Genetics of longitudinal growth data

DOCTORAL THESIS

Jessica M. Coyne

ACADEMIC DISSERTATION
To be presented, with permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public examination in Sali (lecture theatre) 6 (Rm. 3006, 3rd level, Main Building), Fabianinkatu 6 on May 19th 2017 at 12 noon.

Helsinki 2017
Custos:

Professor Asko Mäki-Tanila,
Department of Agricultural Sciences,
University of Helsinki, Finland

Supervisors:

Dr Noirin McHugh,
Teagasc, Animal and Grassland Research and Innovation Centre, Moorepark,
Fermoy, Co. Cork, Ireland

Professor Donagh Berry,
Teagasc, Animal and Grassland Research and Innovation Centre, Moorepark,
Fermoy, Co. Cork, Ireland

Adjunct Professor Jarmo Juga,
Department of Agricultural Sciences,
University of Helsinki, Finland

Professor Esa Mäntysaari,
Natural Resources Institute Finland
(Luke), FI-31600 Jokioinen, Finland

Reviewers:

Professor Ismo Stranden,
Natural Resources Institute Finland
(Luke), FI-31600 Jokioinen, Finland

Dr Björg Heringstad,
Norwegian University of Life Sciences,
(UMB), Department of Animal and Aquacultural Sciences (IHA), Norway

Opponent:

Professor Lars Rönnegård,
Dean of Dalarna University,
Högskolegatan 2, Falun, Sweden
Cover photo © Jessica Coyne/Aoife Mannering, Woodland Print & Signage

Dissertationes Schola Doctoralis Scientiae Circumiectalis, Alimentariae, Biologicae
ISBN 978-951-51-3208-6 (PDF)
ISSN 2342-5423 (Print)
ISSN 2342-5431 (Online)
Electronic publication available at http://ethesis.helsinki.fi

© Jessica Coyne
Teagasc, Moorepark,
Ireland, 2017.
Abstract

The objective of this thesis was threefold: 1) to compare alternative growth functions fitted to pig live-weight data, with particular emphasis on the ability of the growth function to predict future live-weight; 2) to estimate genetic (co)variances for the parameters of the previously determined most appropriate growth function using alternative modelling approaches; 3) to estimate genetic (co)variances parameters pertaining to live-weight, feed intake and two other efficiency traits using Legendre polynomial equations. The final dataset used included 51,893 live-weight and 903,436 feed intake records from 10,201 pigs, collected between the years 2006 and 2012, inclusive, obtained from the Finnish pig breeding company Figen Oy.

Fixed effects and mixed models were applied to three different growth functions, namely von Bertalanffy, Gompertz, and Richards; fixed and mixed model polynomial equations were also considered. Each growth function’s ability to predict future live-weight was determined by excluding a selection of animal live-weight records post 160 days of age, and comparing the predicted live-weight to actual live-weight. The accuracy of fit for each model was determined as the square of the correlation between the actual and predicted weights. The root mean square error (RMSE) values for each model scenario were also estimated. The Gompertz growth function achieved the greatest accuracy squared of modelling pig live-weight (0.997) and lowest RMSE (1.60 kg). When used in a mixed model framework the Gompertz growth function also achieved the greatest accuracy squared of predicting future live-weight records (0.846) with the lowest corresponding RMSE (5.35 kg).

Based on the results from the first study the Gompertz growth function was used to estimate the genetic (co)variance of the function’s parameters asymptotic mature weight (A),
the logarithm of the ratio of mature weight to birth weight \((B)\) and rate of maturation \((k)\). Three alternative approaches were utilised to estimate the variances; a two-step fixed effects approach, a two-step mixed model approach and a one-step mixed model approach. The two-step approach initially used growth function parameter estimates from the first study (paragraph above) and subsequently estimated the variance component parameters for \(A\), \(B\) and \(k\), using a linear mixed model; whereas, the one-step approach used an iterative method to calculate the variance component estimates for the growth function parameters, in a mixed model framework. Results from the genetic analysis using a two-step fixed effects or mixed model approach, and the one-step mixed model approach, highlighted that ample genetic variation exists for all three Gompertz growth function parameters; greater heritability estimates for the Gompertz growth function parameters were obtained from the one-step mixed model approach.

Genetic (co)variances for live-weight, feed intake and two efficiency measures, namely residual feed intake and residual daily gain, were estimated using random regression Legendre polynomial models. Results using the random regression Legendre polynomial models showed that heritability of live-weight, feed intake, residual feed intake and residual daily gain increased in the early growing phase, peaked and subsequently decreased as the age of the animal increased. Ample genetic variation existed for all four traits, indicating the potential to alter curve profiles to meet specific breeding objectives.

Results from this thesis can be implemented into genetic evaluations for pigs, providing comprehensive information on the profile of growth and efficiency throughout the growing period of the animal’s life, thus helping breeders identify genetically superior animals.
Acknowledgements

This PhD provided me with the opportunity to work with a number of exceptionally talented, industrious, dedicated professionals and friends, for which I am extremely grateful. I would like to acknowledge the opportunity presented to me by Teagasc to carry out this work in the Animal and Grassland Research and Innovation Centre at Moorepark. I would also like to acknowledge the Teagasc Walsh Fellowship Scheme for funding the research.

I would like to thank my supervisors, Dr. Noirin McHugh, Prof. Donagh Berry, Prof. Esa Mäntysaari and Adjunct Prof. Jarmo Juga, for all their help, guidance and patience throughout this research. I’m very appreciative of having had the opportunity to work on such an exciting and progressive project with world leaders in computational genetics and genomics. I would like to thank my other co-authors who have contributed to this PhD, Dr. Kaarina Matilainen and Dr. Marja-Liisa Sevon-Aimonen of LUKE, Finland and Dr. Timo Serenius of Figen Oy. I would also like to extend my gratitude to my custos Prof. Asko Mäki-Tanila.

Furthermore, I would like to extend my sincere gratitude to the biometrical genetics department in LUKE, Jokioinen, who looked after me and made me feel so welcome on every visit, ensuring I sampled all Finland had to offer in the line of ice-hockey, dog sledding and cross country skiing. In addition I would like to extend my gratitude to all of the staff and faculty members in the University of Helsinki and Teagasc, Moorepark.

A very special thank you to Mo, Ais, Lou, Deirdre, Audrey, Alan, Tom and all those I met along the way, whose constant enthusiasm, patience, advice and distraction was most appreciated whenever it was needed. To my squad, Justine Deming, Aine Collins and Aoife Buggy; pain, hunger and the will to win united us and we became champions! I can honestly say I wouldn’t swap one blister, strained or exhausted muscle, stupid o’clock freezing start or
nauseating training session for all the tea in China! You ladies are amazing and I am honoured to have rowed in our quad…National Championship winners 2015! I would like to say a huge thank you to Timothy for your patience, support and encouragement.

Finally I would like to thank my family, Dad, Mum, Heather and Genevieve, for all their love and support, and belief in me throughout this project. I wish to dedicate this thesis to my parents, James and Mary, for the major contributions and sacrifices they have made for my education.

Veni, Vidi, Vici.
List of original publications

This thesis is based on the following publications:


### Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>asymptotic mature weight</td>
</tr>
<tr>
<td>ADG</td>
<td>average daily gain</td>
</tr>
<tr>
<td>B</td>
<td>ratio of mature weight to birth weight</td>
</tr>
<tr>
<td>EBV</td>
<td>estimated breeding value</td>
</tr>
<tr>
<td>$h^2$</td>
<td>heritability</td>
</tr>
<tr>
<td>k</td>
<td>rate of maturation</td>
</tr>
<tr>
<td>m</td>
<td>reflection point of parameter A</td>
</tr>
<tr>
<td>REML</td>
<td>restricted maximum likelihood</td>
</tr>
<tr>
<td>RMSE</td>
<td>root mean square error</td>
</tr>
<tr>
<td>SD</td>
<td>standard deviation</td>
</tr>
<tr>
<td>SE</td>
<td>standard error</td>
</tr>
<tr>
<td>EBLUP</td>
<td>empirical best linear unbiased predictor</td>
</tr>
</tbody>
</table>
Table of Contents

1 Introduction ........................................................................................................................................ 1
  1.1 Modelling and predicting phenotypic live-weight ................................................................. 1
  1.2 Genetics of live-weight using fixed effects and mixed model equations ....................... 2
  1.3 Genetics of live-weight, feed intake and efficiency traits using random regression models ........................................................................................................................................ 3
  1.4 Objectives ................................................................................................................................... 3

2 Materials and methods .................................................................................................................. 5
  2.1 Data ............................................................................................................................................. 5
    2.1.1 Animal management ............................................................................................................. 5
    2.1.2 Growth and feed efficiency traits ......................................................................................... 5
  2.2 Analyses ....................................................................................................................................... 7
    2.2.1 Modelling and predicting phenotypic live-weight ............................................................... 7
    2.2.2 Genetic analysis of live-weight using fixed effects and mixed model equations ............... 10
    2.2.3 Genetics of live-weight, feed intake and efficiency traits using random regression models ........................................................................................................................................ 12

3 Results ............................................................................................................................................. 15
  3.1 Modelling and predicting phenotypic live-weight ................................................................. 15
  3.2 Genetic analysis of live-weight using fixed effects and mixed model equations ........... 16
3.2.1 Two-step approach ................................................................. 16
3.2.2 One-step approach ............................................................... 17
3.2.3 Correlations between sire EBV for the two-step and one-step approaches ...... 17

3.3 Genetics of live-weight, feed intake and efficiency traits using random regression models .......................................................................................................................................................................................... 18
3.3.1 Genetic correlations within trait at different ages ..................................... 19
3.3.2 Genetic correlations among traits over time ........................................... 19

4 Discussion .............................................................................................................. 20
4.1 Modelling and predicting phenotypic live-weight ........................................... 20
4.2 Genetic analysis of live-weight using fixed effects and mixed model equations ..... 22
4.2.1 Two-step and one-step approaches .......................................................... 22
4.2.2 Correlations between the two-step and one-step approaches ..................... 22
4.3 Genetics of live-weight, feed intake and efficiency traits using random regression models .......................................................................................................................................................................................... 23
4.3.1 Genetic correlations among traits over time ........................................... 25

5 Conclusion .............................................................................................................. 26

6 Implications .............................................................................................................. 27

7 Bibliography .......................................................................................................... 29
1 Introduction

1.1 Modelling and predicting phenotypic live-weight

Growth can be defined as the relationship between age and lifetime weight of an animal, and can be mathematically modelled using growth functions (Fitzhugh, 1976; Kucuk and Eyduran, 2009). Growth functions have the ability to condense the weight-age relationship into a few biologically interpretable parameters (Brown et al., 1976; Goonewardene et al., 1981). The greatest attribute of a growth function is its ability to predict the animal’s future growth, rather than simply describing the animal’s growth heretofore (Koivula et al., 2008). Parametric growth functions, such as von Bertalanffy (Bertalanffy, 1957), Gompertz (Winsor, 1932) and Richards (Richards, 1959) are suitable to describe and predict growth throughout an animal’s life. Several different growth models have been used to describe the growth pattern and development of body weight in pigs (Knap, 2000; Wellock, 2004; Koivula et al., 2008), cattle (Brown et al., 1976; Beltran et al., 1992; Berry et al., 2005), and sheep (Lewis et al., 2002; Gbangboche et al., 2006; Gbangboche et al., 2008). Studies have also investigated modelling pig live-weight using either fixed effects or mixed models (Craig and Schinckel, 2001; Strathe et al., 2010), with fixed (Afolayan et al., 2006) and random polynomial regressions (Meyer, 2005) also utilised. Model selection to predict growth in livestock is, nonetheless, a challenging task given the broad variety of growth functions, the diverse selection of biological functions that need to be accounted for, and criteria to assess goodness of fit.

Considerable research has been undertaken on the genetic parameters of growth function parameters (Mignon-Grasteau, 1999; Lewis et al., 2002; Koivula et al., 2008). Little information in the literature exists, however, on the modelling of phenotypic live-weight data
and quantifying a growth function’s ability to predict future phenotypic live-weight using either fixed effects or mixed model equations in pigs.

1.2 Genetics of live-weight using fixed effects and mixed model equations

Future prediction of an individual animal or (genetic) family growth profile at both a phenotypic and genetic level has been extensively studied (Meyer, 2005; Sowande and Sobola, 2008; McHugh et al., 2012). Previous results suggest that the Gompertz growth function is generally superior to other growth functions for modelling and predicting future phenotypic animal live-weight (Sevon-Aimonen, 2001). The Gompertz function has three biologically interpretable parameters which are known to be heritable (poultry – Mignon-Grasteau, 1999; sheep – Lewis et al., 2002; pigs – Koivula et al., 2008) and therefore could be modified through genetic selection.

Studies on the estimation of the genetic (co)variances for growth function parameters have mostly used a two-step approach in that growth function parameters are estimated for individual animal growth in a fixed effects framework initially, after which the individual animal function parameter estimates are subjected to mixed model equations implemented for the variance component estimation (Bathaei and Leroy, 1998). A one-step approach has also been investigated (Koivula et al., 2008) where non-linear mixed models were solely used.

To our knowledge, no study has compared variance components of growth function parameters estimated directly from the data to those estimated in a two-stage process where the individual animal growth function parameters are first estimated at a phenotypic level prior to the estimation of genetic (co)variances for these parameters.
1.3 Genetics of live-weight, feed intake and efficiency traits using random regression models

Animal growth and feed intake are key factors determining farm productivity and profitability. Feed costs account for up to 70% of total animal production costs (chickens – Begli et al., 2016); therefore reducing costs without any repercussions on animal growth and performance is of considerable interest to producers. A strong positive genetic relationship exists between live-weight and feed intake (pigs – Nguyen et al., 2004); consequently selecting animals based on either live-weight or feed intake, without cognisance of the other trait, may not result in the selection of the most efficient animals (Begli et al., 2016). Residual feed intake has been suggested as an alternative efficiency measure, defined as, the difference between an animal’s actual feed intake and its expected feed requirements for maintenance and growth (Koch et al., 1963). Residual daily gain has also been proposed as an alternative definition of efficiency explained as the difference between an animal’s actual growth rate and its expected growth rate (Koch et al., 1963). To our knowledge, no study has estimated (co)variance components for pig live-weight, feed intake and efficiency traits using random regression polynomial equations, and examined the interactions of traits, throughout the animal’s growing phase.

1.4 Objectives

The objective of this thesis was threefold:

1) To compare alternative growth functions fitted to pig live-weight data, with particular emphasis on the ability of the growth function to predict future live-weight (Article I);
2) To estimate genetic (co)variances for the parameters of the previously determined most appropriate growth function using alternative modelling approaches (Article II); and
3) To estimate genetic (co)variances parameters pertaining to live-weight, feed intake and two other efficiency traits using Legendre polynomial equations (Article III).

Results from this thesis can be implemented into genetic evaluations for pigs, providing comprehensive information on the profile of growth and efficiency throughout the growing period of the animal’s life, thus helping breeders identify genetically superior animals.
2 Materials and methods

2.1 Data

2.1.1 Animal management

All animals used in this thesis were on trial in the Längelmäki central test station in Finland between the years 2006 and 2012, inclusive (Articles I, II and III). The pigs evaluated in the test station are included in the Finnish national breeding evaluation. Animals ranged from 61 to 102 days of age at entry into the test station and included boars, gilts, and barrows; the average age was 88 days on entry. Two breeds were included in the dataset namely Yorkshire and Landrace. Animals were housed in groups according to their date of entry to the station. Animals were allocated a daily feed allowance just below the expected consumption in an ad libitum feeding regime based on the average live-weight of the group (Koivula et al. 2008); a total of 33 different diets were used, in a phase feeding system, over the course of the data collection (from 2006 to 2012). Pedigree information was available for all animals and the pedigree file consisted of 1,653,082 animals. A sire pedigree was utilised for all three studies and included 3,550 sires, over 4 generations, from 636 founder sires represented in 3,919 litters. The contemporary group applied to the models in Articles II and III was defined as the date of entry to the test station (n = 269).

2.1.2 Growth and feed efficiency traits

Live-weight

A total of 61,715 live-weight records from 12,768 pigs were obtained from the Finnish pig breeding company Figen Oy (Article I, II and III). Live-weight was recorded for each pig on a bi-weekly basis; the number of live-weight records per animal ranged from three to eight, recorded over an 86 to 99 day test period. Animals with less than five live-weight
records during the test period (n=1,034) were discarded, as were animals that failed to remain on test for at least 86 days (n=100). A total of 150 individuals with recorded weight loss between consecutive test-day weight measurements, taken on average two weeks apart, were removed. Only animals that were recorded as finishing the test period alive without any record of sickness throughout the test period were retained (1,283 animals omitted).

*Feed intake*

A total of 1,117,974 feed intake records from 12,768 pigs were obtained for analysis (Article III). Feed intake records were collected on a daily basis from each pig for the duration of their test period (ranging from 86 to 99 days). Pigs with feed intake records greater than ± 3 SD of the mean intake for the group were omitted (32 pigs were omitted).

*Residual feed intake*

Residual feed intake, defined by Koch et al. (1963), describes the difference between an animal’s actual feed intake and its expected feed requirements for maintenance and growth. Residual feed intake was estimated for each pig using a random regression model, where average daily gain (ADG) plus the metabolic live-weight of the pig were regressed onto feed intake (Article III). Predicted live-weight, estimated per pig per day, using a random regression model was used to derive ADG and was calculated for each pig as forward differencing (i.e., the difference in live-weight between two consecutive days of age). Subsequently regression analysis was undertaken using PROC REG (regression analysis; SAS, 2012), where feed intake was included as the dependent variable and ADG and metabolic live-weight (calculated as daily live-weight to the power of 0.75 (live-weight\(^{0.75}\)) were included as regressor variables. The residual estimates from the regression analysis were taken to represent residual feed intake.
**Residual daily gain**

Residual daily gain phenotypes were estimated for each pig using a regression model in PROC REG (regression analysis; SAS, 2012), where ADG was included as the dependent variable and feed intake and metabolic live-weight were both included as the independent variables; the residual values from the regression model were taken to represent residual daily gain (Article III).

Following all edits, the final dataset consisted of 51,893 live-weight observations and 903,436 feed intake, residual feed intake and residual daily gain observations from 10,201 animals (Articles I, II and III).

2.2 **Analyses**

2.2.1 **Modelling and predicting phenotypic live-weight**

Three different growth functions were fitted to the live-weight data for each individual animal (Article I). The three growth functions were the von Bertalanffy, the Gompertz and the Richards growth function and are described in Table 1. Each of the three growth functions were fitted in a fixed effects model framework to each animal separately, and subsequently built up into a mixed model for each growth function. For comparison purposes, fixed effects and mixed model polynomials were also applied to the data. To account for the small absolute value for the average rate of maturation (parameter $k$) in all growth functions equations, and its diminutive variance compared to the other parameters, a scaled time variable was used. Age in days was scaled prior to the analysis by multiplying the age of the animal by a scaling factor (0.015) and was utilised across all six functions. This scaling factor was derived as the average rate of maturation ($k$) obtained from preliminary analysis of the data.
Each of the three growth functions were fitted using a fixed effects model to each animal separately in PROC NLIN (non-linear least square analysis; SAS, 2012). A fixed effects polynomial was fitted in PROC REG (regression analysis; SAS, 2012); linear, quadratic and cubic order polynomials were considered. Additionally the growth functions’ parameters $A$, $B$, $k$ and $m$ (for Richards only) were estimated using a mixed model for each growth function in PROC NLMIXED (non-linear mixed model analysis; SAS, 2012). Mixed model polynomials were also fitted using PROC NLMIXED (non-linear mixed model analysis; SAS, 2012); linear, quadratic and cubic order mixed model polynomials were analysed.

**Table 1** Equations for each growth function, fitted as a fixed effects model

<table>
<thead>
<tr>
<th>Growth function</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Von Bertalanffy</td>
<td>$Y_t = A (1-B \exp^{kt})^3$</td>
</tr>
<tr>
<td>Gompertz</td>
<td>$Y_t = A \exp(-B \exp^{kt})$</td>
</tr>
<tr>
<td>Richards</td>
<td>$Y_t = A (1-B \exp^{-kt})^m$</td>
</tr>
<tr>
<td>Polynomial</td>
<td>Linear</td>
</tr>
<tr>
<td></td>
<td>Quadratic</td>
</tr>
<tr>
<td></td>
<td>Cubic</td>
</tr>
</tbody>
</table>

*where $Y_t$ represents the observed weight of the animal at age $t$ expressed as the rescaled time variable; $A$ represents the limit for each animal as its age approaches infinity, it does not approximate the heaviest weight attained by the animal; Parameter $B$ for the Gompertz function is defined as the ratio of mature weight to birth weight, for the von Bertalanffy and Richards functions parameter $B$ represents the constant of integration.; $k$ is a maturing rate parameter defining the ratio of maximum growth rate to mature weight; $m$ relates the inflection point to $A$.**
Two datasets were used to evaluate each growth functions’ ability to model and predict animal live-weight. The first dataset included all animal live-weight records (exploratory dataset) and was used to evaluate how well each growth function modelled (historical) animal live-weight. The accuracy of the model fit was determined based on the square of the correlation between the actual and predicted live-weight ($r^2_{\hat{W}}$). The root mean square error (RMSE) values for each model scenario were also estimated. The $r^2_{\hat{W}}$ and RMSE were calculated for each individual animal separately and then averaged across the entire population for each growth function.

The second dataset (forward prediction) evaluated how efficiently the growth function predicted future animal live-weight when weight records later in the animal’s life were excluded. The forward prediction dataset was constructed as follows; the exploratory dataset was stratified by year and gender and randomly divided into four evenly sized groups. Cross-validation was performed with the analysis run for each of the four groups separately, for each of the four runs; weight records post 160 days from only one stratum were masked and excluded records predicted for the entire remaining dataset. The square of the correlation between the predicted and actual live-weights ($r^2_{\hat{W}W}$) as well as the RMSE were calculated for the excluded live-weights and average for all four cross-validations obtained to generate a final $r^2_{\hat{W}W}$ and RMSE value. Residual correlations and the bias associated with the three fixed effects growth functions and the fixed effects polynomial equations were also calculated; bias was defined as the mean difference between the actual recorded live-weight and the predicted live-weight.

The number of animals where the model converged for a particular growth function was also considered when choosing the most suitable growth function. The most parsimonious order of the mixed model polynomial equation to adequately model the data
was decided on by comparing the Akaike information criterion of the higher order mixed model polynomial and the immediately lower order fit.

2.2.2 Genetic analysis of live-weight using fixed effects and mixed model equations

(Co)variance components of the growth parameters for fixed and mixed models were estimated using univariate, bivariate and multi-trait linear mixed model in ASReml (restricted maximum likelihood analysis; Gilmour et al., 2009).

2.2.2.1 Two-step approach

Results from the fixed effects model (section 2.2.1) and from the mixed model equation (section 2.2.1), concluded that the Gompertz growth function was superior in both modelling predicting animal live-weight, and therefore, only the Gompertz model was considered for the genetic analysis of live-weight. The Gompertz growth function was fitted to the data to derive individual animal A, B and k parameters with PROC NLIN (non-linear least square analysis; SAS, 2012), or using a mixed model equation in PROC NLMIXED (non-linear mixed model analysis; SAS, 2012) (Article II):

\[ Y_{ij} = A_i \times e^{(-B_i \times e^{-k_i \times t_j})} + e_{ij}, j = 1, \ldots, n_i \]

where the dependent variable \( Y_{ij} \) represents the observed live-weight of the animal \( i \) at \( t_j \) rescaled days of age, \( n_i \) is the number of observations for animal \( i \), parameter \( A \) (kg) describes the live-weight of the animal as its age approaches infinity and represents the mature weight. Parameter \( B \) is the ratio of mature weight to birth weight in log scale. Parameter \( k \) (kg/d per kg mature weight) represents the maturing rate as the ratio of maximum growth rate to mature weight, and \( e_{ij} \) is the residual effect of the animal \( i \) at \( t_j \) days of age.

(Co)variance of the resulting growth parameters for the fixed and mixed models were estimated using a multi-trait linear mixed model in ASReml (restricted maximum likelihood
analysis; Gilmour et al. 2009), with pedigree information for all animals included. Both gender and contemporary group (date of entry to test station, n = 269) were included as fixed effects, with a litter effect (N(0, A\(\sigma^2_l\))), and a sire genetic effect (N(0, A\(\sigma^2_s\))), applied as random effects for all Gompertz function parameters. Heritability (\(h^2\)) estimates for the two-step approaches were calculated using the following formula:

\[
h^2 = \frac{4\sigma^2_s}{\sigma^2_s + \sigma^2_l + \sigma^2_e}
\]

where \(\sigma^2_s\) is the sire genetic variance of the trait, \(\sigma^2_l\) is the common litter variance of the trait, and \(\sigma^2_e\) is the residual variance of the trait.

2.2.2.2 One-step approach

For the one-step analysis, the growth of each pig was modeled using a Gompertz model (Winsor, 1932), but using a multiplicative model approach as detailed in Koivula et al. (2008):

\[
\ln(Y_{ij}) = \ln(g_A + c_A + l_A + a_A + s_A) \times \left(-(g_B + c_B + l_B + a_B + s_B) \times \exp^{-\left(g_k + c_k + l_k + a_k + s_k\right) \times t_j}\right) + \ln(e_{ij})
\]

where \(\ln\) represents the natural log, the dependent variable \(Y_{ij}\) represents the observed live-weight of the animal \(i\) at \(t_j\) rescaled days of age, \(g\) is the fixed gender effect, \(c\) is the fixed contemporary group effect, \(l\) is the random litter effect (N(0, A\(\sigma^2_l\))), \(a\) is the random animal effect (N(0, I\(\sigma^2_a\))), and \(s\) the sire genetic effect (N(0, A\(\sigma^2_s\))). Subscript \(A\) describes that the effect is related to the live-weight of the animal as its age approaches infinity. Similarly, the effects with subscripts \(B\) and \(k\) are related to the ratio of mature weight to birth weight and the maturing rate, respectively, and \(e_{ij}\) is the residual effect (N(0, I\(\sigma^2_e\))) of the animal \(i\) at \(t_j\) days of age.
The restricted maximum likelihood (REML) based empirical best linear unbiased predictor (EBLUP; Wolfinger and Lin, 1997) was utilised to implement the models as described by Vuori et al. (2006). Pseudo heritability \((h^2)\) estimates were calculated for each of the three growth function parameters, \(A\), \(B\) and \(k\):

\[
h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_l^2 + \sigma_a^2}
\]

where \(\sigma_s^2\) is the sire genetic variance of the trait, \(\sigma_l^2\) is the common litter variance of the trait and \(\sigma_a^2\) is the permanent environmental variance of the animal.

For the two-step fixed effects and mixed model approaches, and the one-step mixed model approach, estimated breeding values (EBV) for parameters \(A\), \(B\) and \(k\) were obtained for all sires. These parameter EBV were then used to derive daily sire live-weight profiles (referred to as predicted daily sire live-weights from this point forward) calculated by inserting the sire EBV solutions for \(A\), \(B\) and \(k\), adjusted for the population mean for each parameter, into the Gompertz growth function; daily sire live-weight was estimated from 60 to 200 days of age.

**2.2.3 Genetics of live-weight, feed intake and efficiency traits using random regression models**

Genetic (co)variance parameters for live-weight, feed intake, residual feed intake and residual daily gain were estimated using random regression Legendre polynomials in ASReml (restricted maximum likelihood analysis; Gilmour et al., 2009) (Article III). The following model was fit to each trait:
\[ Y_{ijklmpqrs} = \text{sex}_j + \sum_{k=1}^{n} b_k \text{age}_k + \text{breed}_l + \text{congrp}_m + \text{feed}_p + \sum_{k=1}^{n} \text{sex}_jk \text{age}_k + \sum_{k=1}^{n} \text{breed}_lk \text{age}_k + \sum_{k=0}^{n} \text{sire}_qk \text{age}_k + \sum_{k=0}^{n} \text{litter}_sk \text{age}_k + \sum_{k=0}^{n} \text{permAni}_{rk} \text{age}_k + \text{e}_{ijklmpqrs} \]

where \( Y_i \) was the dependent variable (live-weight, feed intake, residual feed intake or residual daily gain) of the \( i \)th pig, \( \text{sex}_j \) was the fixed effect of the pig’s gender (entire male, female and castrate), \( \sum_{k=1}^{n} b_k \text{age}_k \) was the polynomic function of effect of age with \( \text{age}_k \) being the \( k \)th-order Legendre polynomial on age\( _k \) (d) of the pig, \( \text{breed}_l \) was the breed of the pig (Yorkshire, and Landrace), \( \text{congrp}_m \) was the contemporary group of the pig, defined as date of entry to the test station, \( \text{feed}_p \) represents the dietary supplementation offered to individual group of pigs which varied across the growing phase, \( \sum_{k=1}^{n} \text{sex}_jk \text{age}_k \) models a two-way interaction between the fixed effect of sex along the growth period where \( \text{age}_k \) is the \( k \)th-order Legendre polynomial and \( \sum_{k=1}^{n} \text{breed}_jk \text{age}_k \) models a two-way interaction between the fixed effect of breed along the growth period where \( \text{age}_k \) is the \( k \)th-order Legendre polynomial. The random effects fitted to all models were \( \text{sire} \) \( \mathcal{N}(0, A\sigma_s^2) \), permanent environmental effect of the pig \( \mathcal{N}(0, A\sigma_a^2) \) and a litter effect \( \mathcal{N}(0, A\sigma_l^2) \); where \( \sum_{k=0}^{n} \text{sire}_qk \text{age}_k \) models the sire effects along the growth period where \( \text{age}_k \) is the \( k \)th-order Legendre polynomial, \( \sum_{k=0}^{n} \text{litter}_sk \text{age}_k \) models the litter effects along the growth period where \( \text{age}_k \) is the \( k \)th-order Legendre polynomial, \( \sum_{k=0}^{n} \text{permAni}_{rk} \text{age}_k \) models the permanent environmental effects along the growth period where \( \text{age}_k \) is the \( k \)th-order Legendre polynomial, and \( \text{e}_{ijklmpqrs} \) was the residual effect \( \mathcal{N}(0, I\sigma_e^2) \).
Non-significant fixed effects ($P > 0.05$) were removed from each model by backward elimination. The most parsimonious order of the fixed effect Legendre polynomial was chosen based on the F-statistic value from each order of the polynomial term and also by visual comparison of the resulting curve profile for each model. For the random effects of sire, litter and permanent environmental effect of the pig, the order applied to the polynomial for the sire genetic effect was increased independently of the polynomial for the random litter and permanent environmental effects, (i.e., the sire random effect was increased by $n^{\text{th}}+1$-order Legendre polynomial compared to the $n^{\text{th}}$-order Legendre polynomial for both litter and permanent environment effect). The most parsimonious Legendre polynomial order to adequately model the data was chosen by comparing the log likelihood ratio values of the higher order random regression model and the immediately lower order fit. Eigenvalues of the resulting (co)variance function were also examined for each of the random effects.
3 Results

The edited dataset consisted of 41% boars, 33% gilts, and 26% barrow pigs. The average age (SD in parenthesis) of the pigs entering the test centre was 88 days (7.4 days) with an average weight of 35.2 kg (5.6 kg). The average age (SD in parenthesis), in the edited dataset, of the pigs leaving the test centre was 177 days (8.2 days) with an average weight of 118.0 kg (12.3 kg).

3.1 Modelling and predicting phenotypic live-weight

The proportion of animals where the model fitted converged with biologically sensible parameters for each growth function varied from 55% (Richards) to 100% (polynomials) for the exploratory dataset (Article I). The population mean values (SD in parenthesis) of the model parameters varied by growth function; mean values (SD in parenthesis) for parameter \(A\) for the Gompertz, was 259.54 kg (77.61 kg), parameter \(B\) was 5.50 (0.87) and parameter \(k\) was 0.77 kg/d per kg mature weight (0.17 kg/d per kg mature weight). The coefficient of variation for parameters \(A\) and \(k\) for the Gompertz growth function were 30% and 22%, respectively.

The accuracy squared \((r_w^2)\) for the exploratory dataset, ranged from 0.989 (Richards) to 0.998 (cubic polynomial); a high \(r_w^2\) (0.997) and a low RMSE was estimated for the Gompertz growth function (1.66 kg) indicating it best fit the exploratory dataset. Results for the Gompertz function when forward predicting live-weight revealed the \(r_{w_w}^2\) was lower (0.683) and had a RMSE value five times larger (8.51 kg) compared to the initial modelling results. When forward predicting live-weight, the Gompertz function marginally underestimated live-weight (on average by -0.009 kg to -0.003 kg), and weak correlations (|0.12|) existed between the phenotypic animal live-weight and the prediction error of the calculated future live-weight.
Strong positive correlations existed between the three growth function parameter estimates, $A$, $B$ and $k$, for the fixed effects and mixed model Gompertz equations. The fixed effects model estimated a moderate negative correlation ($r = -0.41$) between parameters $A$ and $B$; however for the mixed model equations the corresponding correlation was 0.29. The Gompertz function with integration constant ($B$) and rate of maturation ($k$) fitted as random effects was superior to all other mixed models in predicting future live-weight with an $r^2_{\text{pred}}$ and RMSE of 0.9619 and 2.60 kg, respectively. The mixed model Gompertz growth function, with parameters $A$ and $k$ fitted as random effects, slightly over-estimated live-weight, on average by 0.59 kg to 3.97 kg. Near zero correlations (0.01 to 0.02) existed between the phenotypic animal live-weight and the prediction error of the calculated future live-weight with the Gompertz mixed models.

### 3.2 Genetic analysis of live-weight using fixed effects and mixed model equations

#### 3.2.1 Two-step approach

The co-efficient of genetic variation for the two-step fixed effects approach was 10%, 14% and 9%, for parameters $A$, $B$ and $k$, respectively. The coefficient of genetic variation estimates for $A$ (6%), $B$ (5%) and $k$ (4%) for the two-step mixed model was lower than the corresponding two-step fixed effects approach (Article II). Lower heritability estimates (SE in parenthesis) were observed for all growth function parameters when the two-step fixed effects approach (ranging from 0.10 (0.03; parameter $A$) to 0.33 (0.04; parameter $B$) compared to the two-step mixed model approach (ranging from 0.17 (0.03; parameter $A$) to 0.32 (0.04; parameter $B$).
3.2.2 One-step approach

Moderate to large heritability estimates were observed for the three Gompertz growth function parameters $A$ (0.40), $B$ (0.69) and $k$ (0.45). Weak to moderate correlations existed between the three growth curve parameters (-0.07 to -0.39) estimated using the one-step approach.

3.2.3 Correlations between sire EBV for the two-step and one-step approaches

Moderate to strong correlations existed between the sire EBV for parameter $A$, ranging from 0.31 (two-step fixed effects approach and the one-step mixed model approach) to 0.73 (fixed effects and the mixed model two-step approach) (Article II). Across the two-step fixed effects and mixed model approach, and the one-step mixed model approach, strong correlations were evident for sire EBV for parameter $B$ ranging from 0.75 (two-step fixed model and the one-step mixed model) to 0.89 (two-step mixed effects model and the one-step mixed model). The weakest correlation between sire EBV for the three Gompertz growth function parameters existed for parameter $k$ and ranged from 0.08 (two-step fixed model and the one-step mixed model approach) to 0.37 (two-step mixed effects and the one-step mixed model).

Moderate to strong correlations were observed between sire live-weight EBV calculated using the Gompertz growth curve from 60 to 200 days of age across all three approaches. The correlation between the sire live-weight EBV predicted using the two-step fixed effects and one-step mixed model approach ranged from 0.75 (day 200) to 0.81 (day 60), and between the one-step mixed model approach and the two-step mixed model ranged from 0.91 (day 60) to 0.95 (day 200).
3.3 Genetics of live-weight, feed intake and efficiency traits using random regression models

A fourth order random regression Legendre polynomial on the fixed effect of age provided the best fit for live-weight, feed intake and residual feed intake; for residual daily gain a fifth order Legendre polynomial was best (Article III). For live-weight, a quadratic random regression Legendre polynomial best described the additive genetic effect, while a linear random regression Legendre polynomial was the most parsimonious for both litter and permanent environmental component. Although a quartic random regression Legendre polynomial appeared to provide the best fit to all three random effects for both feed intake and residual feed intake, however results from the log likelihood test showed that the quartic order did not improve the fit to the data, therefore a cubic random regression Legendre polynomial was applied for both feed intake and residual feed intake. For residual daily gain, a quadratic order Legendre polynomial was applied to all three random effects.

The genetic variance for live-weight, feed intake and residual feed intake followed a similar trend throughout the pig’s growing phase, increasing with age with a more pronounced increase at older ages, especially for feed intake and residual feed intake. In contrast, the trend in genetic variance for residual daily gain was almost a mirror image, reducing as the animal’s age increased. Litter and permanent environmental variance associated with live-weight, feed intake and the two other efficiency traits decreased as the age trajectory of the animals increased.

Heritability estimates (SE in parenthesis) for live-weight ranged from 0.25 (0.04) on day 73 to 0.50 (0.03) on day 122, and decreased steadily thereafter. Low to moderate heritability estimates were evident for feed intake ranging from 0.07 (0.03) on day 66 to 0.25 (0.02) on day 170. The estimated heritability for residual feed intake was generally lower
than those reported for live-weight and feed intake and ranged from 0.04 (0.01) day 96 to 0.17 (0.02) day 159. For feed intake and residual feed intake, heritability estimates declined rapidly after day 170 and day 158, respectively. Heritability estimates for residual daily gain increased to a maximum value of 0.42 (0.03) on day 104 in the early stages of the pig’s growing phase but decreased steadily thereafter to a minimum value of 0.26 (0.03) on day 188.

3.3.1 Genetic correlations within trait at different ages

Within all traits, genetic correlations were strongest (0.99) between adjacent ages, but weakened as the interval between ages increased (Article III). Strong negative genetic correlations between the beginning and end of the test period were estimated for residual daily gain, whereas for other traits moderate positive genetic correlations were estimated. Interestingly, observations for live-weight, feed intake and residual feed intake at age 66 are more genetically correlated to observations at age 196 than age 136.

3.3.2 Genetic correlations among traits over time

Moderate to strong genetic correlations were evident among all four traits in the early stage of the test period (day 66 to day 86) but weakened with age. The strongest correlations were observed between live-weight and feed intake, ranging from 0.58 (day 197) to 0.88 (day 115) and, between feed intake and residual feed intake from 0.65 (day 153) to 0.92 (day 66). Live-weight was moderately to strongly positively correlated with both residual feed intake (0.46; day 96) and residual daily gain (0.96; day 105), respectively. Moderate to strong positive genetic correlations existed between residual feed intake and residual daily gain (0.35 on day 132 to 0.70 on day 89).
4 Discussion

The Gompertz growth function adequately modelled and predicted pig live-weight. Furthermore, a Gompertz growth function in a one-step mixed model framework estimated the greatest heritability for the three growth function parameters, $A$, $B$ and $k$. Finally random regression Legendre polynomial models fit the data adequately and ample genetic variation was estimated indicating the potential to alter curve profiles for live-weight, feed intake, residual feed intake and residual daily gain to meet specific breeding objectives. Results from this thesis can be implemented into genetic evaluations for pigs, providing comprehensive information on the profile of growth and efficiency throughout the growing period of the animal’s life, thus helping breeders identify genetically superior animals.

4.1 Modelling and predicting phenotypic live-weight

The growth functions investigated in this study (i.e., von Bertalanffy, Gompertz, and Richards) have been commonly used to model live-weight gain in many livestock species (cattle – Berry et al., 2005; pigs – Koivula et al., 2008; sheep – Lambe et al., 2006; Gbangboche et al., 2008). The Brody growth function (Lambe et al., 2006; Gbangboche et al., 2008) and the logistic growth function (Lambe et al., 2006) have also been studied extensively but previous studies have concluded that the von Bertalanffy, Gompertz and Richards growth functions were superior for describing animal growth compared to all other growth functions.

Differences existed between the growth functions when their ability to predict future animal live-weight in the forward prediction dataset was considered. The ability of the mixed model equations to forward predict live-weight was, in all cases, superior to the fixed effects models. Mixed model equations account for the population mean but also the individual animal deviations from that mean, thereby partitioning the variance more efficiently
compared to the fixed effects models. The superiority of mixed models is particularly important when population growth rate is starting to plateau. The fixed terms in the mixed model use data on contemporaries to model this plateauing effect; thereby also influencing the predicted future growth trajectory of the individual animals, without sufficient data to inform the algorithm of the current growth rate and imminent plateau. Previous studies (poultry – Mignon-Grasteau et al., 1999; sheep – Lewis et al., 2002) have exploited fixed effects models for the development of growth curves in a range of species. Gossett et al. (2007) reported that the mixed model equations, when incorporated into the Gompertz growth function, were the best type of models to model the growth curve of premature human infants. Similar results were observed across different species when the mixed model Gompertz growth functions’ ability to describe and summarise a given dataset, but also to predict future live-weight, was examined (pigs – Wellock, 2004; Koivula et al., 2008; sheep – Lambe et al., 2006).

In comparison to growth functions, polynomial equations have, however, no biologically interpretable parameters and therefore, depending on the purpose of the function, may not be the most suitable choice for describing growth patterns. In contrast to polynomial equations, biological interpretable growth functions are better in data extrapolation; non-linear functions have a built in intelligence which allows the growth curve to reach an actual asymptotic mature weight. Towards the end of life, when there were fewer data points, in a mixed model framework the random effect solutions will regress towards the fixed effects profile, which causes the animal growth curves to mimic the growth pattern of the contemporaries. In contrast, when modelling incomplete data, the polynomial models are not restricted to biological limits, since no assumptions are made about the shape of the growth curve relative to time; this may explain their poor forward predictive ability of live-weight in this thesis.
4.2 Genetic analysis of live-weight using fixed effects and mixed model equations

4.2.1 Two-step and one-step approaches

The sire variance estimated for live-weight from the two-step and one-step mixed model approaches were lower than the sire variance estimated for live-weight using the fixed effects model. One potential reason for the larger sire variance estimated for live-weight with the two-step fixed effects approach, could be attributable to the partitioning of the variances in the models; a mixed model will regress individual random animal deviations towards the mean and therefore, will result in less variation in the second step for variance component estimation. In addition only one residual variance was calculated for the one-step approach, and therefore the variance not explained by sire and litter may be included in the random animal effect rather than in the residual variance. Several international studies in different species are in agreement that non-linear mixed models allowed for more accurate and precise estimation of animal growth parameters compared to fixed effects models, due to their ability to reduce bias generally caused by the early removal of heavier pigs (sheep – Bathaei and Leroy, 1998; pigs – Craig and Schinckel, 2001; ducks – Schinckel et al., 2004).

The greater heritability estimates associated with the Gompertz growth function parameters, asymptotic mature weight \( A \) and rate of maturation \( k \), for both the one-step and two-step mixed model approaches compared to the two-step fixed effects approach, again, could be explained by the superior partitioning of residual variance by the mixed model compared to the fixed effects model.

4.2.2 Correlations between the two-step and one-step approaches

The negative correlation between sire EBV for asymptotic mature weight and rate of maturation across the two-step fixed effects and mixed model, and the one-step mixed model
approaches, could be exploited by pig producers to produce faster growing animals that reach lower mature weights, thereby reducing the age at slaughter of finishing animals but also enabling producers to increase stocking density due to the lower mature weight of the breeding stock. A strong positive association between parameters $B$ and $k$ for the two-step fixed effects Gompertz growth function, could be biologically interpreted as lighter pigs are more likely to grow faster at a young age and subsequently have greater maturing rates.

Selecting on an individual trait without taking cognisance of its relationship to other traits can have deleterious consequences; therefore a sire’s predicted daily live-weight profile may be more beneficial and informative as it allows breeders to identify sires that deviate from the mean population curve at certain stages of growth. Although correlations between EBV from two-step models vary for different parameters, selecting sires on their predicted live-weight profiles for both two-step approaches would result in the selection of similar sires based on the strong positive correlations between predicted sire live-weights across all ages (0.91 to 0.96). However the weakening correlation between the two-step and one-step predicted sire live-weights as age increases suggests that sires would rank differently as animals reached maturation, specifically from 150 days on. One possible explanation for this is the weak correlation recorded between EBV for parameter $A$ in the two-step and one-step approach.

4.3 Genetics of live-weight, feed intake and efficiency traits using random regression models

Across species, random regression polynomial models have been documented as superior to multi-trait models in modelling variance components, due to their ability to analyse (co)variances between, or at, every age or time point (sheep – Wolc et al., 2011; pigs – Wetten et al., 2012; cattle – Mota et al., 2013; poultry – Begli et al., 2016). In addition,
Legendre polynomials have been favored over normal polynomials in many studies as the orthogonal properties associated with Legendre polynomials assist model convergence (Smyth, 1998; Meyer, 2000). The order of the random regression Legendre polynomials fitted to live-weight varies across studies and species (pigs – Schnyder et al., 2001; Huisman et al., 2002). An important point of information regarding the random regression Legendre polynomials is, although a higher order may provide a superior fit to the data, the substantial increase in computational resource required to estimate the higher order may not be justified (Schnyder et al., 2001).

Additive genetic, litter and permanent environmental variance increased steadily over time for live-weight, feed intake and residual feed intake, which corroborates results from other studies on these traits estimated using random regression models in pigs (Huisman et al., 2002) and poultry (Begli et al., 2016). Few studies (Huisman et al., 2002) have reported the genetic, litter and permanent environmental variances estimated using random regression models in pigs for live-weight, feed intake and efficiency traits. However, genetic and permanent environmental variances reported previously using multi-trait models (Wetten et al., 2012) followed a similar trend to the trend in variances observed in this thesis. Residual variance for live-weight, feed intake, residual feed intake and residual daily gain varied as age increased, though not to the same magnitude as genetic, litter and permanent environmental variances which contrasts to results published in pigs by Wetten et al. (2012).

The heritability estimates for live-weight in the present study were within the range, albeit on the upper end, than those reported in previous studies on growing pigs using both random regression models (Huisman et al., 2002) and multi-trait models (Gjerlaug-Enger et al. 2011; Wetten et al., 2012). Reduced heritability estimates of feed intake may be explained by an increase in mean feed intake of the individual pigs towards the latter stages of the test period which could be causing greater variability in the recording of the phenotype.
Eigenfunctions provide information on potential changes in the age trajectory in response to selection of a trait (Meyer and Hill, 1997), and have previously been applied to live-weight records in cattle (Berry et al., 2007) and pigs (Schnyder et al., 2001). Analysis of eigenvalues and eigenfunctions of the additive genetic (co)variance matrices in the present study revealed that ample variability exists in the shape of profiles for live-weight, feed intake, residual feed intake and residual daily gain. Across all traits the intercept term accounted for a large proportion of genetic variation (55.5 to 86.8%); this suggests that the height of the profiles for the four traits can be modified through breeding, thereby allowing pigs to grow faster and to heavier weights.

4.3.1 Genetic correlations among traits over time

Genetic correlations between live-weight and feed intake were stronger in the early stage of the trial period and suggest that a high genetic growth capacity is closely related to greater feed intake during the early stages of growth. The strong genetic correlation between feed intake and residual feed intake in the present study is consistent with a similar study in pigs (Saintilan et al., 2013); these results suggest that the underlying genetic correlations influence the potential for change among live-weight, feed intake and the efficiency traits. The strong genetic correlations identified between the four traits (i.e., live-weight, feed intake, residual feed intake and residual daily gain) suggest that selection for one trait will impact an animal’s performance on the other traits. For example, selecting for heavier live-weight will increase overall live-weight output of the system, but, it will also increase feed intake as heavier animals tend to consume more feed and increased feed costs will negatively affect the system’s profitability. A solution to this problem is to include both traits in a breeding objective; this will allow producers to identify and breed fast growing animals that require less feed. The use of random regression models allows for this selection to occur across the animal’s lifetime.
5 Conclusion

The Gompertz function was the best growth function for modelling and predicting animal live-weight. Mixed model equations were superior to the fixed effects models when comparing modelling and prediction of live-weight, and estimation of genetic (co)variance for growth function parameters. The best model to use for variance component estimation for the Gompertz growth function parameters was the one-step mixed model. This was due to the model’s simultaneous iterative approach to solving the individual animal growth curves for all fixed and random effects, and suggests the model tries to find the optimal balance between fixed and random effects. Assigning EBV to these growth function parameters and implementing the parameters into national genetic evaluation programs could allow for more accurate EBV for growth related traits. Random regression Legendre polynomial models fit the data adequately and moderate to strong heritability estimates and genetic correlations, both within and among traits, were estimated for live-weight, feed intake, residual feed intake and residual daily gain. These results suggest ample genetic variation exists and genetic change can be achieved through selection. Further improvement of live-weight, feed intake, residual feed intake and residual daily gain could be achieved by developing a management decision tool using the information from the current study to align the management of animals more closely with their growth potential.
6 Implications

Based on the results from the present thesis, the Gompertz can accurately model and future predict animal live-weight, particularly when fitted using a mixed model and could be implemented as a management support tool for livestock producers. A decision support tool based on fitted growth functions could be used to identify faster growing animals that require less time to reach target mature weights. Additionally the decision support tool could identify the slow growing animals, aiding producers in making important feeding and slaughter decisions for these animals. A slow growing animal, for example, could be chronically sick and, if left unattended, could infect contemporaries. The growth functions could also be used to predict, based on body weight and age, when gilts will reach maturity or for use in management decision to ensure target weights are being achieved so the animal reaches the appropriate breeding weight at a suitable age. Pig unit growth curves could also be built into abattoir systems to determine animal supply profiles and coordinate the collection of animals suitable for slaughter in different pig units. This can thus be used to maximise the full exploitation of the abattoir production systems and minimise periods of over or under supply.

The three Gompertz parameters are heritable and genetic variation exists; therefore it is possible to identify the genetically superior animals to be parents of the next generation and aid breeders in altering the shape of the population growth curve. The mixed models allow random components to be fit to individual animals; therefore, with a centralised national database, an additional series of random terms could be fitted to reflect pig unit or pig unit by time. This can be used to compare performance of individual pig units or even performance within pig unit over time. Because differences in performance can be due to genetics of management, the mixed models should also account for the genetic merit of the pig herd. Not only could such information be useful in elucidating management practices influencing
performance but could also be useful in detecting pig units with possible high pathogen loads, or regions of individual pig units with high pathogen load, or even if evaluated a potential accumulation of pathogen load over time.

The random regression Legendre polynomials used, fit a covariance between weight measures on the same animal across time. The scope of the random regression Legendre polynomials was further expanded to include genetic relationships among animals which could subsequently be used to estimate breeding values, or measures of genetic merit, for individual animals for each day of life. Further improvement of live-weight, feed intake, residual feed intake and residual daily gain could be achieved by incorporating this information into the previously discussed management support tool and help align the management of the animals more closely with their genetic growth potential. Further studies could include slaughter information, such as carcass conformation and fat, and examine the relationship between the genetic contribution to carcass traits and the actual phenotype being received by meat processors. Additionally, genomic information on live-weight, feed intake, residual feed intake and residual daily gain, should be investigated to identify whether certain areas of the genome are activated during different stages of an animal’s growth phase, or if the same genes are responsible for the trait throughout an animal’s life.


Huisman, A. E., Veerkamp, R. F. and Van Arendonk, J. A. M. 2002. Genetic parameters for various random regression models to describe the weight data of pigs. Journal of


McHugh, N., Evans, R. D., Fahey, A. G. and Berry, D. P. 2012. Animal muscularity and size are genetically correlated with animal live-weight and price. Livestock Science, 144, 11-19


Richards, F. J. 1959. A flexible growth function for empirical use. Journal of Experimental Botany, 10, 290-301


regression model for daily feed intake of performance tested French Landrace and Large White growing pigs. Genetics Selection Evolution, 33, 635-658


