & \frac{\partial^2 l_i}{\partial a_i \partial b_i} & \frac{\partial^2 l_i}{\partial a_i \partial c_i} \\ \frac{\partial^2 l_i}{\partial a_i \partial b_i} & \frac{\partial^2 l_i}{\partial b_i^2} & \frac{\partial^2 l_i}{\partial b_i \partial c_i} \\ \frac{\partial^2 l_i}{\partial a_i \partial c_i} & \frac{\partial^2 l_i}{\partial b_i \partial c_i} & \frac{\partial^2 l_i}{\partial c_i^2} \end{pmatrix}$$

$$= \frac{1}{\sigma_e^2} \begin{pmatrix} \sum_{j=1}^{r_i} -A_{ij}^2 & \sum_{j=1}^{r_i} \frac{\varepsilon_{ij}}{a_i} B_{ij} - A_{ij} B_{ij} & \sum_{j=1}^{r_i} \frac{\varepsilon_{ij}}{a_i} C_{ij} - A_{ij} C_{ij} \\ \sum_{j=1}^{r_i} \frac{\varepsilon_{ij}}{a_i} B_{ij} - A_{ij} B_{ij} & \sum_{j=1}^{r_i} \varepsilon_{ij} \left(\frac{B_{ij}^2}{d(\boldsymbol{\theta}_i, t_{ij})} + \frac{B_{ij}}{c_i} \right) - B_{ij}^2 & \sum_{j=1}^{r_i} \varepsilon_{ij} \left(\frac{B_{ij} C_{ij}}{d(\boldsymbol{\theta}_i, t_{ij})} + \frac{C_{ij} - B_{ij}}{c_i} \right) - B_{ij} C_{ij} \\ \sum_{j=1}^{r_i} \frac{\varepsilon_{ij}}{a_i} C_{ij} - A_{ij} C_{ij} & \sum_{j=1}^{r_i} \varepsilon_{ij} \left(\frac{B_{ij} C_{ij}}{d(\boldsymbol{\theta}_i, t_{ij})} + \frac{C_{ij} - B_{ij}}{c_i} \right) - B_{ij} C_{ij} & \sum_{j=1}^{r_i} \varepsilon_{ij} \left(\frac{C_{ij}^2}{d(\boldsymbol{\theta}_i, t_{ij})} - \frac{2C_{ij}}{c_i} + \frac{(t_{ij} - b_i)C_{ij}}{c_i^2} \right) - C_{ij}^2 \end{pmatrix}$$

$\hat{\Sigma}_{\boldsymbol{\theta}_i^{MLE}}$: the estimated variance matrix from $[-\mathbf{H}_i]^{-1}$ evaluated at $\boldsymbol{\theta}_i^{MLE}$;

$\bar{\Sigma}_{\boldsymbol{\theta}}$: 2 times of average of variance matrix $\hat{\Sigma}_{\boldsymbol{\theta}_i^{MLE}}$ for pigs which could get maximum likelihood estimate for $\boldsymbol{\theta}_i$ using its own data.

Although the asymptotic value a_i conditional on all others follows a normal posterior distribution, the posterior distributions of parameters b_i and c_i don't follow any known parametric family (Liu, 2000). Liu (2000) also found that drawing the vector (a_i, b_i, c_i) in a single tri-variate Metropolis-Hastings (M-H) algorithm had converged faster than drawing a_i from its full conditional posterior distribution and then drawing the vector (b_i, c_i) in a bi-variate M-H step, and then drawing a_i, b_i, c_i one by one in sequence in single-variate M-H steps. Therefore, the tri-variate random walk M-H algorithm was used to draw the vector $\boldsymbol{\theta}_i = (a_i, b_i, c_i)$. The jumping distribution is specified as a normal distribution $J(\boldsymbol{\theta}_i | \boldsymbol{\theta}_i^c) = N(\boldsymbol{\theta}_i | \boldsymbol{\theta}_i^c, \bar{\Sigma}_{\boldsymbol{\theta}})$ with mean equal to the current value $\boldsymbol{\theta}_i^c$ and variance matrix equal to $\bar{\Sigma}_{\boldsymbol{\theta}}$. The importance ratio for the M-H algorithm simplifies to $\alpha = \frac{p(\boldsymbol{\theta}_i^* | \mathbf{y})}{p(\boldsymbol{\theta}_i^c | \mathbf{y})}$ because the jumping distribution $J(\boldsymbol{\theta}_i^* | \boldsymbol{\theta}_i^c) = J(\boldsymbol{\theta}_i^c | \boldsymbol{\theta}_i^*)$ is symmetric.

Convergence diagnosis and inference. Three parallel Markov chains with over-dispersed starting values were run in this study. The length of chains was set to 50,000 iterations. Statistics of the potential scale reduction factor (Gelman and Rubin, 1992) from the ‘coda’ package in R (R, 2010) were used for convergence diagnosis. Once estimates of the potential scale reduction factor were below 1.3 for all interested scalar parameters and remained below 1.3 after that, the three chains were diagnosed as converged at that iteration. The three chains converged before 30,000 iterations. To be conservative, the second halves of the 20,000 iterations after convergence from all three chains were collected and treated as samples from the target distribution.

For each separate analysis of BW and DFI for boars and gilts, the 30,000 posterior samples were collected from the three chains for scalar parameters of variance components, the fixed effect for generation 5, and average animal genetic effects for the LRFI and CTRL lines for Gompertz curve parameters at generation 5. For each of 30,000 posterior samples, new variables of heritability of the three Gompertz parameters and genetic correlations between Gompertz parameters were calculated from corresponding variance components; the Gompertz parameters for the LRFI and CTRL lines at generation 5 were calculated as the sum of the fixed effect for generation 5 and average animal genetic effects for each line at generation 5; line differences (LRFI-CTRL) of Gompertz parameters were calculated as the difference between average animal genetic effects for the lines at generation 5. The marginal posterior distributions of new variables of interest were obtained from these 30,000 newly calculated posterior samples. All inferences were based on these 30,000 samples.

Results

Estimates of Genetic Parameters for Gompertz Curve Parameters

Table 5.1 shows means and standard deviations of posterior distributions for variance components, heritability, and genetic correlations for the three Gompertz curve parameters for BW and DFI for boars and gilts. Estimates of residual variance were similar between boars and gilts and were 3.92 and 3.44 kg² for BW for boars and gilts, and 0.183 and 0.170 (kg/d)² for DFI for boars and gilts.

Estimates of genetic and environmental variance components for DFI were smaller in magnitude for boars than for gilts (Table 5.1) but 95% credible intervals for these estimates are overlapped for boars and gilts. Estimates of environmental variance components for BW for boars were smaller than for gilts but estimates of genetic variance components for BW for boars were greater than for gilts (Table 5.1), however, 95% credible intervals for estimates of genetic and environmental variance components are overlapped for boars and gilts.

Heritability is the ratio of genetic variance to phenotypic variance, which is equal to genetic variance plus environmental variance for Gompertz curve parameters. Estimates of heritability of Gompertz curve parameters of mature daily feed intake and inflection point for DFI were similar between boars and gilts, however, the estimate of heritability of the decay parameter for DFI was 0.81 for boars and 0.53 for gilts but 95% credible intervals for these two estimates are overlapped. Estimates of heritability of Gompertz curve parameters of mature body weight, inflection point, and decay parameter for BW were greater for boars than for gilts but 95% credible intervals for these estimates are overlapped for boars and gilts.

Estimates of genetic correlations between growth curve parameters for DFI for boars and gilts were greater than 0.7, except that the estimate of the genetic correlation between the inflection point and the decay parameter for DFI for boars was 0.37. Estimates of genetic correlations between growth curve parameters for BW for boars and gilts were greater than 0.9, except that the estimate of the genetic correlation between mature body weight and the decay parameter for BW for gilts was 0.74, but with a big standard deviation of 0.18.

Table 5.1 Posterior means and standard deviations of variance components and genetic parameters for Gompertz curve parameters for DFI and BW for boars and gilts

Parameter ¹	Boars				Gilts			
	BW ²		DFI ²		BW ²		DFI ²	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
σ_e^2	3.92	0.07	0.183	0.001	3.44	0.07	0.170	0.001
R_{aa}	4324	780	0.32	0.06	6875	1289	0.40	0.18
R_{ba}	2120	375	7	1	3758	654	15	7
R_{bb}	1150	184	210	41	2152	342	742	295
R_{ca}	1524	267	8	2	2958	499	23	9
R_{cb}	838	132	172	50	1667	265	783	331
R_{cc}	644	97	424	102	1328	212	1795	491
G_{aa}	7103	1788	0.95	0.19	5340	2453	1.38	0.45
G_{ba}	3162	844	16	4	2211	1231	43	17
G_{bb}	1512	414	472	118	1080	627	1478	648
G_{ca}	2325	626	32	7	1477	933	44	19
G_{cb}	1106	307	351	153	787	478	1324	711
G_{cc}	887	235	1852	347	663	377	2158	956
h_{aa}^2	0.61	0.09	0.74	0.07	0.42	0.14	0.75	0.15
h_{bb}^2	0.56	0.10	0.68	0.09	0.32	0.14	0.64	0.19
h_{cc}^2	0.57	0.09	0.81	0.06	0.32	0.14	0.53	0.17
$gcorr_{ba}$	0.96	0.01	0.75	0.07	0.90	0.08	0.93	0.10
$gcorr_{ca}$	0.92	0.03	0.76	0.06	0.74	0.18	0.79	0.16
$gcorr_{cb}$	0.95	0.02	0.37	0.13	0.91	0.07	0.71	0.22

¹ σ_e^2 : residual variance; For parameters a (mature BW or DFI), b (inflection point), c (decay parameter), G and R : genetic and environmental covariance matrix; $gcorr$: genetic correlations; h^2 : heritability

²BW: body weight; DFI: daily feed intake

Estimates of Line Differences for Gompertz Curve Parameters

Table 5.2 shows means and standard deviations of the posterior densities of the Gompertz curve parameters for the LRFI and CTRL lines at generation 5 and the posterior probability of the line differences (LRFI-CTRL) of Gompertz curve parameters being greater than zero. Histograms of marginal posterior distributions for the line differences between LRFI and CTRL lines for the Gompertz curve parameters for DFI and for BW are in Figures 5.2 and 5.3, respectively. The LRFI boars had a significantly ($p = 0.08$) lower mature daily feed intake (2.97 vs. 3.10 kg/d), and a significantly ($p = 0.03$) earlier inflection point (88 vs. 92 d) for DFI than CTRL boars (Table 5.2). Boars from the LRFI line also had a greater decay parameter (69 vs. 66 d) for DFI, but this difference was not significant ($p = 0.77$). Similarly, compared with CTRL gilts, LRFI gilts had a significantly lower mature feed intake (2.76 vs. 2.96 kg with $p = 0.04$), and an earlier inflection point (73 vs. 78 d with $p = 0.11$). The LRFI gilts had a lower decay parameter for DFI (88 vs. 90 d with $p = 0.35$) than CTRL gilts (Table 5.2). Line differences of decay parameter for gilts and for boars were opposite in sign, but neither was significantly different from zero ($p = 0.35$ for gilts and $p = 0.77$ for boars). Line differences for decay parameters for DFI for boars and gilts are shown clearly in Figures 5.2 (e) and (f).

Boars from the LRFI line had a lower mature body weight (288 vs. 299 kg with $p = 0.11$), an earlier inflection point (187 vs. 191 d with $p = 0.16$), and a lower decay parameter (128 vs. 130 d with $p = 0.27$) than CTRL boars for BW (Table 5.2). Gilts from the LRFI line also had a lower mature body weight than CTRL gilts (304 vs. 319 kg with $p = 0.12$), but a similar inflection point (213 vs. 213 d with $p = 0.46$), and a greater decay parameter (160 vs. 155 d with $p = 0.80$) for BW than CTRL gilts (Table 5.2). However, the line differences (LRFI-CTRL) for these three Gompertz parameters for BW were not significantly greater than zero ($p > 0.1$) for either boars or gilts. Estimates of the mature body weights and the decay parameters from the current study are within the range of ~180 to ~320 kg for the mature body weight and ~200 to ~63 days for the decay parameter, which were summarized in Figure 3 of Knap (2000), noting that the decay parameter is equal to $1/\text{growth rate parameter}$ of Knap (2000).

Table 5.2 Posterior means and standard deviations of Gompertz curve parameters for LRFI and CTRL lines for DFI and BW at generation 5 by summing the fixed effect of generation and average animal genetic effects for each line for each posterior sample

Sex	Parameter ¹	Line ²	BW ³			DFI ³		
			Mean	SD	Pr>0 ⁴	Mean	SD	Pr>0 ⁴
Boars	<i>a</i>	LRFI	288	9		2.97	0.09	
		CTRL	299	9		3.10	0.08	
		LRFI-CTRL	-11	9	0.11	-0.13	0.09	0.08
	<i>b</i>	LRFI	187	4		88	2	
		CTRL	191	4		92	2	
		LRFI-CTRL	-4	4	0.16	-4	2	0.03
	<i>c</i>	LRFI	128	3		69	5	
		CTRL	130	3		66	4	
		LRFI-CTRL	-2	3	0.27	3	4	0.77
	<i>a</i>	LRFI	304	13		2.76	0.10	
		CTRL	319	12		2.96	0.09	
		LRFI-CTRL	-15	13	0.12	-0.21	0.11	0.04
Gilts	<i>b</i>	LRFI	213	7		73	4	
		CTRL	213	7		78	4	
		LRFI-CTRL	0.01	6	0.46	-5	4	0.11
	<i>c</i>	LRFI	160	5		88	6	
		CTRL	155	5		90	6	
		LRFI-CTRL	5	5	0.80	-2	5	0.35

¹ *a* is the mature BW or DFI; *b* is the inflection point (days); *c* is the decay parameter (days)

² LRFI is low RFI line; CTRL is control line; LRFI-CTRL is the difference between lines

³ BW: body weight; DFI: daily feed intake

⁴ Posterior probability of the line difference being bigger than 0

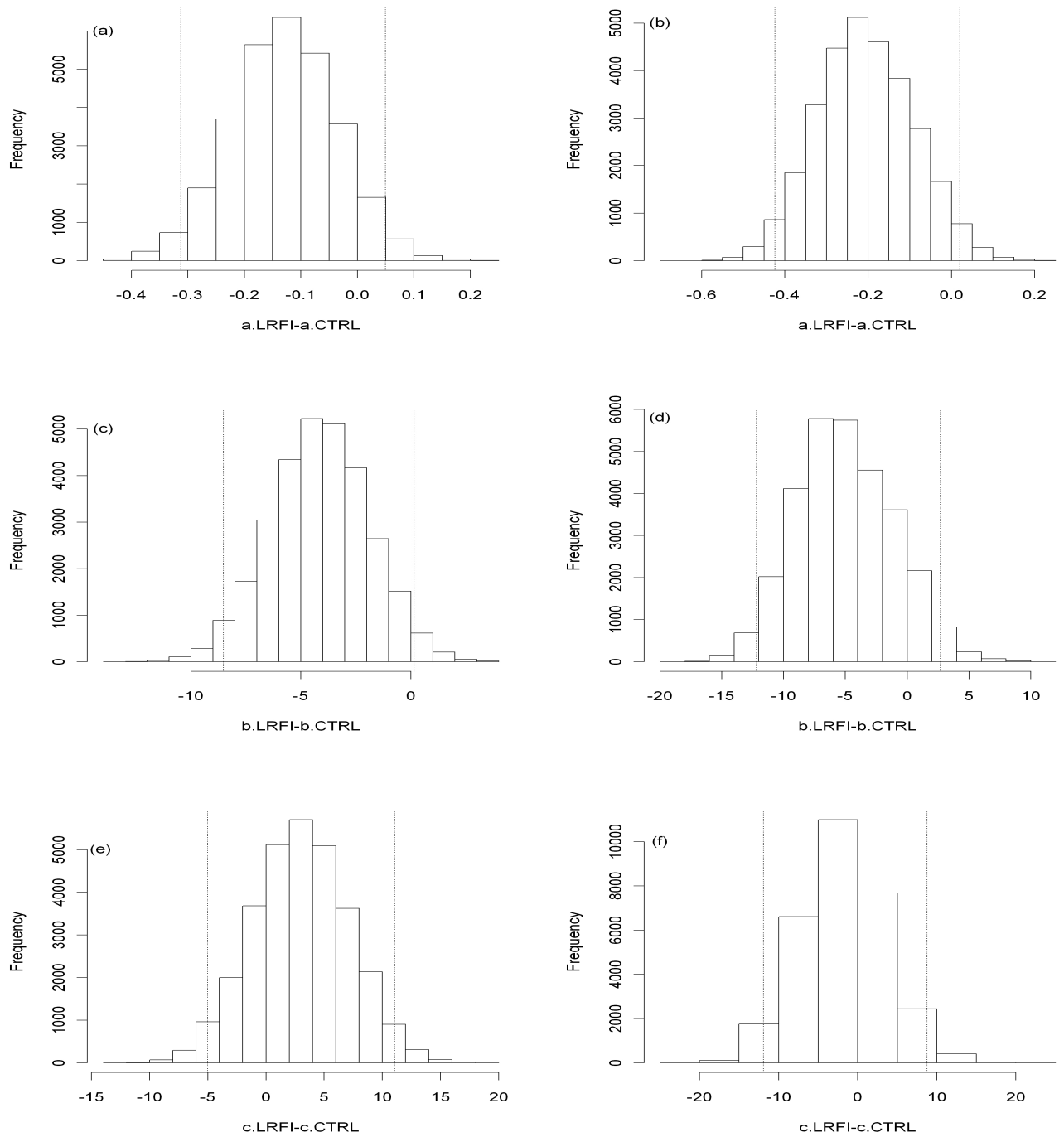


Figure 5.2 Histograms of marginal posterior distributions for the line differences between the lower residual feed intake line and the control line (LRFI-CTRL) for Gompertz curve parameters (a, b, and c) for daily feed intake for boars (left panel) and gilts (right panel), with dotted vertical lines for the 2.5 and 97.5 % quantiles

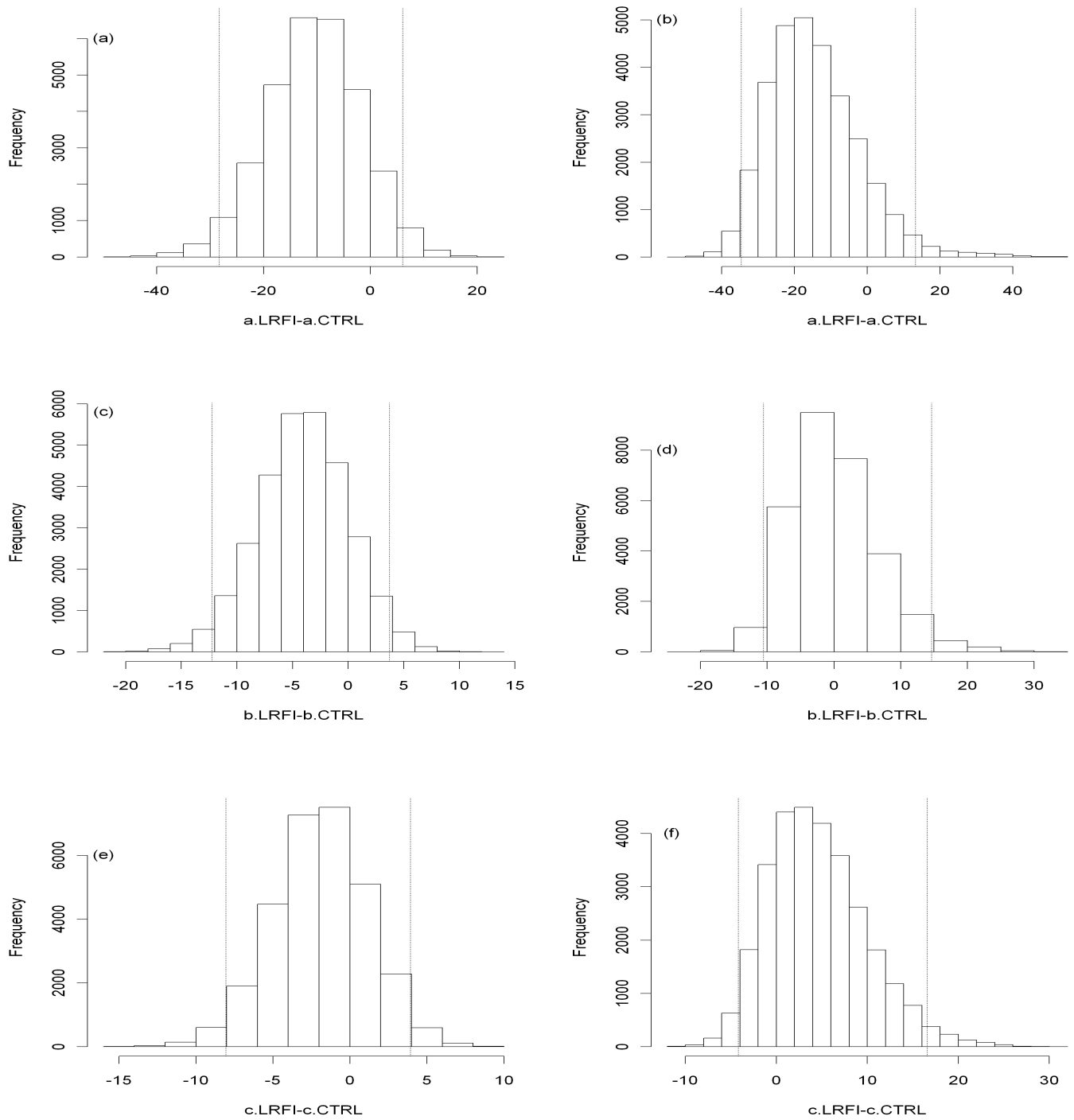


Figure 5.3 Histograms of marginal posterior distributions for the line differences between the lower residual feed intake line and the control line (LRFI-CTRL) for Gompertz curve parameters (a, b, and c) for body weight for boars (left panel) and gilts (right panel), with dotted vertical lines for the 2.5 and 97.5 % quantiles

Estimates of Population Curves with Age

For each of 30,000 posterior samples, estimates of Gompertz curve parameters for LRFI and CTRL lines for DFI and BW at generation 5 were calculated as the sum of the fixed effect of generation and average animal genetic effects for each line. For each sample, since the fixed effect of generation was common to both lines, differences in Gompertz curve parameters between the two lines were entirely determined by differences in average animal genetic effects. Figure 5.4 shows estimates of average genetic Gompertz curves and associated 90% point-wise credible intervals for LRFI and CTRL lines for DFI and BW in generation 5. They were derived as the mean and 5% and 95% quantiles of the 30,000 Gompertz curves at each day of the growth trajectory from 90 to 210 d of age. Each of 30,000 curves was formed from Gompertz curve parameters for LRFI and CTRL lines from each of 30,000 posterior samples.

Figure 5.4 visualizes the effect of selection for reduced RFI on genetic population curves of growth and feed intake along the growth trajectory from 90 to 210 d of age. Compared with the CTRL line, the LRFI line had a lower DFI curve for both boars and gilts, especially in the later part of the growth period (Figure 5.4 (a) and (b)). In the later part of the growth period, 90% credible intervals for LRFI and CTRL lines for DFI did not overlap each other for either boars or gilts (Figure 5.4 (a) and (b)). Line differences for DFI (LRFI - CTRL) at 105, 135, 165, and 195 d of age were 0.00, -0.05, -0.08, and -0.11 kg/d for boars and -0.04, -0.06, -0.09, and -0.11 kg/d for gilts (Figure 5.4 (a) and (b)).

Compared with CTRL boars, LRFI boars had a slightly lower body weight curve in the later part of the growth period, but 90% credible intervals for LRFI and CTRL lines overlapped each other (Figure 5.4 (c)). In comparison with CTRL gilts, LRFI gilts had a lower body weight curve in the later part of the growth period, with 90% credible intervals for LRFI and CTRL lines that did not overlap (Figure 5.4 (d)). Line differences for BW (LRFI - CTRL) at 105, 135, 165, and 195 d of age were 0.24, 0.14, -0.14, and -0.62 kg for boars and -0.34, -1.44, -2.85, and -4.44 kg for gilts (Figure 5.4 (c) and (d)). In summary, selection for reduced RFI has led to a lower daily feed intake curve and a lower body weight curve, especially in the later part of the growth period. Line differences for DFI and BW

were small at the beginning of the growth period from ~90 days of age and became larger at the later growth period.

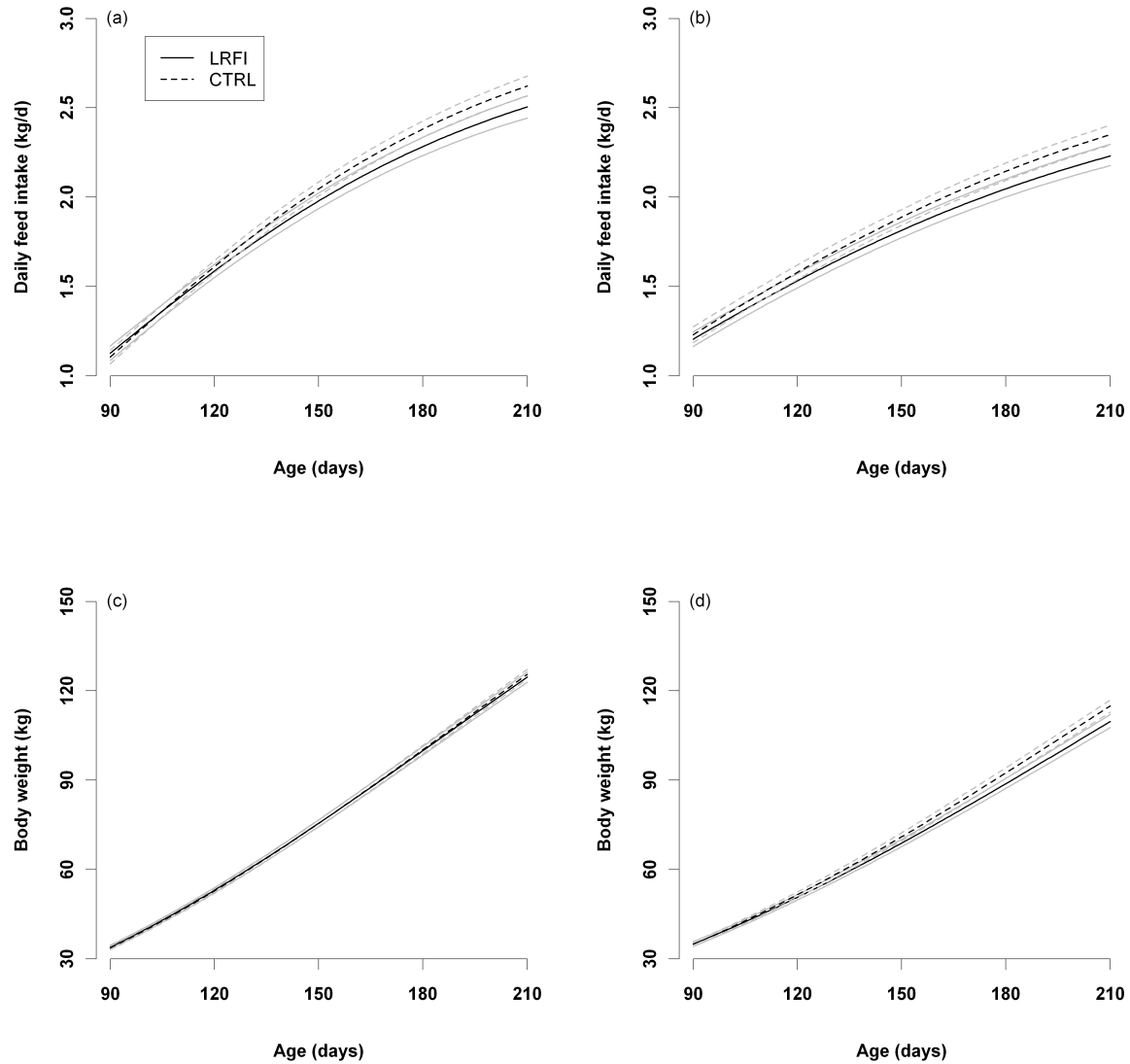


Figure 5.4 Estimated average genetic Gompertz curves and associated 90% point-wise credible intervals for the lower residual feed intake line (LRFI) and the control line (CTRL) for daily feed intake for boars (a) and gilts (b), and for body weight for boars (c) and gilts (d)

Discussion

A two-stage method is often used to investigate genetic variation of nonlinear growth curve parameters (Barbato, 1991; Kachman et al., 1988; Koivula et al., 2008). For the two-

stage analysis, growth curve parameters are estimated based on each individual's own data in the first stage and genetic analyses are implemented on these estimated growth parameters in the second stage. As an appealing alternative to evaluate genetic variation of nonlinear curve parameters, the Bayesian method (Blasco et al., 2003; Varona et al. 1998) integrates the two stages of the analysis. Hierarchical Bayesian analysis of BW and DFI curves by the Gompertz function were investigated in the current study.

The two-stage method is simple, but the analyses of the first and the second stages are completely separated from each other. This may result in different results between the two-stage method and the Bayesian method for combining these two stage analyses, especially when the growth curve parameters for some animals can not be estimated based on its own data. In the present study, Gompertz curve parameters could be estimated for 353 of 586 boars and for 240 of 495 gilts. The scale matrix of the inverse Wishart prior distribution for covariance matrix **G** and **R** for DFI and BW for boars and gilts were from the 3-trait analyses of Gompertz curve parameters of the 353 boars and 240 gilts using the two-stage method. They are very different from the posterior means (Table 5.1) in the Bayesian analysis which used all 586 boars and 495 gilts.

An analytic or numerical study of posterior distribution for the Bayesian analysis is often not realizable because the posterior distribution typically has high dimensions. As a result, Monte Carlo Markov Chain methods are often used to explore the posterior distribution. This method may be computational demanding, but inferences are easy and flexible for any new variable of interest from the posterior distributions of parameters that are obtained from the Monte Carlo Markov chains after convergence. For example, new samples of marginal posterior distributions of new variables of heritability and genetic correlations between the three Gompertz parameters in the current study were derived from posterior distributions of the corresponding variance components. Then the inferences for heritability and genetic correlations can be based on these new samples of marginal posterior distributions.

Estimates of genetic parameters and line differences for the three Gompertz parameters had smaller posterior sample standard deviations for boars than for gilts (Tables 5.1 and 5.2, and Figures 5.2 and 5.3). In other words, they were estimated more accurately for boars than those for gilts. The reason is that there were more data for boars.

The relationship matrix from individuals in all generations was used to calculate the inverse of the relationship matrix. Only the columns and rows of this inverse of relationship matrix corresponding to pigs with phenotypic data were used in the Bayesian analysis. For estimating genetic parameters and selection response for Gompertz curve parameters for BW and DFI, using this inverse is sufficient because it takes into account all needed relationships. In principle, if predictions of genetic effects for pigs without the phenotypic data are of interest, the whole inverse of relationship matrix could be included in the Bayesian analysis.

Webb (1998) suggested a direction of selection of pigs to increase feed intake at an early age but decrease it at a later age. This corresponds to a lower mature feed intake, an earlier inflection point, and possibly greater decay parameters for the Gompertz curves (Figure 5.1) for DFI. It seems that selection for reduced RFI has resulted in such change in the DFI curve (a lower daily feed intake curve at the later growth period) (Figure 5.4). Further research is needed to investigate the optimum magnitude of the change on Gompertz curve parameters for growth, feed intake, and body composition to achieve efficient production of lean meat.

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CHAPTER 6. GENERAL CONCLUSIONS AND DISCUSSION

Summary

The objectives of this dissertation were addressed in four chapters with four complementary research projects. The data used for each project were from a selection experiment for reduced RFI in Yorkshire pigs at Iowa State University. These four research projects are connected to fulfill the overall objectives of this dissertation, which were to evaluate the effects of selection for reduced RFI, estimate genetic parameters, and explore different statistical and genetic models to make best use of longitudinal measurements of DFI, BW, BF, and LMA to improve feed efficiency in pigs. From a methodological perspective, these four research projects are sequentially progressing from simple to complex to serve different levels of needs in breeding programs to handle these longitudinal measurements.

In chapter 2, a simple quadratic regression of DFI on age was fitted for individual pigs. Missing daily FI data were imputed using the polynomial fitted values, and then ADFI was computed by averaging daily FI during the test period. Similarly, a simple linear regression of weekly BW on age was fitted for each pig, and the slope of the linear regression was used as a measure of ADG for that pig. For BF and LMA, only the last measures, at off-testing, were used for each pig. By further analyses of these single summaries or measures for individual pigs, RFI had a sizable heritability of 0.29, and selection for reduced RFI was shown to have significantly decreased the amount of feed required for a given rate of growth and backfat and, thus, has improved FE. The method of reducing the longitudinal measurements of DFI, BW, BF, and LMA to single summaries or measures of ADFI, ADG, BF, and LMA for individual pigs certainly meets the need for genetic evaluation of RFI if the aim is to improve average performance over the growing period, and also fits the framework of the traditional selection index approach.

To investigate a better model to predict DFI and BW curves for individual pigs than fitting a simple quadratic and linear regression of daily FI and weekly BW on age separately for each individual pig, as done in chapter 2, different RR models and non-linear mixed models, which use the data from all pigs simultaneously, were evaluated in chapter 3. The

pigs used in chapter 3 were from generation 5 of the selection experiment and the genetic relationships between animals were ignored. The quadratic polynomial RR model was identified to be best for DFI and BW after evaluating 40 RR models with different orders of polynomials of age and Gompertz non-linear mixed models based on predicted residual sum of squares. The results from this research were used in two ways. First, the quadratic polynomial RR model is now used in the ongoing selection experiment to predict DFI and BW curves for individual pigs and to summarize ADFI and ADG based on these predictions. Second, quadratic order polynomials were chosen for RR genetic analyses in chapter 4.

In chapter 4, the RR genetic analyses with quadratic order of Legendre polynomials of age and splines were applied to the data from all generations of the selection experiment to estimate genetic parameters for DFI, BW, BF, and LMA along the growth trajectory. From the RR genetic analyses with Legendre polynomials of age, estimates of heritability from 91 to 210 d of age ranged from 0.10 to 0.37 for boars and 0.14 to 0.26 for gilts for DFI, from 0.39 to 0.58 for boars and 0.55 to 0.61 for gilts for BW, from 0.48 to 0.61 for boars and 0.61 to 0.79 for gilts for BF, and from 0.46 to 0.55 for boars and 0.63 to 0.81 for gilts for LMA. The genetic analyses of longitudinal measurements of DFI and BW by linear RR models can be easily implemented using existing software such as ASREML (Gilmour et al., 2006). However, the parameters of the RR models don't have a biological meaning and give limited insight in the biological data-generating process. Non-linear mixed models such as the Gompertz growth model can overcome these shortcomings, although they are more difficult to fit. In chapter 5, the hierarchical Bayesian method was applied to investigate genetic variation in the parameters of the Gompertz non-linear mixed model for DFI and BW. Estimates of heritability for three Gompertz curve parameters (asymptotic value, inflection point, and decay parameter) were 0.74, 0.68, and 0.81 for boars and 0.75, 0.64, and 0.53 for gilts for DFI, and 0.61, 0.56, and 0.57 for boars and 0.42, 0.32, and 0.32 for gilts for BW. The effect of selection for reduced RFI on growth and feed intake curves was evaluated genetically by the linear RR model in chapter 4 and by the Gompertz non-linear mixed model in chapter 5. Both models showed that selection for reduced RFI has resulted in a lower feed intake curve and a lower body weight curve, especially towards the end of growth period.

Discussion

Estimates of Line Differences (CTRL-LRFI) in Growth and Feed Intake Curves

Estimates of line differences obtained from the different analyses implemented in this thesis are summarized in Figure 6.1.

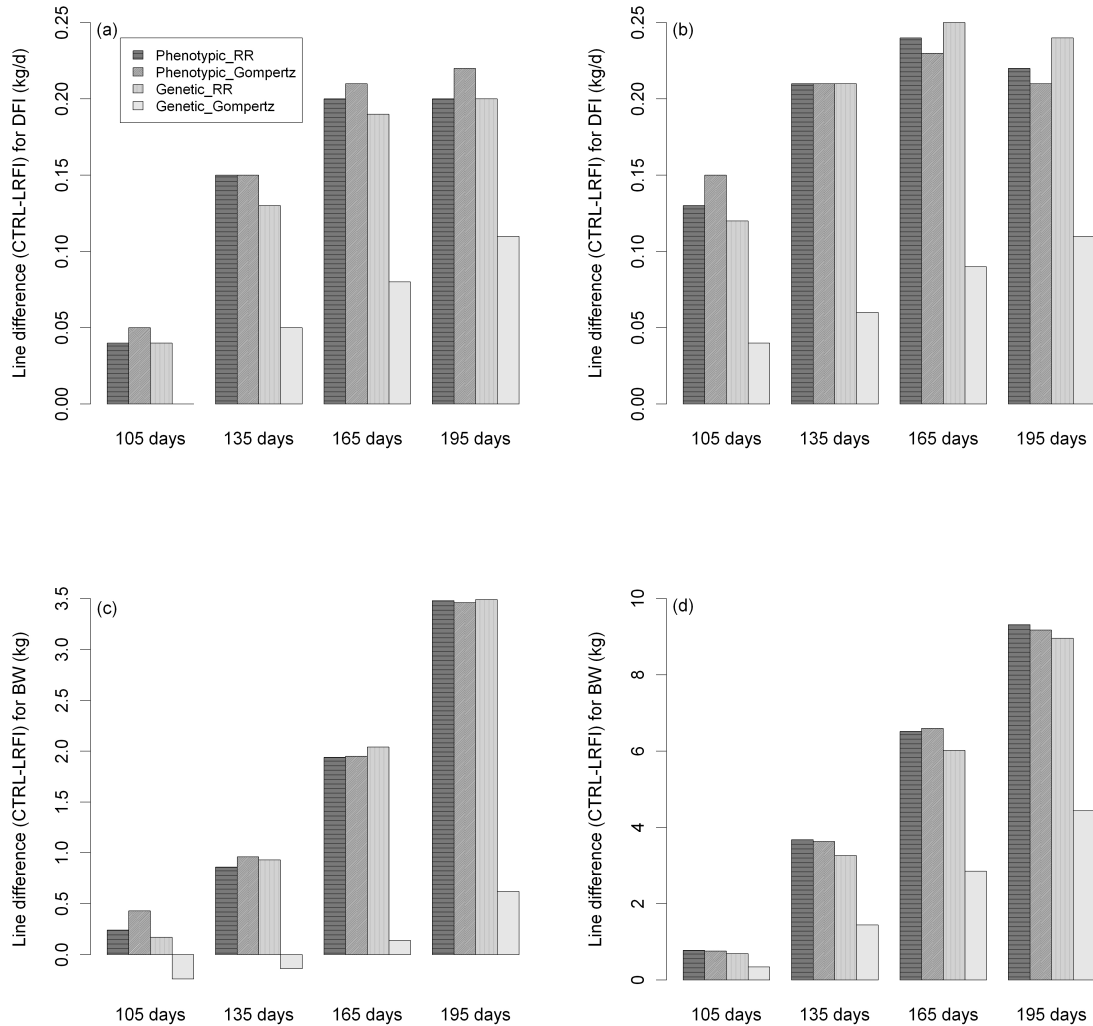


Figure 6.1 Estimates of line differences (CTRL-LRFI) for daily feed intake for boars (a) and gilts (b), and for body weight for boars (c) and gilts (d). Phenotypic_RR: Phenotypic analysis of generation 5 data only by quadratic polynomial random regression model in chapter 3. Phenotypic_Gompertz: Phenotypic analysis of generation 5 data only by Gompertz nonlinear mixed model in chapter 3. Genetic_RR: Genetic analysis by quadratic polynomial random regression model in chapter 4. Genetic_Gompertz: Genetic analysis by Gompertz nonlinear mixed model in chapter 5

In chapter 3, the quadratic polynomial random regression model and the Gompertz nonlinear mixed model were implemented for BW and DFI data for pigs from the LRFI and CTRL lines in the 5th generation of the selection experiment. The analyses in chapter 3 are phenotypic analyses without genetic effects and pedigree information involved. Separate fixed population curves were fitted for the LRFI and CTRL lines for both the random regression model and the Gompertz model in chapter 3. Line differences were directly measured by the differences of fixed population curves for LRFI and CTRL lines at generation 5 of the selection experiment. Estimates of line differences (CTRL-LRFI) at 105, 135, 165, and 195 d of age were very similar between phenotypic analyses by the random regression model and by the Gompertz model for DFI and BW for boars and gilts (Figure 6.1).

In chapter 4, genetic analyses by the quadratic polynomial random regression model were applied to BW and DFI data for pigs from all generations of the selection experiment, with second-order Legendre polynomials of age as fixed curves for each generation and random curves for additive genetic and permanent environment effects. Estimates of genetic population curves for DFI and BW for boars and gilts of the LRFI and CTRL lines at generation 5 of the selection experiment were calculated as the sum of estimates of the fixed curve and average EBV by line. Because the fixed curve was common to both lines, differences in population curves between the two lines were entirely determined by differences in average EBV. Estimates of line differences (CTRL-LRFI) at 105, 135, 165, and 195 d of age based on differences in average EBV from genetic analyses including the common fixed curve for both lines in chapter 4 were very similar with those from phenotypic analyses, which included separate fixed population curves for the LRFI and CTRL lines in chapter 3 (Figure 6.1). This shows that including the genetic effect and accounting for relationships had a small effect on evaluating line differences. However, the standard errors of the estimates of line differences may be overestimated if genetic relationships are not taken into account. This needs to be investigated further.

In chapter 5, genetic analyses by the hierarchical Gompertz nonlinear mixed model using Bayesian method were applied to the same set of BW and DFI data as in chapter 4. The

model for the three Gompertz curve parameters (asymptotic value, inflection point, and decay parameter) was fitted with fixed effects of generation and random effects of additive genetic and environmental effects. Estimates of average genetic Gompertz curves for DFI and BW for boars and gilts of the LRFI and CTRL lines at generation 5 of the selection experiment were calculated as the mean of 30,000 Gompertz curves. Each of 30,000 curves was formed from estimates of Gompertz curve parameters for LRFI and CTRL lines from each of 30,000 posterior samples. Because the fixed effect of generation was common to both lines, differences in Gompertz curve parameters between the two lines were entirely determined by differences in average EBV for each posterior sample. Compared with phenotypic analyses by the quadratic polynomial random regression model and the Gompertz nonlinear mixed model in chapter 3 and genetic analyses by the quadratic polynomial random regression model in chapter 4, the magnitude of estimates of line differences for BW and DFI curves by Bayesian analyses was much smaller (Figure 6.1), although the trend of estimates of line differences was similar, i.e. small line differences at the beginning of the growth period and larger differences later in the growth period. Wright et al. (2000) found that traditional REML/BLUP approach (residual maximum likelihood/best linear unbiased prediction) and Bayesian inferences can produce very different predictions of random animal genetic effects for linear mixed model analyses of a selection experiment in animal breeding. The pen within group effect was not fitted in the Gompertz nonlinear mixed model in chapter 5, in contrast to the random regression model in chapter 4 because it caused convergence problems. This may introduce some bias for estimates of line differences, although we expect this bias is small because pigs from the two lines were mixed in pens. Further research is needed to investigate the discrepancy of the magnitude of estimates of line differences between the random regression model by the REML/BLUP approach and the Gompertz nonlinear mixed model by the Bayesian method.

Residual Feed Intake and Traditional Selection Approaches

Johnson et al. (2003) mentioned that one reason for the lack of change in energetic efficiencies for animal production is that most measurements in breeding programs are for traits of output characteristics in the production system. Residual feed intake was advocated

by Johnson et al. (2003) as one of the tools, besides quantitative trait loci mapping, to enhance efficiency in beef cattle. The concept of RFI was first proposed by Koch et al. (1963) as an alternative measurement of feed efficiency for beef cattle. In recent decades, the number of research projects on RFI has increased for most livestock species. A possible reason is that the importance of feed efficiency has triggered the livestock breeding companies to invest more to record individual feed intake, besides traditionally measured body weight, backfat, and loin muscle area. Most RFI research projects in pigs (Johnson et al., 1999; Mrode and Kennedy, 1993; Von Felde et al., 1996) have focused on estimating genetic parameters of RFI. These studies are useful because for a trait such as RFI to be used as a possible selection criterion in breeding programs, it must be heritable and have sizeable genetic variability, besides economic importance. However, little effort has been devoted to research on implementation of RFI in selection programs for improving feed efficiency. One major reason is that maintenance of a selection experiment for RFI for research purposes is labor intensive and costly. However, such a selection experiment for RFI certainly will provide insight into how to incorporate RFI in a breeding program. The RFI selection experiment in Yorkshire pigs at Iowa State University, along with a similar RFI selection experiment in Large White pigs in France (Gilbert et al., 2007), is implementing single trait selection of RFI. The evaluation of direct and correlated response of selection for RFI on production and carcass traits provides more information for breeding companies on the possibility of using RFI for genetic improvement of feed efficiency in pigs.

Traditional selection approaches in the pig industry often do not include direct measurements of feed intake and efficiency (Clutter and Brascamp, 1998). An increase of feed efficiency is as a correlated response of selection for increased output only. To speed up improvement of feed efficiency of lean production for the pig industry, extending these selection approaches to include some measures of feed intake and efficiency may be a possible and acceptable way in the near future. Including ratio measurements of feed efficiency ($ADG/ADFI$) or its reciprocal feed conversion ratio ($ADFI/ADG$) into the selection index with component traits of ADG , BF , and LMA is not valid (Gunsett, 1984) because the joint distribution between a component trait and the ratio is not normal and prediction of genetic merit based on the linear index is not valid. Residual feed intake is a

linear combination of feed intake and production traits with coefficients usually from a phenotypic regression of feed intake on production traits. Kennedy et al. (1993) and Van der Werf (2004) discussed the genetic and statistical properties of RFI, and showed that inclusion of RFI as a component trait into the selection index is equivalent to a selection index with feed intake and its component traits.

Although including RFI as a component trait of selection indices does not add response in comparison with selection indices that have feed intake as one of the component traits, research on RFI can lead to a more informative biological understanding of feed efficiency. Results in chapter 2, such as heritability of RFI, genetic correlations between RFI and production traits, and direct and correlated responses of RFI selection on production and carcass traits, provide an understanding of the effect of RFI selection on component traits of feed efficiency and carcass body composition. Further studies on the effect of reduced RFI (improvement of feed efficiency) in the RFI selection experiment at Iowa State University have been extended to several other aspects, such as difference between lines for feeding behavior and sow performance, and must be extended to more aspects. The ultimate goal of RFI research is to understand the genetic, genomic, physiological, and behavioral basis of feed efficiency. In some sense, the ultimate goal of research on RFI is to make the RFI concept redundant.

Linear Random Regression Models

Previous research on RFI and selection index approaches with the classical traits of ADFI and ADG implicitly ignored heterogeneity of variance for feed intake and production traits and the correlation between them over the pig's growth trajectory. This implicit assumption is an outcome of lack of models to properly handle longitudinal measurements on feed intake and production traits. In contrast, random regression models (Kirkpatrick et al., 1990) allow variances and covariances to change over the pig's growth trajectory. The multi-trait random regression models of DFI, BW, and BF in chapter 4 allow genetic and residual variation in each trait and correlations between traits to vary together over the pig's growth trajectory (Schaeffer, 2004). It is an alternative for these longitudinal measurements in breeding programs besides previous residual feed intake and traditional selection approaches with

classical traits. No literature was found that evaluated longitudinally measured performance traits and feed intake in pigs by a multi-trait random regression model. The estimates of heritability of DFI, BW, BF, and LMA, and genetic correlations between them provide insight of how these genetic parameters vary over the pig's growth trajectory.

When analyzing longitudinal data by random regression models, two popular choices are spline and Legendre polynomials. In chapter 4, the random regression polynomial model was chosen for further analyses because the random regression spline models had, in most cases, more erratic estimates of phenotypic variance and heritability than the random regression polynomial model although, in most of cases, the spline models had a smaller BIC values than the random regression polynomial model. This may be because the RR spline model is so flexible that it overfits noise of the data. In the animal breeding field, no studies have compared the RR spline model with the RR polynomial model based on model fitting behavior on estimates of phenotypic variance and heritability.

When analyzing longitudinal data by random regression spline models, how to select the number of knots and their placement is an important question. Specifically, for the natural cubic regression splines, boundary knots should not be placed at the minimum and maximum of time points in the data if limited data exist at those time points. In chapter 4, when the boundary knots were placed at the minimum and maximum days of age in the data across all pigs, where records were very sparse, random regression spline models had inflated estimates of phenotypic variance and heritability in the middle of the longitudinal range, despite an abundance of data in that range. However, after moving the boundary knots inside, to places where still a good proportion of data exists, sparse records beyond the boundary knots had less influence on the model fit between the boundary knots. Literature comparison on this result is not possible because no literature was found on the effect of placement of boundary knots for random regression spline models.

Gompertz Nonlinear Mixed Model and Linear Plateau Model

In chapter 5, Bayesian analyses of a Gompertz nonlinear mixed model were applied to longitudinal DFI and BW data for boars and gilts. In principle, the same Bayesian methodology can also be applied to longitudinal ultrasonic measurements of BF and LMA in

pig breeding programs. However, in generation 5 of this RFI selection experiment, BF and LMA were only measured once when pigs were taken off test, which is the main reason why Bayesian analyses were not applied to BF and LMA in chapter 5. Estimates of feed intake, growth, and body composition curves of individual pigs are required to evaluate efficiency of daily lean meat production along the growth trajectory. No previous literature has genetically evaluated longitudinal DFI and BW data in pigs by Bayesian analyses of a nonlinear mixed model. Evaluation of the genetic variation of Gompertz curve parameters for DFI and BW can be helpful to investigate the possibility of selection on these curve parameters to improve feed efficiency in the future.

The concept of the linear plateau model was proposed by Whittemore and Fawcett (1976) to describe the relationship between daily lean growth rate, daily fat growth rate, and daily energy intake. The main points of the linear plateau model were introduced in chapter 1. The maximum rate of daily protein deposition (maxPD) for a pig was assumed to be constant, throughout the growth period up to commercial slaughter weights (Whittemore and Fawcett, 1976). Instead of the assumption of constant maxPD along the growth period, Emmans and Kyriazakis (1997) used the Gompertz function to model potential protein growth of pigs and the derivative of the Gompertz curve described the maxPD. (Emmans and Kyriazakis, 1997) described a trend of maxPD for the entire growth period, with maxPD increasing rapidly in the early stage, plateauing during the growing-fattening stage, and then decreasing towards zero at maturity (Luiting and Knap, 2006). Luiting and Knap (2006) declared that the Gompertz model (Emmans and Kyriazakis, 1997) is the most appropriate method for the description of maximum rate of daily protein deposition, after comparing several pig growth models, included the linear plateau model (Whittemore and Fawcett, 1976). In this sense, the Gompertz nonlinear model is more appropriate to use in breeding programs than the linear plateau model.

The Gompertz pig growth model (Emmans and Kyriazakis, 1997) is deterministic. To use it in the breeding programs, the Gompertz nonlinear model needs to be stochastic to accommodate individual pig variation. In the current study, the Gompertz models for BW and DFI are stochastic with random genetic and environmental effects fitted for the parameters of the Gompertz model.

Implications and Future Work

The objective of a pig production company is the efficient production of quality lean pork (Clutter and Brascamp, 1998). As a result, managing the shape of feed intake and growth curves will become increasingly important for altering feeding strategies in commercial animal production, and for the development of effective animal breeding strategies. The studies in this dissertation can help the swine industry to directly select on shapes of growth and feed intake curves for improving efficiency of pork production. Further research is needed to use these longitudinal measurements of performance traits to best serve the swine industry. Several possible directions on additional research are discussed below.

Implementation of Direct Selection on Performance Curves

The result that selection for reduced RFI led to lower feed intake and body weight curves, as found in chapter 4 (linear RR models) and in chapter 5 (Gompertz non-linear mixed models), show that it is possible to change shapes of feed intake and growth curves through selection. Webb (1998) suggested a direction of selection for changing the shape of the feed intake curve as increasing feed intake at an early age but decreasing it at a later age. How to select and change the curves of DFI, BW, BF, and LMA together toward desired directions must be investigated further because these traits are correlated. A possible approach is index selection with estimates of breeding values based on the genetic effects of the intercept, linear, and quadratic terms of age from a multi-trait RR model or of curve parameters from a multi-trait Gompertz model. For feed intake and performance traits, the genetic variance and covariance matrix for the intercept, linear, and quadratic terms of age from a multi-trait RR model was estimated in chapter 4 and a genetic variance and covariance matrix for Gompertz curve parameters could be estimated by multi-trait evaluation of the Gompertz model using the methodology from chapter 5. How to derive index weights for changing the feed intake and performance curves together in desired directions needs further research.

Costs and Returns for Measuring Feed Intake and Performance Traits Longitudinally

The cost of longitudinal measurements of feed intake, growth, backfat, and loin muscle area by electronic feeders and real time ultrasound scanning are high. The wealth of data generated by these automatic measuring systems certainly requires more trained persons on statistics and quantitative genetics to tackle and derive valuable information from them. This will also add salary costs for the breeding companies. Given the low rates of investment return in the pig industry, these cost barriers are one major reason preventing breeding companies to measure the data longitudinally unless they have to. In recent years, prices of feedstuff have skyrocketed because of competition on land for food and biofuel production. On the return side, measuring feed intake for individual pigs over the growth period could increase the rate of genetic improvement for efficient lean meat production 15 to 20% (Webb, 1998). Future work is needed to investigate the costs and returns from longitudinal measurements of feed intake and performance traits in order to better inform the pig industry whether to take these measurements or not.

Functional Mapping

The difficulty and expense of measuring feed intake and performance traits longitudinally on large numbers of animals prevents the swine industry to explore and invest further on directly selection on shapes of performance and feed intake curves. However, the rapid development of genotyping technologies, accompanied by a dramatic decrease of genotyping costs, provides opportunities to address these issues. If the genetic variants, e.g. quantitative trait loci (QTLs) or nucleotides (QTNs), responsible for the difference in shapes of performance and feed intake curves are identified, selection on these curves based on genetic markers becomes increasingly possible. The general statistical and genetic framework of identifying genetic variants that underlie these dynamic curves is called functional mapping (Ma et al., 2002; Malosetti et al., 2006; Wu et al., 2003, 2004). Traditional mapping approaches are usually designed to analyze phenotypic data at a single time point. Functional mapping can be viewed as an extension of the traditional mapping methods to a mathematical function. Wu and Lin (2006) thoroughly reviewed functional mapping approaches. Lusk (2007) investigated the association of two single nucleotide polymorphisms in the leptin gene

with growth curve parameters for BW and BF in beef cattle. Within the framework of functional mapping, gene by gene interactions for these functional parameters can also be tested.

With pig production becoming more and more an international business, breeding stock is raised more and more in different locations with different conditions around the world. Thus, potential interactions between genotype and environment become an increasing issue. Feed intake is one of the primary ways for pigs to cope with changing environments (Luiting, 1999), and the growth and body composition will change as well. Within the scope of functional mapping, we could also test gene by environment interaction for these function parameters.

Selection on Purebreds to Optimize Feed Intake and Performance Curves of Crossbreds

In the pig industry, selection is mostly in purebred nucleus herds but crossbreds formed from these purebred lines are used for commercial production. The crossbreds are typically raised in variety of environmental conditions with disease challenges compared to the well-controlled environmental conditions that the purebreds are raised in. Therefore, selection on purebred performance is often not very effective at improving crossbred performance. Dekkers (2007) summarized that the genetic correlation between purebred performance and crossbred performance in pigs is low, ranging from 0.4 to 0.7. In addition, purebred lines are often separated into sire and dam lines, with sire lines selected for growth performance and feed efficiency, and dam lines typically selected for reproduction performance. Further research is needed to investigate how to genetically change the performance and feed intake curves in sire and dam lines in order to optimize the performance and feed intake curves in commercial crossbreds. Dekkers (2007) proposed a marker assisted selection strategy for improving crossbred performance by using estimates of marker effects based on crossbred performance. In principle, this methodology could also be applied to optimize the performance and feed intake curves in crossbreds. Estimates of effects of genetic variants (QTLs, QTNs, or markers) responsible for differences in shapes of performance and feed intake curves could be based on crossbred data. This will require additional genotyping and phenotyping on crossbred pigs besides in purebred nucleus herds.

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