Genetic analysis of growth and feed intake patterns in pigs

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Genetic analysis of growth and feed intake patterns in pigs

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Genetic Analysis of Growth and Feed Intake Patterns in Pigs

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Abstract. Objective of this thesis was to quantify genetic differences in performance patterns of pigs by means of random regression models. Emphasis was on growth and feed intake patterns in pigs. Genetic parameters for weight, daily gain and daily feed intake were estimated using random regression models, where traits were modeled on a continuous scale, i.e. age, days on test or weight. Interactions between weight, daily gain, and daily feed intake during a trajectory were studied. The possibilities to change (part of) performance pattern of pigs through selection were investigated using simulation. Random regression models provide a method to analyze longitudinal records in animal breeding that reveal specific patterns of change over a trajectory. Advantages of the application of random regression models were a higher accuracy of selection, the use of information of the course of traits, and the possibility to change the course of a trait through selection. Measurements of live weight, daily gain, and daily feed intake taken at different points along this trajectory cannot be regarded as repeated measurements of the same trait. It is possible to change patterns of weight, daily feed intake, and daily gain over an age trajectory through genetic selection; the extent of change depends on the genetic correlation structure. A set of multivariate random regression models can be set up, yielding estimated breeding values for traits of interest along a trajectory, e.g. a weight - or age trajectory. These estimated breeding values for different points along a trajectory can be considered as estimated breeding values of separate traits. A breeding goal that incorporates all these traits can be set up, putting more emphasis on that part of the trajectory that we want to change. Random regression models are a helpful tool in identifying and selecting animals that show desired patterns for a combination of traits.

Voorwoord

Het in dit proefschrift beschreven onderzoek is uitgevoerd bij de Leerstoelgroep Fokkerij en Genetica van Wageningen Universiteit. Meerdere mensen hebben bijgedragen aan de totstandkoming, een aantal wil ik hier met name noemen.

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Contents

Chapter 1

General Introduction

Pig breeding programs have been very successful in achieving genetic improvement of economically important traits, especially daily gain, back fat thickness, feed efficiency and in the last decade, litter size (Merks, 2000). Selection of pigs was mainly aimed at improving economic efficiency of pig production per kg pork through improving leanness and feed efficiency of growing pigs (Webb, 1998). These traits are likely to stay important in future breeding programs. At present, broader breeding goals are applied. Breeders are aiming at a more robust pig; efficient production under all relevant circumstances must be achieved. A more robust pig is expected to be more able to meet changes in future demands, such as different housing conditions, lower dependence on medicines and digestion of more feed types. The need for a more robust pig is driven by an increase in consumer awareness and a continuous globalization in pig breeding. Pigs of high quality must be produced under all production circumstances and environmental conditions. This need for a more robust pig means that we have to refine our breeding tools and that we need to collect additional information.

Due to the introduction of electronic feeders, with or without the inclusion of a weight scale (e.g.: de Haer et al., 1992; Ramaekers, 1996; McSweeney et al., 2001), it is possible to gather detailed information on feed intake, feed intake behavior and weight changes of each individual animal. Up to today pigs for the production of pork are selected on total weight gain and total feed intake during a certain test period. This test period generally consists of a fixed age or fixed weight interval. From total gain and total feed intake during test, average daily gain, average daily feed intake, and possibly feed conversion ratio or feed efficiency for that particular period are derived. Such an evaluation system neglects possible variation between animals in growth, feed intake and efficiency patterns, therefore it is not possible to utilize this information when animals are selected. When electronic feeders (with or without weight scales) are used, opportunities to aim selection at performance patterns instead of at performance averages arise (Kalm et al., 1996). With the generation of opportunities to collect all this extra information, new opportunities for selection arise. It becomes possible to identify differences in performance patterns. Genetic variation in performance patterns can be utilized to select animals that have a more desired genetic performance pattern.

To cope with all this information collected on performance patterns, formerly used models are not sufficient. Advanced models that use longitudinal data to estimate genetic performance patterns, need to be developed and applied. Kirkpatrick and Heckman (1989)

suggested the use of covariance functions for traits that are measured on a continuous scale (e.g. time or weight) in a two-step analysis. Firstly, different measurements of the same trait along a trajectory were assumed to be different traits and a variance-covariance matrix was estimated for these "different" traits. After that, functions were fitted on this variance-covariance matrix; these functions then described variances and covariances at all points within the scale of the analysis. Meyer and Hill (1997) extended this method to a method were covariance functions were directly estimated from the data. Several authors (e.g. Van der Werf et al., 1998) used this kind of random regression model, where measurements of the same trait along a trajectory are modeled using random coefficients on a continuous scale. Schaeffer et al. (2000) applied random regression models for the genetic evaluation of dairy cattle, modelling lactation as function of days in milk. This resulted in greater flexibility, more accurately estimated breeding values (EBV's) and more stable EBV's over time. Andersen and Pedersen (1996) were the first to apply random regression models in pigs, to describe growth and feed intake curves for pigs. However, only phenotypic curves were described. Several studies used random regression models to model genetic daily feed intake of growing pigs as function of either days on test or age, with diverging results. Some concluded that changing feed intake patterns through selection would be a very difficult operation (Schnyder, 2001), whereas others conclude that changing feed intake patterns through selection would be a viable option (Hall et al., 1999; Schulze et al., 2002). Sevón-Aimonen et al. (1997) were the first to apply a random regression model to estimate genetic parameters for growth traits in pigs. They showed that genetic differences in gain patterns exist between pigs. However, only estimates for the weight trajectory 30 to 90 kg were shown. The challenges are to estimate genetic parameters for weight and feed intake over a longer trajectory, to investigate genetic relations between both traits at different ages and weights. If genetic relations between weight and feed intake are known at different points along a trajectory, genetic efficiencies can be derived. Possible variation in efficiency along an age- or weight trajectory could be studied.

Objectives and outline

Objective of this thesis was to quantify genetic differences in performance patterns of pigs by means of random regression models. Emphasis will be on weight and feed intake

patterns in growing pigs. Genetic parameters for weight, daily gain and daily feed intake will be estimated using random regression models, where traits were modeled on a continuous scale, i.e. age, days on test or weight. Interaction between weight, daily gain, and daily feed intake during the trajectory will be studied. The possibilities to change (part of) the growth curve of pigs through selection will be investigated making use of simulation.

In *Chapter 2* a multivariate model and various random regression models are compared on their ability to describe weight data of growing pigs. Data analysed in this study were weights of growing pigs, recorded at different stages of their life. Estimates of genetic parameters for weight as a function of age are presented. In *Chapter 3* genetic parameters for daily feed intake patterns of ad libitum fed growing gilts are presented. Various orders of fit were considered to describe daily feed intake as function of days on test, and are compared based on Schwarz's Bayesian Information Criterion (Schwarz, 1978). Six different daily feed intake traits were defined to study genetic differences in daily feed intake patterns. In *Chapter 4* routinely recorded live weight and daily feed intake on a large number of animals in a commercial environment is analyzed. With this data it is possible to study patterns in growth and feed intake and to study how these traits interact during the test period. The aim is to estimate genetic parameters for live weight, daily feed intake, and daily gain over an age trajectory and genetic parameters that describe the interactions between these traits. In *Chapter 5* the objective is to investigate the possibilities to change (part of) the growth curve of pigs through selection. Simulation is used to determine the impact of genetic correlation structure, recording strategy, and missing records on achieved changes in growth curve and the accuracy of breeding value estimation. In *Chapter 6*, daily gain and daily feed intake are modeled as function of weight. Data are the same data as is used in Chapter 4. Objective of this study is to describe daily gain and feed intake as a function of weight using random regression models, to derive feed efficiency at different weights from daily gain and daily feed intake. The second objective was to estimate genetic parameters for daily gain, daily feed intake and feed efficiency at different ranges of live weight. In *Chapter 7* the use of random regression models in pig breeding is discussed. Examples of the benefits of random regression models are given, and shortcomings of random regression models are discussed. Suggestions for further research are put forward, the possibilities to breed a more balanced pig using random regression technology are underlined.

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Chapter 2

Genetic parameters for various random regression models to describe the weight data of pigs

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Abstract

Different random regression models have been advocated for the fitting of covariance structures. It was suggested that a spline model would fit better to weight data than a random regression model that utilizes orthogonal polynomials. Objective of this study was to investigate which kind of random regression model fits best to weight data of pigs. Two random regression models that described weight of individual pigs, one using orthogonal polynomials, and the other using splines, were compared. A comparison with a multivariate model, Akaike's Information Criterion (**AIC**), and the Bayesion-Schwarz Information Criterion (**BIC**) were used to select the best model. Genetic, permanent environmental and total variances increased with age. Heritabilities for the multivariate model ranged from 0.14-0.19, for both random regression models heritabilities were fluctuating around 0.17. Both genetic and phenotypic correlations decreased when the interval between measurements increased. The spline model needed fewer parameters than the multivariate and polynomial models. Akaike's Information Criterion was least for the spline model and greatest for the multivariate model. Bayesian-Schwarz Information Criterion was least for the polynomial model and greatest for the multivariate model. Residuals of all models were normally distributed. Based on these results, it is concluded that random regression models provide the best fit to pig weight data.

Key Words: Body Weight, Genetic Parameters, Models, Pigs, Regression

Introduction

Many phenotypes, such as body composition, body weight, and feed intake, of an individual pig change with age. There is evidence that changes in performance of animals with age are influenced by genetic factors (e.g. Mrode and Kennedy, 1993; Atchley, 1998; Atchley et al., 1997). From an animal breeding point of view, interest lies in genetic parameters that describe the change of such traits in time. These genetic parameters reflect to what extent and how genetic changes in performance patterns over time can be achieved by selection.

Kirkpatrick et al. (1990) showed that phenotypic changes with age could be represented as a function of time. Traditionally traits that are measured in time are analyzed with a multitrait model, defining the phenotypic values at distinct ages as different traits. One advantage of random regression models over multivariate models is that for random regression models it is possible to calculate (co)-variances between or at every age or time-point. Compared to a multivariate model, a random regression model estimates variances and covariances smoother and with less bias (Kirkpatrick et al., 1990). In comparison a random regression model needs fewer parameters to describe the same data as a multivariate model. Random regression models provide a method for analyzing independent components of variation that reveal specific patterns of change over time. Two curve-fitting methods use patterned covariance matrices in the analysis of longitudinal data, i.e. random regressions and spline fitting. The advantage of spline functions is that those functions do not exhibit the end-effects of a polynomial, which tends to bend more sharply at the extremities (Verbyla et al., 1999). Information on pig growth using these methods is very limited. Objective is to investigate which kind of random regression model best fits to weight data of pigs.

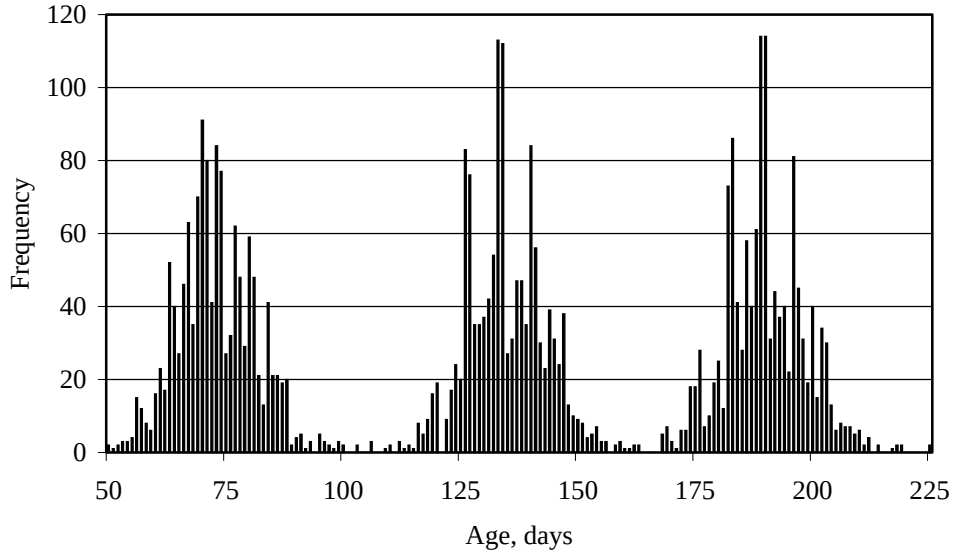

Figure 1. Distribution of weight recordings over the ages in the data set.

Material and Methods

General

Originally the data set contained measurements on 3445 animals, all boars. Selecting the boars which had at least 25 paternal half sibs resulted in a data set that contained 1315 animals, which were weighed three times. The first weight was taken at the beginning of the test period, when pigs were approximately 25 kg, and 9 wk old. The second weight was taken after 8 wk in the test period when the pigs weighed approximately 75 kg. The last weight coincides with the end of the test period, 8 wk later, when the pigs weighed approximately 130 kg. Distribution of weight recordings over age (in days) is shown in Figure 1. The boars were from two different lines, a sow-line and a boar-line. For all animals, sire and dam were known. Data were collected from March 1995 until December 1998. Pigs were group-housed and had ad libitum access to feed. On average each sire had 33 offspring, resulting in about 100 records per sire.

Statistics

All models were fit as a sire-model using ASREML (Gilmour et al., 2000). General model was:

$$y_{ijk} = Fixed + Sire_{ik} + PE_{jk} + e_{ijk} \quad [1]$$

where y_{ijk} represents the weight of offspring j of sire i at age k, *Fixed* is representing the fixed effects described under the heading *Fixed Effects*, $Sire_{ik}$ represents the effect of sire i at age k, PE_{jk} represents the effect of individual animal j at age k, and e_{ijk} is the random residual term which is modeled as a constant over time. The sire component describes ¼ of the genetic variance, and is the genetic component of the model. Three possible ways to model the sire component were considered: 1) in a multivariate model with each measurement treated as a separate trait, resulting in three traits; 2) in a random regression model, where the sire component was fitted as a function of age using a polynomial; and 3) in a random regression model, where the sire component was fitted as a function of age using a spline. The PE-component is the same for all models and accounts for repeated observations on the same individual; this component includes ¾ of the genetic variance. Fixed effects are the same for all models.

Fixed Effects

Fixed effects were the same for all models. Fixed effects were fitted as a function of age. Fixed effects were (between brackets are the number of classes). A second order polynomial on age for the line (2) effect; a first order polynomial on age for the measurement (3) effect; a first order polynomial on age for the date (129) of measurement effect; and a spline-term with 50 knots, which were evenly spaced over the age range, as average curve.

Individual Animal Effect

Individual animal effect was modeled similarly for all models, to account for covariances between repeated records on the same animal. Individual animal effect was fit using a second order polynomial, because there are three measurements for each individual animal. Polynomials of choice were Legendre polynomials, Legendre polynomials are defined for the range of -1 to +1. For the j-th age (a_j) standardized to this range, a_j^*, the r-th polynomial is given as (e.g., Spiegel, 1968)

$$\Phi\left(a_j^*\right)_r = \frac{1}{2^r}\sqrt{\frac{2r+1}{2}}\sum_{m=0}^{r/2}(-1)^m\binom{r}{m}\binom{2r-2m}{r}\left(a_j^*\right)^{r-2m} \quad [2]$$

where *m* is an index number needed to determine the *r*-th polynomial. This gives individual animal effect as:

$$PE_{jk} = \sum_{r=0}^{2}\beta_{jr}\Phi\left(a_j^*\right) \quad [3]$$

where PE_{jk} is the individual animal *j* at age *k*, a_j^* is the standardized age on which the polynomials are modeled (see [2]) and β_{jr} is the set of random regression coefficients for individual animal *j*. Variance-covariance matrix for individual animal effect was calculated as $\mathbf{P} = \mathbf{\Phi}'\mathbf{B}_{PE}\mathbf{\Phi}$, where $\mathbf{B}_{PE}$ is the estimated variance-covariance matrix of the polynomial effects and $\mathbf{\Phi}$ is a matrix containing the polynomial coefficients for the ages of interest (e.g. 70d, 100d, 130d, 160d, and 190d). These ages were chosen because 70d roughly coincides with average age at first measurement, 130d roughly coincides with average age at second measurement, 190d roughly coincides with average age at third measurement, 100d and 160d are in the middle of two measurements. Thus these ages approximately cover the age trajectory.

Sire Effect

Multivariate Model For the multivariate model, each measurement was treated as a different trait. Resulting in three traits. Then the multivariate model for the k-th measurement y_{ijk} recorded on individual animal j, which is offspring of sire i is

$$y_{ijk} = Fixed + A_{ik} + PE_{jk} + e_{ijk} \quad [4]$$

with Fixed representing the fixed effects concerning y_{ijk}, as described above. The A_{ik} stands for the random effect of sire *i* for measurement *k*, PE_{jk} stands for the random effect of the individual animal *j* at age *k*, and is modeled using a second order polynomial function of age (see [3]), and e_{ijk} is the random residual term, which is constant over time and traits.

Polynomial Model Records from all ages were analyzed simultaneously by fitting a random regression model with age at weighing as co-variable. A set of functions on age for each sire was fitted as random effect. A random regression model was fitted on orthogonal polynomials of age. A fourth order polynomial was fitted for each sire. We choose a fourth order polynomial because then variance components of the polynomial still were significantly different from zero. Polynomials of choice were Legendre polynomials, see

[2]. This gives a model for weight y_{ijk} recorded for sire *i* and individual animal *j* at age *k*, a^*_{ijk} on the standardized age scale, as

$$y_{ijk} = Fixed + \sum_{r=0}^{l-1} \beta_{ir} \Phi\left(a^*_{ijk}\right)_r + PE_{jk} + e_{ijk} \qquad [5]$$

with *Fixed* representing the fixed effects pertaining to y_{ijk}, as described above. The β_{ir} denoting the set of *l* random regression coefficients for sire *i*, and PE_{jk} denoting the effect of individual animal *j* at age *k* modeled as a second order polynomial function of age (see [3]), e_{ijk} is denoting the random residual term. Sire variance-covariance matrix for ages of interest was calculated as

$\mathbf{G}_{polynomial} = \Phi' \mathbf{B} \Phi$ where $\mathbf{G}_{polynomial}$ is the sire variance-covariance matrix for ages of interest, Φ a matrix containing the random effects of the polynomial for the ages of interest (70, 100, 130, 160, and 190d) and, **B** the estimated variance-covariance matrix of the polynomial coefficients. Genetic variance-covariance matrix was equal to 4 times the sire variance-covariance matrix, $\mathbf{G}_{polynomial}$.

Spline Model A cubic spline is a smooth curve over an interval formed by linked segments of cubic polynomials at certain knot-points, such that the whole curve and its first and second differentials are continuous over the interval (Green and Silverman, 1994).

The ASREML package of Gilmour et al. (2000) fits splines as described by Verbyla et al. (1999). Natural cubic splines can be incorporated into the standard mixed model (White et al, 1999, Verbyla et al., 1999). For a complete overview see Verbyla et al. (1999). This gives a model for weight y_{ijk} recorded for sire *i* and individual animal *j* at age t_{ijk}

$$y_{ijk} = Fixed + b_{i0} + b_{i1} t_{ijk} + \sum_{l=2}^{q-1} b_{il} z_l\left(t_{ijk}\right) + PE_{jk} + e_{ijk} \qquad [6]$$

with *Fixed* representing the fixed effects –as described above- pertaining to y_{ijk}, b_{i0} denoting the intercept for sire *i*, b_{i1} denoting the slope for sire *i* and b_{il} the random regression coefficient for sire *i* at knot *l*. The t_{ijk} denote the age of measurement, $z_l(t_{ijk})$ represents the spline coefficient for age t_{ijk}. And PE_{jk} denotes effect of individual animal *j* at age *k*, modeled as a third order polynomial function of age (see [3]). Finally, e_{ijk} is the random residual term.

Sire variance-covariance matrix for ages of interest was calculated as $\mathbf{G}_{spline} = \beta' \mathbf{Z} \beta$ where $\mathbf{G}_{spline}$ is the sire variance-covariance matrix for ages of interest,

β a matrix containing the random effects of the spline for the ages 70, 100, 130, 160, and 190d, and **Z** the estimated variance-covariance matrix of the spline coefficients. Genetic variance-covariance matrix was equal to 4 times the sire variance-covariance matrix, $\mathbf{G}_{spline}$.

Model Comparison

Selection of models was based on Akaike's Information Criterion (Akaike, 1973). Akaike (1973) proposed a simple and useful criterion called Akaike's Information Criterion (**AIC**) for selecting the best-fit model among alternative models.

AIC = -2 log (maximum likelihood) + 2 (number of model parameters) [7]

Differences between AIC values are important, not the absolute size of AIC values. The model with the lowest AIC is considered as the best one. Various experiences verify the applicability of AIC in model selection (Wada and Kashiwagi, 1990; Burnham and Anderson, 1998).

Another widely used Information Criterion, is the Bayesian-Schwarz Information Criterion (**BIC**) which takes into account model uncertainty as well. Bayesian-Schwarz Information Criterion is stricter than AIC. The BIC is defined as:

BIC = -2 log (maximum likelihood) – log (n)*(number of model parameters) [8]

where n is equal to the number of records used in the analysis (Burnham and Anderson, 1998).

Results

Distribution of the weight recordings over age is shown in Figure 1. From Figure 1 it is clear that measurements are from three discrete periods of growth. Description of the data is in Table 1. The SD for age was about the same for all three weightings, around 8.7d. Average live weight increased from 26.2 kg at the first weighing to 130.4 kg at the last weighing. Average age at first weighing was 72.9d and average age at the last weighing was 190.0d. Standard deviation for live weight increased from the first weighing to the last weighing. Number of weight records (n=1315) is the same for all three measurements. Live weight ranged from 14.0 kg at the first weighing to a maximum of 172.2 kg at the last weighing. Age at weighing is ranged from 49d at the first weighing to a maximum of 233d at the last weighing. There was some overlapping of ages for the different measurements.

Table 1. Description of the data

Measurement [c]		Average	SD	Minimum	Maximum
1	age [a]	72.9	8.54	49	117
2	age	134.7	8.87	99	177
3	age	190.0	8.73	162	233
1	weight [b]	26.3	3.60	14.0	40.0
2	weight	76.3	8.37	50.4	103.6
3	weight	130.5	13.53	75.0	172.2

[a] in days.

[b] in kilograms.

[c] n = 1315 for all weighings.

Table 2. Estimated multivariate variance components for live weight

Measurement	Variance components			
	Genetic	Permanent environment	Error	Total
1	1.405	3.982	4.686	10.072
2	8.189	34.467	4.686	47.342
3	24.300	99.282	4.686	128.268

Table 3. Heritabilities, genetic and phenotypic correlations [a] for live weight estimated with the multivariate model. In brackets the SE for the estimates

Measurement	1	2	3
1	0.14 (0.066)	0.53 (0.055)	0.48 (0.073)
2	0.61 (0.018)	0.17 (0.072)	0.99 (0.006)
3	0.23 (0.009)	0.56 (0.019)	0.19 (0.077)

[a] Heritabilities on the diagonal, genetic correlations above the diagonal, phenotypic correlations below the diagonal.

Table 4. Variance components for live weight estimated with the polynomial model

Age	Variance components			
	Genetic	Permanent environment	Error	Total
70	1.408	2.213	4.609	8.230
100	4.916	19.452	4.609	28.977
130	6.204	37.238	4.609	48.052
160	13.616	50.757	4.609	68.983
190	22.544	101.646	4.609	128.799

Table 5. Heritabilities, genetic and phenotypic correlations a for live weight estimated with the polynomial model

Age, days	70	100	130	160	190
70	0.17	0.963	0.736	0.378	0.407
100	0.559	0.17	0.777	0.395	0.408
130	0.554	0.836	0.13	0.882	0.865
160	0.467	0.669	0.832	0.20	0.983
190	0.287	0.347	0.569	0.839	0.18

[a] Heritabilities on the diagonal, genetic correlations above the diagonal, phenotypic correlations below the diagonal.

Table 6. Variance components for live weight estimated with the spline model

Age, days	Variance components			
	Genetic	Permanent environment	Error	Total
70	1.532	2.107	4.676	8.315
100	3.736	18.421	4.676	26.833
130	7.944	32.124	4.676	44.744
160	13.296	48.364	4.676	66.335
190	19.812	109.082	4.676	133.569

Multivariate Model

Variance components estimated with the multivariate model are shown in Table 2. Both the genetic and the permanent environmental variance components increased over time. Heritabilities, genetic correlations and phenotypic correlations are shown in Table 3. Heritability is increasing over time. It was least (0.14) at the first weighing, and greatest (0.19) at the third weighing. Genetic correlation was greatest (0.99) between the second and third weights. Genetic correlation was least (0.48) between the first and third weights. Phenotypic correlations ranged from 0.23 between the first and third weights to 0.61 between the first and second weights.

Polynomial Model

Variance components for the polynomial model are calculated at the ages: 70d; 100d; 130d; 160d and 190d of age and are shown in Table 4. The estimated genetic, permanent environmental and total variance components are increasing over time. It can be seen that total variance and permanent environmental variance decrease slightly at an early age and then increase.

Estimated heritabilities for the whole period are in Figure 2. One can see that heritability is highest at the beginning, subsequently dropping, then increasing again, and after that fluctuate around a value of 0.17. In Table 5 are the heritabilities and correlations for the ages: 70d, 100d, 130d, 160d, and 190d. For the ages in Table 5 heritability was least (0.13) at 130d of age and greatest (0.20) at 160d of age. Genetic correlations between adjacent ages were high and decreased slightly as the interval between ages increased. Phenotypic correlations between adjacent ages are somewhat lower than the genetic correlations. Phenotypic correlations also declined more markedly as the interval between ages increased.

Spline Model

Variance components for the spline model calculated at 70d, 100d, 130d, 160d, 190d of age are shown in Table 6. The estimated genetic, permanent environmental and total variance components increased over time. Genetic variance increased over the whole period.

Estimated heritabilities for the entire period are in Figure 2. The heritability is greatest at the beginning, subsequently dropping, then slightly increasing again, and after that decreasing again. Heritability fluctuated around 0.17 and has a tendency to decrease, as pigs grow older. In Table 7 are the heritabilities and correlations between weight at 70d,

Table 7. Heritabilities, genetic and phenotypic correlations [a] for live weight estimated with the spline model

Age, days	70	100	130	160	190
70	0.18	0.711	0.529	0.451	0.436
100	0.537	0.14	0.956	0.877	0.807
130	0.539	0.828	0.18	0.973	0.916
160	0.460	0.657	0.820	0.20	0.978
190	0.280	0.323	0.552	0.839	0.15

[a] Heritabilities on diagonal, genetic correlations above diagonal, phenotypic correlations below diagonal.

Table 8. Loglikelihood, Akaike's Information Criterion (AIC), and Bayesian-Schwarz Information Criterion for each model

Model	Loglikelihood	AIC [a]	BIC [b]	model parameters
multivariate	-7,649.82	33.58	48.10	336
polynomial	-7,632.96	7.86	0	340
spline	-7,635.03	0	25.72	334

[a] Akaike's Information Criterion, see [7].

[b] Bayesion-Schwarz Information Criterion, see [8].

100d, 130d, 160d, 190d of age. For the ages in Table 7 heritability was least (0.14) at 100d of age and greatest (0.20) at 160d of age. Genetic correlations between adjacent ages were high and slightly decreased, as the interval between ages becomes greater. Genetic correlations between adjacent ages at a later stage of the test period were greater than genetic correlations at the early stage of the test period. Phenotypic correlations between adjacent ages were greatest and decreased when ages became further apart. Phenotypic correlations between adjacent ages were somewhat lower than the genetic correlations between adjacent ages. Phenotypic correlations declined more rapidly as the interval between ages became greater.

Model Comparison

Loglikelihoods, AIC, and BIC for the three models are shown in Table 8. Loglikelihood was least for the polynomial model and greatest for the multivariate model.

The number of estimated parameters was least for the spline model and greatest for the polynomial model. Akaike's Information Criterion was least for the spline model and greatest for the multivariate model. Bayesian-Schwarz Information Criterion was least for the polynomial model and greatest for the multivariate model.

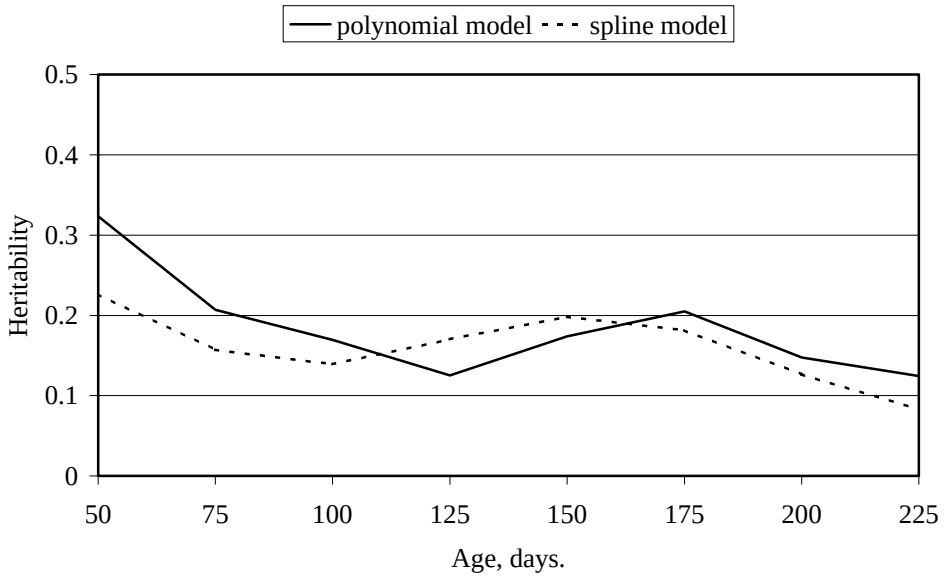

Figure 2. Estimated heritabilities for the polynomial model and the spline model for the ages in the data set.

Discussion

Sevón-Aimonen et al. (1997) used third degree polynomials to estimate genetic parameters for growth traits in pigs, their heritability estimates ranged within 0.14 through 0.21. Which is comparable to the heritability estimates in this study. Meyer (2000) modeled weight of Australian beef cattle with random regression models, and concluded that random regression models were well suited to the analysis of growth data.

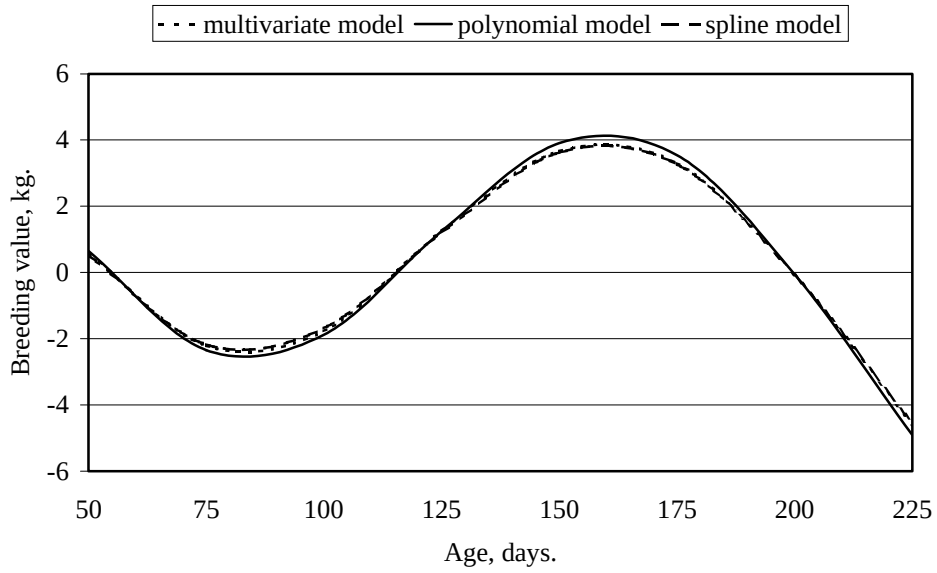

Figure 3. Estimated effect of the fixed spline term for the multivariate model, the polynomial, and the spline model.

When comparing the results obtained with the polynomial and multivariate models, the variance components estimated with both models are similar. Heritabilities estimated from the polynomial model show a somewhat different pattern than corresponding estimates from the multivariate model. It seems, when comparing Figures 1 and 4, heritabilities estimated with the polynomial model are somewhat greater when there is less information. The genetic correlations estimated with the polynomial model are comparable with the genetic correlations estimated with the multivariate model. The same holds for the phenotypic correlations, although it seems that phenotypic correlations estimated with the polynomial model at a later age are higher than the phenotypic correlations estimated with the multivariate model.

When comparing the results obtained with the spline model and the results obtained with the multivariate model, the variance components estimated with both models are in agreement with each other. Heritabilities estimated with the spline model were somewhat higher than the heritabilities estimated with the multivariate model. The genetic correlations estimated with the spline model were similar with the genetic correlations estimated with the multivariate model. The same holds for the phenotypic correlations.

When comparing both random regression models, it can be seen that the spline model requires fewer parameters than the polynomial model. The total variance estimated with the polynomial model is increasing more rapidly then the total variance estimated with the spline model (Table 4 and 6). Variance components at 70d, 100d, 130d, 160d, 190d of age similar for both random regression models (Tables 4 and 6). The phenotypic correlations are likewise similar for the polynomial and the spline model, which probably results from the permanent environment effect being modeled the same in both models. Genetic correlations are somewhat greater in the spline model compared to the polynomial model. In general, correlations estimated with the polynomial model and the spline model show the same pattern and are similar. In both random regression models, genetic and phenotypic correlations are decreased when the interval between ages increased.

In Figure 3 is the estimated fixed spline term for all three models. This spline term is about the same for all three models. In Figure 3 the effect of measurements done at a certain weight instead of at a certain age can be seen. First we see the effect of the pig that reaches 25 kg at an early age and then the pigs that reached 25 kg at a later stage in their life. Subsequently we see the effect of the pigs that reached 75 kg at an early age and then the pigs that reached 75 kg at a later age. The same occurs at the third measurement.

The two model selection criteria applied, AIC and BIC, are not in agreement on which model is best. But they both show that a random regression model performs better than a multivariate model on this data.

Forcing the error term to be constant over time and traits for all models is not correct, because variances are increasing from beginning to end of the test. By doing so, the variance heterogeneity is forced into the PE term. This PE term takes into account repeated records on the same individual. A better way of modeling the error term would be to model a separate error term for each day, independent of error terms at other days.

Implications

Variance of live weight is increasing during lifetime of a pig; the total variance at the end of the test-period is about 20 times higher as the variance at the beginning of the test-period. Both random regression models fit better to the data than the multivariate model. Residuals of all models had a normal distribution. Random regression models gave better

estimates, and take into account that measurements are not all done at the same age. Even with the data we had, 3 measurements per individual animal, the random regression models did a better job than the traditional multivariate model.

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Chapter 3

Genetic parameters for daily feed intake patterns of growing Dutch Landrace gilts

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Abstract

Daily feed intake (DFI) was described as a function of days on test using a spline random regression model. Order of fit for the spline random regression model was varied, models were compared using Schwarz's Bayesian Information Criterion. The objective was to investigate whether there are genetic differences in DFI patterns. Data were DFI records of growing gilts, which had ad libitum access to food. Gilts were 94 days old at start of test. All gilts were from a Dutch Landrace line. Number of random regression coefficients were varied from zero to nine for both random effects, the model with four random regression coefficients resulted in the most optimal fit. Six traits were derived to capture differences in DFI patterns. Heritability for DFI decreased from 0.53 at five days on test to 0.24 at 95 days on test. Genetic correlations between DFI at five days on test and 95 days on test, and between DFI at 50 days on test and 95 days on test were low (around 0.3). The results clearly demonstrated that DFI at different days on test cannot be regarded as repeated measurements of a single trait with constant variance and heritability. Based on the results presented it can be concluded that changes in feed intake patterns through selection are possible.

Keywords: regression, models, pigs, feed intake, patterns.

Introduction

The phenotype of individual animals changes during growth and aging. These changes occur in a broad range of traits such as body composition, body weight and feed intake. For an animal breeder genetic parameters that describe changes in an animal during growth and aging are of interest. These genetic parameters give information about the possibility to genetically change performance patterns. Normally traits that are measured over time are analyzed using a multiple trait model, with phenotypic values at several specific ages as different traits. Kirkpatrick et al. (1990) modeled phenotypic changes as a function of time, using the fact that measurements are ordered in time, which gave better estimates of covariances between different ages. Estimates of covariances between trait-values at two ages are improved by using information about covariances at other ages. The infinite-dimensional model introduced by Kirkpatrick et al. (1990) provided more accurate estimates of variation in traits. The infinite-dimensional model fits a continuous covariance function to an existing covariance matrix. Sevón-Aimonen et al. (1997) estimated genetic parameters for growth traits in pigs, using a random regression model. Huisman et al. (2002) applied random regression models to estimate genetic parameters for live weight in growing pigs.

Eissen et al. (1999) showed that a linear model sufficiently described daily feed intake (DFI) to get an accurate estimate for the level of DFI from 28 kilograms to 108 kilograms of body weight. Several studies used random regression models to describe DFI of growing pigs (Schnyder, 2001; Hall et al,. 1999;Von Felde et al, 1996). Questions that could be answered using random regression techniques: Are there differences in daily feed intake patterns between pigs? And, is it possible to change these patterns through selection?

DFI is expected to increase from the start of the growing period, following a diminishing returns pattern (Kanis and Koops, 1990) and reaches a plateau before mature weight. Introduction of electronic feeders allowed for accurate measures of individual feed intake in a group housing system. This made it possible to study DFI patterns of individual pigs in a commercial environment.

Objective is to describe DFI as a function of days on test, using a spline random regression model. Order of fit for the spline random regression model will be varied to

determine the best model. Increasing the number of random coefficients (that is knotpoints) will result in a better model to fit the data.

Material and Methods

Data

Data were recorded on an experimental farm of the Institute for Pig Genetics (IPG), The Netherlands, from September 1996 until December 1999. Performance records of 257 gilts were used. IVOG® (Insentec, Marknesse, The Netherlands) feeding stations were used to measure feed intake for each animal. Cumulative DFI records were obtained using the methods of Eissen et al. (1998). After methods of Eissen et al. (1998) were applied, all records with less than 1 kg of DFI or more than 3 kg of DFI were discarded from the analysis; also excluded from the analysis were DFI records recorded after day 100 on test. This resulted in approximately 56 DFI records per gilt. Pigs had ad libitum access to feed and were group housed, 10 gilts per pen. All animals were from a pure Dutch Landrace line, and started test at an average age of 94 d. At least parents and grandparents were known for each animal. In total the pedigree-file consisted of 389 animals. The first date that a gilt appeared in the data set was considered to be her first day on test.

Random Regression Model

A cubic spline is a smooth curve over an interval formed by linked segments of cubic polynomials at certain knotpoints (Green and Silverman, 1994). Verbyla et al. (1997) showed that spline functions can be incorporated in the standard mixed model. A random regression model using spline functions for the random part was used to model DFI as a function of days on test. The model has two random parts; one for the animal effect; and another that accounts for repeated measurements on the same animal, the so-called "permanent environment". This resulted in the following model:

$$y_{ij} = Fixed + a_{i0} + a_{i1}t_{ij} + \sum_{l=2}^{q-1} a_{il} z_l(t_{ij}) + p_{i0} + p_{i1}t_{ij} + \sum_{l=2}^{q-1} p_{il} z_l(t_{ij}) + e_{ij} \quad [1]$$

with y_{ij} representing daily feed intake of animal i at day on test j, q the number of knotpoints, *Fixed* representing the fixed effects pertained to y_{ij}, a_{i0} representing the intercept

for animal *i*, a_{i1} representing the slope for animal *i* and a_{il} represents the estimate for the spline-coefficient of animal *i* at knotpoint *l*, p_{i0} representing the intercept for permanent environment *i*, p_{i1} representing the slope for permanent environment *i* and p_{il} represents the estimate for the spline of permanent environment *i* at knot *l*, $z_l(t_{ij})$ are the random spline coefficients for age t_{ij}, t_{ij} is the age at which daily feed intake is measured, and e_{ij} representing the error term for y_{ij}. Data were divided in 14 periods of approximately 7 days, and a separate error term was estimated for each period, $e_{ij} \sim N(0, \mathbf{I}\times\sigma^2_e)$, where **I** is an identity matrix of size 14×14.

Fixed effects were a spline term on days on test with 100 knotpoints; an effect of pen (12 classes); and the interaction between month and year of recording (16 classes) and a class-effect of age at recording (169 classes). In matrix notation

$$\mathbf{Y} = \mathbf{X\beta} + \mathbf{Z_s a} + \mathbf{Z_s p} + \mathbf{e} \quad [2]$$

where **Y** was a vector containing the observations, **β** was the vector containing the fixed effects, **X** was an incidence matrix which indicates for each observation the fixed effects by which it was influenced. $\mathbf{Z_s}$ was an incidence matrix containing the spline coefficients for each observation in blocks of animals, **a** was a matrix containing the estimates for genetic spline effects and **p** was a matrix containing the estimates for permanent environment spline effects; **e** was a vector with error terms. The estimated breeding values over days on test for animals:

$$\mathbf{EBV_{i,t}} = \mathbf{Z_{s,all} \cdot a_i} \quad [3]$$

where $\mathbf{EBV_{i,t}}$ was the vector containing estimated breeding values for every day on test *t* for animal *i*, $\mathbf{a_i}$ was a vector containing the estimated spline effects for animal *i*, $\mathbf{Z_{s,all}}$ was a matrix containing spline coefficients for all days on test. The genetic variance-covariance matrix of all days on test equaled $\sigma^2_a = \mathbf{Z_{s,all} \cdot \Sigma_a \cdot Z_{s,all}'}$, permanent environmental variance-covariance matrix of all days on test equaled $\sigma^2_p = \mathbf{Z_{s,all} \cdot \Sigma_p \cdot Z_{s,all}'}$. Where $\mathbf{\Sigma_a}$ and $\mathbf{\Sigma_p}$ were the estimated variance-covariance matrices of the spline effects for the genetic and the permanent environment. Variances at day on test *t* was $\sigma^2_{a,t} = \mathbf{Z_{s,t} \cdot \Sigma_a \cdot Z_{s,t}'}$, genetic covariance between days on test *t* and *t+1* was equal to $\sigma_{at,at+1} = \mathbf{Z_{s,t} \cdot \Sigma_a \cdot Z_{s,t+1}'}$. Permanent environmental variance can be calculated in the same way, replacing $\mathbf{\Sigma_a}$ with $\mathbf{\Sigma_p}$. The error variance in each period followed a normal distribution, $e_{ij} \sim N(0,\sigma^2_e)$. Covariances between error in different periods were considered to be zero. For all models knotpoints were evenly spread over the test period. All models were fitted using ASREML (Gilmour et al., 2000).

Comparison of models

The number of knotpoints was varied for both random effects – keeping the fixed effects the same for all models – to investigate which model fitted best to the data. The number of knotpoints was varied from 0 to 9; all combinations of both random effects resulted in 100 random regression models. The model with 0 knotpoints is the model with only fixed effects. Deciding which model described the data best based on Loglikelihood ignores differences in the number of parameters that has to be estimated. Several information criterions have been proposed that do take the number of estimated parameters into account. The Bayesian information criterion takes the number of estimated parameters and the size of the data set into account, and is somewhat more stringent than Akaike's information criterion (Akaike, 1973). The Bayesian information criterion (**BIC**) is defined as (Schwarz, 1978):

$$BIC = -2 \times Loglikelihood - number\ of\ model\ parameters \times log\ (n^*) \quad [4]$$

Where $n^* = n - p$, n was the number of observations in the data set and p was the number of fixed effects. When Δ is the absolute difference between the value for **BIC** for two models, then if $\Delta \leq 2$ then there is substantial support for no difference between the two models. If $\Delta \leq 4$ and $\Delta \leq 7$ then there is considerably less support for no difference between the two models and if $\Delta > 10$ then there is essentially no support for no difference between the two models (Burnham and Anderson, 1998).

Derived traits

Six derived traits were defined in an attempt to capture the differences in feed intake patterns. DFI_average is the average of DFI at days 1 to 100 on test; DFI_variance is the variance in DFI at days 1 to 100 on test. DFI05 is DFI at day 5 on test, DFI50 is DFI at day 50 on test and DFI95 is the DFI at day 95 on test. Further, DFI95_05 is DFI at day 95 minus DFI at day 5 on test. These traits were chosen because the whole range in test days was represented, as well as the variation in DFI and possible differences in DFI between beginning and end of test.

Table 1. Average daily feed intake, standard deviation of daily feed intake and included days on test for the 14 periods.

Period	days on test	Average DFI	standard deviation
1	1-8	1.51	0.32
2	9-15	1.60	0.33
3	16-22	1.67	0.38
4	23-29	1.77	0.39
5	30-36	1.81	0.42
6	37-43	1.92	0.42
7	44-50	2.00	0.43
8	51-57	2.08	0.43
9	58-64	2.13	0.44
10	65-71	2.21	0.44
11	72-78	2.21	0.43
12	79-85	2.23	0.46
13	86-92	2.21	0.45
14	93-100	2.20	0.45

Results

Averages

Average DFI was about 1.5 kg in the first week on test and reached a plateau at week 10 on test (Table 1); average DFI at the plateau was about 2.2 kg. The SE of average DFI started at a value of 0.32 kg and reached a plateau after week 5 at a value of approximately 0.43 kg (Table 1).

Model choice

The values of the **BIC** criterion for each model were plotted relative to the maximum value found for **BIC** (Figure 1). It is clear that the biggest improvement in **BIC** was achieved when going from the model with no random effects to the model with one

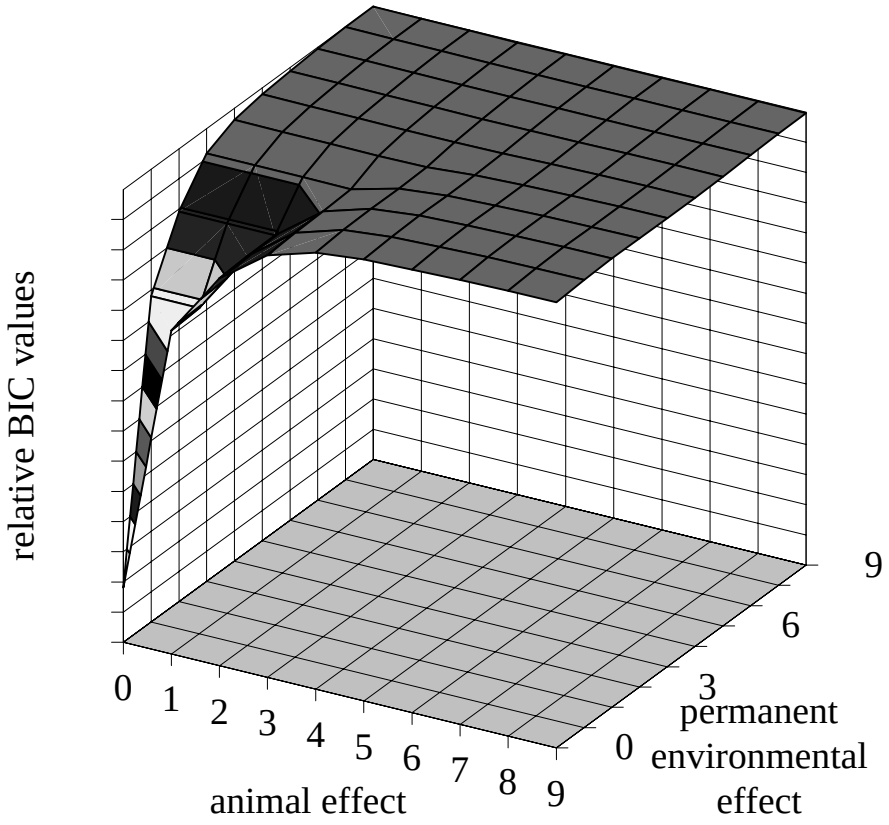

Figure 1. Relative BIC values for the different random regression models.

knotpoint (that is only an estimate of DFI level) for both the animal and the permanent environmental effect. Adding more knotpoints resulted in diminishing returns in the value of the **BIC**. The values for **BIC** start to plateau at the model that included four knotpoints for both random effects. After that, adding extra knotpoints only lead to minor improvements in model fit. The highest value of **BIC** was found for the model with nine knotpoints for the animal and the permanent environmental effect. However this value was only slightly higher than the value found for the model with four knotpoints for both random effects. Because of this all further reported results in this section relate to the model with four knotpoints for both random effects.

Table 2. Heritabilities (on diagonal) and genetic correlations (below diagonal) and between derived traits for the model with four knotpoints for both random effects [A].

	DFI_avg	DFI_var	DFI05	DFI50	DFI95	DFI95_05
DFI_avg	0.22					
DFI_var	-0.19	0.30				
DFI05	0.66	-0.22	0.53			
DFI50	0.89	-0.47	0.37	0.28		
DFI95	0.59	0.67	0.30	0.29	0.24	
DFI95_05	-0.11	0.73	-0.65	-0.10	0.54	0.29

[A] DFI_avg is DFI_average and DFI_var is DFI_variance.

Genetic parameters

The genetic correlations between the derived traits and the heritabilities of the derived traits were given in Table 2. Highest heritability (0.53) was found for DFI05, lowest heritability (0.22) was found for DFI_average. Heritabilities for the other derived traits were all in the region of 0.3. Highest genetic correlation was found between DFI_average and DFI50 (0.89) and lowest genetic correlation was found between DFI95_05 and DFI05 (-0.65). DFI_average had higher genetic correlation with DFI05 and DFI50 than with DFI95. The genetic correlation between DFI05 and DFI50 was slightly higher (0.37) than the genetic correlation between DFI05 and DFI95 (0.30), and DFI50 and DFI95 (0.29). Selection on DFI_average will result in higher DFI at days five, 50 and 95 on test. Only selection on DFI95 will result in higher values for DFI_variance and DFI95_05, while selection on DFI05 will result in lower values for DFI95_05. The genetic correlation between DFI at different days on test was high (0.8-1.0) when days were close together (Figure 2), but decreased to roughly 0.3 when days on test were approximately 40 days apart. This indicates that DFI at different days on test cannot be seen as a repeated measurement of the same trait, with the same variance. Phenotypic correlations between DFI at different days on test was highest at the start of test – up to 50 days on test – and in the last part of test (Figure 2). For the largest part of test phenotypic correlations between different days on test were below 0.4 (Figure 2). This low phenotypic correlation is associated with high estimates for the error variances, and low estimates for the permanent environmental effect. Both arose from high fluctuations in DFI.

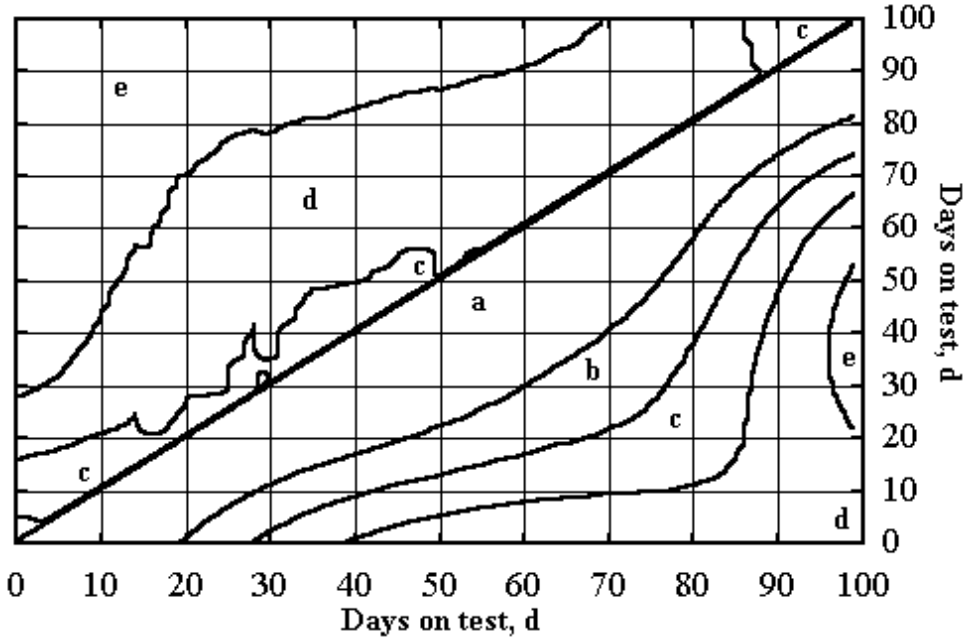

Figure 2. Estimated correlations between DFI at different days on test, genetic correlations below diagonal, phenotypic correlations above diagonal, (a) 0.8-1.0; (b) 0.6-0.8; (c) 0.4-0.6; (d) 0.2-0.4; and (e) 0.0-0.2.

Discussion

DFI was sufficiently described by a model that incorporates four knotpoints for the animal and the permanent environmental effect. Other studies show that a second order of fit, using polynomials on age – comparable to the model with three knotpoints for both effects -, was sufficient to describe weekly averaged DFI (Andersen and Pedersen, 1996; Schnyder, 2001). From Figure 1 it is clear that moving from a model with three knotpoints for both random effects to a model with four knotpoints for both random effects resulted in a substantial increment of **BIC**, indicating a better fit when a random regression model with four knotpoints is applied.

For three of the six derived traits the average estimated breeding values (EBV's) of the 10 highest-ranking animals were plotted in Figure 3. The 10 highest-ranking animals for DFI_average followed a similar pattern as the 10 highest-ranking animals for DFI50. The traits DFI95 and DFI95_05 and the traits DFI05 and DFI_variance showed a similar shape of their EBV pattern. For the three plotted traits dissimilarities between patterns were obvious. The 10 highest-ranking animals for DFI05 had a decreasing EBV for DFI, while the 10 highest-ranking animals for DFI50 had an increasing EBV for DFI from day one to day 30 on test, after day 30 on test EBV's were decreasing again. For DFI95, EBV's for DFI were decreasing until day 30 on test, after day 30 EBV's were increasing again.

Voluntary feed intake is depending on a lot of factors; such as body weight, breed, sex and temperature (Quiniou et al., 2000; Zijlstra and Scott, 2000). It is difficult to say what the most favorable feed intake pattern is, in general it is more desirable to select for animals that are able to eat a lot when growth is linear, because that is when maximum protein is deposited (Schinckel and De Lange, 1996). According to Webb (1998), pigs are too fat because the feed intake capacity is not in balance with the pig's potential to grow. Pigs eat too little prior to reaching 40 kg of live weight and too much after reaching 70 kg of live weight. The consequence of this in-equilibrium between growth and feed intake is a pig that becomes too fat. Results show that this can be changed through selection, selection on DFI05 would result in pigs that eat more at start of test and eat less towards end of test (Figure 3). High (average) DFI has a positive genetic correlation with average daily gain on test, and a negative genetic correlation with lean percentage (Labroue et al., 1997). Several studies (Von Felde et al., 1996; Hall et al., 2000) estimated genetic correlations between average daily gain and feed intake over test and between backfat and feed intake over test. Both show that the genetic correlation between backfat and DFI increased over test, while the genetic correlation between average daily gain and DFI was roughly equal over test. Von Felde et al. (1996) also showed an increasing negative genetic correlation between DFI and carcass lean content, and an increasing positive genetic correlation between DFI and lean growth rate. Considering the increase in genetic correlation between backfat and DFI, selection for higher early feed intake with no change in later feed intake results in more efficient lean growth. Genetic correlations between DFI at different days on test are not equal to one, they were not even close to unity. Which means that the pattern of DFI is under genetic control and not just average DFI. Genetic correlation was below 0.5 when

days on test were 30 days or more apart. Changing feed intake patterns is possible considering the estimated genetic correlations (see Table 2 and Figure 2).

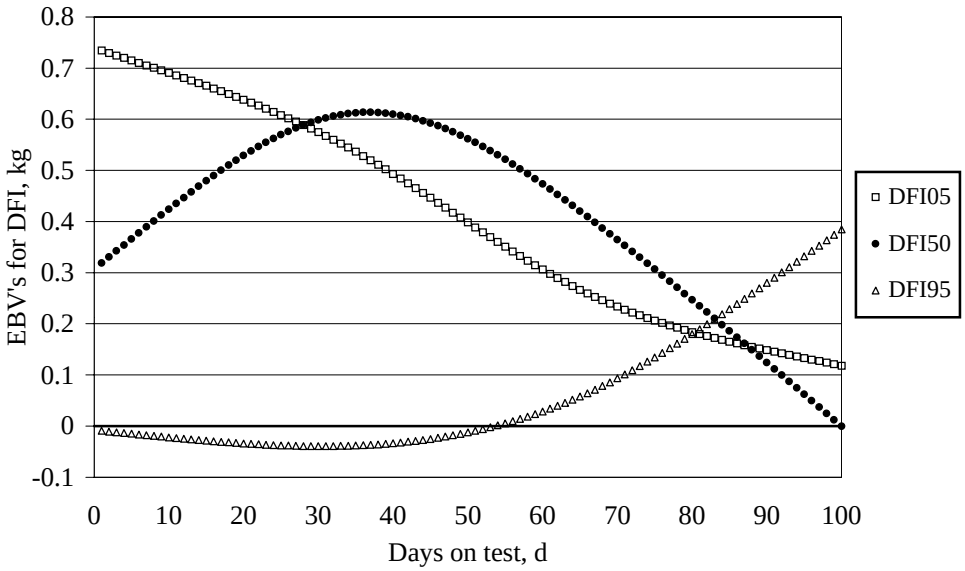

Figure 3. Estimated breeding values for DFI on days on test for the 10 highest-ranking animals for DFI05, DFI50 and DFI95.

Conclusions

Average DFI increases from the start of the growing period, following a diminishing returns pattern (Table 1). The optimum fit to the data is achieved with the model with four knotpoints for the animal and the permanent environment effect. Differences between **BIC** values were small when moving from the model with four knotpoints to models with more than four knotpoints. Variances were increasing over test period. Heritability of DFI decreased over test period. Genetic correlations between DFI at different days on test vary from 0.3, when days were furthest apart, to 1.0 when days were close together (Figure 2). From the results presented here it is clear that DFI cannot be

treated as the same trait throughout test, with constant heritability and variance. Based on these results it is possible to change feed intake patterns through selection.

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Chapter 4

A multivariate random regression model on age for live weight, daily feed intake, and daily gain of growing pigs

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Abstract

The aim of this study was to estimate genetic parameters for live weight, daily feed intake, and daily gain over an age trajectory using a multivariate random regression model. Boars were tested for a 7-week period, with additional week prior to test being an adjustment period to their new environment. Pigs entered the test at an average age of 128 d ± 4 d. On average each boar had approximately 34 valid daily weight records and 50 daily feed intake records. Heritability estimates for live weight, daily feed intake, and daily gain at different ages, and genetic and phenotypic correlations between different ages for live weight, daily feed intake, and daily gain were presented, as well as genetic and phenotypic correlations for all age and trait combinations. Correlations between live weight and daily feed intake at various age combinations were fairly constant, genetic (0.8) and phenotypic (0.15). Genetic correlation between live weight and daily gain at a given age increased over age. Genetic correlations between live weight at a given age and daily gain at different ages was fairly constant. The phenotypic correlation between live weight at a given age and daily gain was higher when the daily gain measurement was before the live weight measurement, and lower when the daily gain measurement was after the live weight measurement. Estimates for the genetic correlation between daily feed intake and daily gain at different ages showed similar values for all age combinations. Phenotypic correlations between daily feed intake and daily gain showed in increase over age. Live weight, daily feed intake, and daily gain cannot be considered to be the same trait over test. Extrapolating estimates yields lower genetic correlations between ages for the same trait, which is indicating that altering curves through selection is a viable option. The estimated genetic correlation of approximately 0.35 between daily gain and daily feed intake indicates that it is possible to increase daily gain through selection without increasing daily feed intake.

KEYWORDS: pigs; covariance; regression; age; feed intake; weight gain; body weight.

Introduction

Major costs in producing pork are associated with feed and time taken to reach a desired slaughter weight (Webb, 1998). Pig breeding programs aim to reduce these costs by selecting the most efficient pig. Selection of breeding pigs can be based on the ratio between feed intake and gain, where these two traits are measured over a fixed weight- or time-interval. Average daily feed intake or average daily gain over that fixed interval are then the traits often considered in breeding programs.

Scale equipped feed stations allow collection of daily feed intake and daily weight data on individual animals. This data will allow animal breeders to consider differences in performance during growth and ageing, these differences are of interest for example when pigs are selected for different markets. Such information is not taken into account in current selection programs. Traditionally measurements of traits at different ages or weights were analyzed as different traits, e.g. birth weight, weaning weight, and slaughter weight in pigs. Interest lies in genetic parameters that describe these differences in growth and feed intake curves between animals.

Genetic parameters that describe the change of traits over time or weight can be estimated using a random regression model (Kirkpatrick et al., 1990; Van der Werf et al., 1998). With a random regression model it is possible to treat different measurements along a trajectory, e.g. an age or a weight trajectory, as an expression of the same characteristic that can be described by a continuous covariance function.

QAF Meat Industries routinely records live weight and daily feed intake on a large number of animals in a commercial environment, yielding an unique data set to study performance patterns in pigs. More precise: growth and feed intake patterns, and the interaction between these two traits. The aim of this study was to describe the course of live weight, daily feed intake and daily over an age trajectory, and to estimate genetic parameters for live weight, daily feed intake and daily at different ages using a multivariate random regression model.

Material and Methods

General

Boars were tested for a 7-week period after pigs had been given an adjustment period of one week prior to test. Pigs entered the test at an average age of 128 d ± 4 d. Based on live weight at start of test, pigs were assigned to a certain feeding level. Meaning that pigs could eat their predicted energy requirements for maintenance plus extra feed for growth (targeted at 80% of ad libitum intake). Pigs were of three different sire lines each with a different genetic background. Data were collected between February 2001 and October 2001 and pigs were tested in 29 weekly batches, which contained approximately 60 animals, evenly distributed over two pens. In each pen there were three electronic feeder stations, one of the electronic feeder stations was equipped with a weight scale. For a detailed description of the feeder stations see McSweeney et al. (2001).

Individual feeding event records on each pig were used to derive daily records. Daily feed intake was determined by summing all individual feed intake records of a pig that appeared on the same calendar day. Daily live weight was determined by averaging the individual weight records of a pig that appeared on the same calendar day. Improper values for daily weight and daily feed intake were excluded from the analysis, this was done based on the deviation of the individual recording from the average trait value on that test day. After excluding pigs without pedigree information, the data set contained records on 1589 boars. In total there were 53756 daily weight records and 80311 daily feed intake records (Table 1). On average each boar had approximately 34 valid weight records and 50 valid daily feed intake records for the full eight-week recording period that all animals completed.

Pedigree of animals was traced back for two generations, resulting in a pedigree file of 3307 animals, including the animals with records. The animals without records consisted of 246 sires and 1242 dams. Pigs in the data set originated from 822 litters and 106 sires.

Random regression model

In the random regression analysis for live weight and feed intake, random effects were modeled as function of age using spline functions. The program ASREML (Gilmour et

Table 1. Number of live weight and daily feed intake records per week on test.

Week on test	Average age (d)	Number of weight records	Average weight (kg)	SD weight (kg)	Number of feed intake records	Average feed intake (kg/d)	SD feed intake (kg/d)
0	124	6793	70.3	8.6	8734	1.59	0.66
1	131	6910	76.3	9.1	10231	1.94	0.46
2	138	6760	82.1	9.2	10502	2.03	0.45
3	145	6665	87.3	9.3	10473	2.08	0.49
4	152	7120	92.9	10.0	10497	2.17	0.49
5	159	7004	98.0	10.2	10405	2.21	0.52
6	166	6766	103.4	10.4	10387	2.25	0.56
7	173	5738	108.2	10.6	9082	2.31	0.59

al., 2001) fits splines as described by Verbyla et al. (1999). This resulted in the following model:

$$y_{ijk} = Fixed + u_{i0} + u_{i1}t_{ij} + \sum_{l=2}^{q-1} u_{il} z_l(t_{ij}) + p_{i0} + p_{i1}t_{ij} + \sum_{l=2}^{q-1} p_{il} z_l(t_{ij}) + e_{ik}$$

where y_{ijk} was the trait – live weight or daily feed intake - recorded on animal i at age j within week k, *Fixed* represented the fixed effects for each trait as described in the next section, u_{i0} represented the intercept for animal i, u_{i1} represented the slope for animal i, u_{il} represented the random regression coefficient for animal i at knot l. The p_{i0} represented the intercept for permanent environment i, p_{i1} represented the slope for permanent environment i, p_{il} represented the random regression coefficient for permanent environment i at knot l. Permanent environment i reflects the non-genetic effect of animal i. The $z_l(t_{ij})$ represented the spline coefficients for knot l at animal i and age j, q was an index number for the knotpoints. Finally, e_{ik} is the random residual term, for an observation at animal and permanent environment i in week k, where weeks k (k=10) were defined based on the age of the animal, which is not equal to the weeks on test. The starting point was $l=2$, because the slope and the intercept are considered to be the first two knotpoints. In matrix notation the model can be described as:

$\mathbf{y} = \mathbf{X\beta} + \mathbf{Z_s u} + \mathbf{Z_s p} + \mathbf{e}$

Where **y** is a vector containing the observations, **β** is the vector containing the fixed effects, **u** is a vector containing the estimates for genetic spline effects and **p** is a vector containing the estimates for permanent environment spline effects; **e** is the vector with error terms. **X**, and $\mathbf{Z_s}$ are incidence matrices relating **y** to **β**, **u**, and **p**. $\mathbf{Z_s}$ contains the coefficients for each observation in blocks of animals. If an animal has observations on *t...t+4*, than the block for this animal has a size of 5 × number of knotpoints.

The genetic variance-covariance matrix (**A**) of all ages between animals in the analysis is $\mathbf{A}=\mathbf{S}\cdot\mathbf{\Sigma_a}\cdot\mathbf{S'}$, permanent environmental variance-covariance (**P**) matrix of all ages in the analysis equals $\mathbf{P} = \mathbf{S}\cdot\mathbf{\Sigma_p}\cdot\mathbf{S'}$. Where $\mathbf{\Sigma_a}$ and $\mathbf{\Sigma_p}$ are the variance-covariance matrices of the estimated spline coefficients for the genetic and the permanent environmental effects. **S** is a matrix with rows containing coefficients for all ages in the analysis, equal to [1 t_{ijk} $z(t_{ijk})$], and columns corresponds to the number of knotpoints applied. Variances at any age t_{ijk} can be calculated as $\sigma^2_{a,t} = \mathbf{S_t}\cdot\mathbf{\Sigma_a}\cdot\mathbf{S_t'}$, while the genetic covariance between ages t_{ijk} and t_{ijk}' equals $\sigma_{a,t;a,t'} = \mathbf{S_t}\cdot\mathbf{\Sigma_a}\cdot\mathbf{S_{t'}'}$. Permanent environmental covariances can be calculated using the same method.

Fixed effects

All fixed effects were modelled as a function of age using splines, where the maximum number of knotpoints for each fixed effect was eight. Knotpoints for each fixed effect were evenly spread over the age trajectory. Significance of the fixed effects was determined using SAS' PROC GLM (SAS, 1988). As soon as a spline coefficient was non-significant, all higher order fits were considered to be non-significant as well.

The significant fixed effects for live weight were: line as a spline term with three knotpoints, week of test as a spline term with four knotpoints, feed level as a spline term with three knotpoints, and weekly batch as a spline term with five knotpoints. The significant fixed effects for feed intake were: line, week of test as a spline term with four knotpoints, feed level as a spline term with four knotpoints, and weekly batch as a spline term with eight knotpoints.

Derivation of gain

Daily gain was equal to live weight at age $t + 1$ minus live weight at age t, divided by $((t + 1) – t)$, which is equal to 1. Using the estimates of the variance components for live weight, (co-)variances for daily gain can be calculated using var(b-a)=var(a)+var(b)-

2×cov(a,b), where a equals the weight at age *t* and b equals weight at age *t* + 1; var(a) equals the variance of weight at age *t*, var(b) equals the variance of weight at age *t* + 1, cov(a,b) equals the covariance between weights at age *t* and *t* + 1, and var(b-a) equals the variance of gain between ages *t* and *t* + 1. In matrix notations this is equal to $\sigma^2_{A:DG} = \mathbf{S}_* \cdot \mathbf{\Sigma}_a \cdot \mathbf{S}_*'$. Where $\sigma^2_{A:DG}$ is the genetic covariance matrix for daily gain at ages *t*, $\mathbf{S}_*$ is derived from **S** as $\mathbf{S}_*(t+1)=\mathbf{S}(t+1)-\mathbf{S}(t)$, where *t* are the rows with spline coefficients corresponding to age *t*, columns correspond to number of knotpoints applied and $\mathbf{\Sigma}_a$ is the covariance matrix estimated for the genetic spline coefficients for live weight. Permanent environmental variance at any age *t* is then calculated in the same way, substituting $\mathbf{\Sigma}_a$ for $\mathbf{\Sigma}_p$. Covariance between ages for daily gain were derived using the same methodology as for live weight and daily feed intake.

Results

Results are shown when pigs were 124, 131, … 166 and 173 days of age because these were the average ages for the adjustment week and each of the following weeks on test.

Table 2. Heritabilities, genetic and phenotypic correlations for live weight. [A]

Age	124d	131d	138d	145d	152d	159d	166d	173d
124d	**0.25**	0.98	0.94	0.88	0.81	0.75	0.69	0.64
131d	0.77	**0.25**	0.99	0.95	0.91	0.86	0.81	0.77
138d	0.66	0.80	**0.23**	0.99	0.96	0.93	0.89	0.86
145d	0.56	0.75	0.85	**0.22**	0.99	0.97	0.95	0.92
152d	0.49	0.70	0.83	0.88	**0.23**	0.99	0.98	0.96
159d	0.44	0.65	0.78	0.85	0.90	**0.26**	1.00	0.98
166d	0.38	0.57	0.70	0.78	0.85	0.92	**0.28**	1.00
173d	0.31	0.47	0.59	0.67	0.76	0.86	0.93	**0.28**
total variance	39.2	41.3	49.0	60.0	66.5	71.5	79.6	95.6

[A] Heritabilities are bold and on the diagonal, genetic and phenotypic correlations respectively above and below the diagonal.

Live weight

Estimated heritability for live weight was approximately 0.25 over the age trajectory, and was somewhat higher at the early and late ages (Table 2). Estimates for the genetic correlations between different ages were high (0.64-1.00), and slightly decreasing when ages were further apart. Estimates for the phenotypic correlations showed the same pattern, but were clearly lower compared to the estimates for the genetic correlations (0.31-0.93) indicating that environmental correlations decreased faster with increasing age interval than genetic correlations. Both the genetic and the phenotypic correlations tended to be higher (i.e. a stronger correlation between ages) near the end of the test period.

Table 3. Heritabilities, genetic and phenotypic correlations for daily feed intake. [A]

age	124d	131d	138d	145d	152d	159d	166d	173d
124d	**0.12**	0.96	0.87	0.78	0.74	0.75	0.78	0.75
131d	0.18	**0.17**	0.98	0.92	0.90	0.90	0.88	0.77
138d	0.15	0.22	**0.17**	0.99	0.97	0.96	0.91	0.75
145d	0.12	0.19	0.23	**0.16**	1.00	0.98	0.92	0.73
152d	0.09	0.17	0.21	0.23	**0.15**	0.99	0.94	0.75
159d	0.06	0.14	0.18	0.21	0.23	**0.11**	0.97	0.83
166d	0.04	0.10	0.14	0.17	0.20	0.22	**0.08**	0.93
173d	0.01	0.05	0.09	0.12	0.16	0.19	0.22	**0.06**
total variance	0.313	0.206	0.212	0.249	0.249	0.263	0.274	0.329

[A] Heritabilities are bold and on the diagonal, genetic and phenotypic correlations respectively above and below the diagonal.

Daily feed intake

Heritability estimates for daily feed intake ranged from 0.06 to 0.17 (Table 3), with highest estimates between the ages of 131d and 145d (0.17), and continuously decreasing estimates after 152d of age (0.15 to 0.06). Estimates for the genetic correlations ranged from 0.73 to 1.00, and again were highest between adjacent ages and decreasing when ages were further apart. Estimates for phenotypic correlations were lower and ranged from 0.01 to 0.23. Low phenotypic correlations between daily feed intake at different ages (Table 3) were

mainly due to the high error variances. High estimates for error variances (excluding permanent environmental effects) represent large fluctuations in daily feed intake from one day to the next.

Table 4. Heritabilities, genetic and phenotypic correlations for daily gain. [A]

age	124d	131d	138d	145d	152d	159d	166d	173d
124d	**0.06**	1.00	0.99	0.95	0.91	0.85	0.81	0.79
131d	0.99	**0.09**	1.00	0.98	0.94	0.90	0.86	0.84
138d	0.97	0.99	**0.10**	0.99	0.96	0.92	0.89	0.86
145d	0.73	0.82	0.87	**0.17**	0.99	0.97	0.95	0.93
152d	0.25	0.39	0.49	0.85	**0.17**	0.99	0.98	0.97
159d	-0.09	0.05	0.16	0.62	0.94	**0.12**	1.00	0.99
166d	-0.26	-0.11	-0.01	0.48	0.87	0.99	**0.09**	1.00
173d	-0.34	-0.20	-0.10	0.40	0.82	0.97	1.00	**0.08**
total variance	0.122	0.083	0.067	0.038	0.039	0.057	0.078	0.096

[A] Heritabilities are bold and on the diagonal, genetic and phenotypic correlations respectively above and below the diagonal.

Daily gain

Heritability estimates for daily gain increased from 0.06 at 124d of age to 0.17 at the middle of the age-trajectory and then decreased to 0.08 at 173d of age (Table 4). Estimates for genetic correlations between daily gain at different ages were high (0.79 to 1.00). Estimates for phenotypic correlations ranged from –0.34 to 1.00, where the higher values were found between adjacent ages and the lowest values when ages were furthest apart. Positive phenotypic correlations existed in two blocks of different ages: 124d to 145d (0.25 to 0.99) and 152d to 173d (0.40 to 1.00).

Table 5. Estimates for genetic and phenotypic correlations between live weight and daily feed intake at different ages.

		daily feed intake							
	age	124d	131d	138d	145d	152d	159d	166d	173d
				genetic correlation					
live weight	124d	0.80	0.76	0.70	0.62	0.60	0.61	0.64	0.63
	131d	0.84	0.81	0.74	0.66	0.64	0.66	0.69	0.68
	138d	0.85	0.82	0.75	0.68	0.66	0.68	0.72	0.71
	145d	0.84	0.81	0.75	0.68	0.66	0.68	0.73	0.73
	152d	0.82	0.80	0.74	0.67	0.65	0.68	0.72	0.73
	159d	0.80	0.78	0.72	0.65	0.64	0.67	0.71	0.72
	166d	0.77	0.75	0.70	0.63	0.62	0.65	0.70	0.71
	173d	0.75	0.73	0.67	0.61	0.60	0.63	0.68	0.69
	age			phenotypic correlation					
live weight	124d	0.14	0.16	0.14	0.12	0.10	0.09	0.07	0.05
	131d	0.15	0.17	0.16	0.14	0.13	0.12	0.10	0.09
	138d	0.14	0.17	0.17	0.15	0.14	0.14	0.13	0.11
	145d	0.14	0.17	0.17	0.16	0.16	0.15	0.15	0.14
	152d	0.14	0.18	0.18	0.17	0.17	0.17	0.17	0.16
	159d	0.14	0.18	0.19	0.18	0.19	0.19	0.19	0.18
	166d	0.14	0.18	0.19	0.19	0.20	0.20	0.21	0.20
	173d	0.13	0.18	0.19	0.19	0.20	0.21	0.21	0.21

Live weight and daily feed intake

Estimates of the genetic correlations between live weight and daily feed intake decreased slightly with age when both traits were recorded at the same age (Table 5). In general genetic correlations were positive and high (0.60 to 0.85), meaning that an animal with a high live weight had a high daily feed intake. Live weight had somewhat lower genetic correlations with daily feed intake recorded on the median ages in comparison to daily feed intake measured at 124d, 131d, and 166d, 173d of age. Phenotypic correlations between live weight and daily feed intake recorded at the same age were slightly increasing

over age, from 0.14 at 124d of age to 0.21 at 173d of age. Phenotypic correlations between live weight and daily feed intake were highest at the end of the age-trajectory, and lowest between live weight recorded at beginning of age trajectory and daily feed intake recorded at end of age trajectory.

Table 6. Estimates for genetic and phenotypic correlations between live weight and daily gain at different ages.

		Daily gain							
	age	124d	131d	138d	145d	152d	159d	166d	173d
				genetic correlation					
live weight	124d	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
	131d	0.23	0.23	0.23	0.23	0.22	0.21	0.20	0.20
	138d	0.39	0.39	0.39	0.39	0.37	0.36	0.34	0.33
	145d	0.52	0.52	0.52	0.51	0.50	0.48	0.46	0.45
	152d	0.61	0.62	0.62	0.62	0.60	0.58	0.56	0.55
	159d	0.67	0.69	0.69	0.69	0.68	0.67	0.65	0.64
	166d	0.72	0.74	0.74	0.75	0.75	0.73	0.72	0.71
	173d	0.75	0.77	0.78	0.80	0.80	0.78	0.77	0.76
	age			phenotypic correlation					
live weight	124d	-0.12	-0.15	-0.16	-0.23	-0.23	-0.19	-0.17	-0.15
	131d	0.22	0.20	0.17	0.04	-0.11	-0.19	-0.22	-0.24
	138d	0.47	0.45	0.43	0.27	0.02	-0.14	-0.22	-0.25
	145d	0.61	0.60	0.59	0.44	0.15	-0.07	-0.17	-0.22
	152d	0.66	0.67	0.67	0.57	0.30	0.07	-0.04	-0.10
	159d	0.64	0.68	0.70	0.68	0.46	0.25	0.14	0.08
	166d	0.56	0.63	0.67	0.75	0.62	0.44	0.33	0.28
	173d	0.45	0.54	0.60	0.78	0.75	0.61	0.52	0.46

Live weight and daily gain

Genetic correlations between live weight and daily gain recorded at the same age increased over age, from 0.05 at 124d of age to 0.76 at 173d of age (Table 6). Live weight at

Table 7. Estimates for genetic and phenotypic correlations between daily feed intake and daily gain at different ages.

		daily gain							
	age	124d	131d	138d	145d	152d	159d	166d	173d
				genetic correlation					
daily feed intake	124d	0.32	0.33	0.34	0.34	0.34	0.34	0.33	0.33
	131d	0.32	0.33	0.34	0.34	0.34	0.34	0.33	0.33
	138d	0.31	0.32	0.32	0.33	0.33	0.32	0.32	0.31
	145d	0.29	0.30	0.30	0.31	0.31	0.31	0.30	0.30
	152d	0.30	0.31	0.31	0.32	0.32	0.31	0.31	0.30
	159d	0.32	0.33	0.34	0.34	0.34	0.34	0.33	0.33
	166d	0.36	0.37	0.38	0.39	0.39	0.38	0.37	0.37
	173d	0.39	0.40	0.40	0.41	0.41	0.41	0.40	0.39
	age			phenotypic correlation					
daily feed intake	124d	0.02	0.03	0.03	0.04	0.04	0.04	0.03	0.03
	131d	0.04	0.05	0.06	0.08	0.08	0.06	0.05	0.05
	138d	0.06	0.07	0.08	0.10	0.10	0.08	0.07	0.06
	145d	0.06	0.08	0.09	0.12	0.11	0.09	0.08	0.07
	152d	0.08	0.09	0.10	0.14	0.14	0.11	0.10	0.09
	159d	0.09	0.11	0.12	0.16	0.15	0.13	0.11	0.10
	166d	0.10	0.12	0.13	0.17	0.17	0.14	0.12	0.11
	173d	0.10	0.12	0.13	0.18	0.17	0.14	0.12	0.11

a specific age had fairly constant genetic correlations with daily gain recorded at varying ages. However, genetic correlations increased from 0.05 between live weight at 124d of age and daily gain at all ages to 0.77 between live weight measured at 173d and daily gain measurements over the whole age-trajectory. Phenotypic correlations showed a different pattern compared to the genetic correlations. The phenotypic correlations between live weight recorded at a given age and daily gain measured at different ages was higher when the daily gain measurement was before the live weight measurement. The phenotypic correlations between daily gain measured at a specific age and live weight measurements were highest for live weight recorded towards the end of the age trajectory. Phenotypic

correlations were higher when the live weight measurement preceded the daily gain measurement, e.g. correlation for daily gain at age 152d and live weight at age 124d was equal to –0.23 while the correlation for live weight at age 124d and daily gain at age 152d was equal to 0.66 (Table 6).

Daily feed intake and daily gain

Estimates for the genetic correlations between daily feed intake and daily gain at different ages showed similar values for all age combinations (0.29 to 0.41, Table 7.). There was a slight increase in the genetic correlation between daily feed intake and daily gain recorded at the same age from 159d to 173d of age. Phenotypic correlations between daily feed intake and daily gain recorded at the same age showed an increase with increasing age, daily feed intake at older ages had a higher phenotypic correlation with daily gain at all ages.

Discussion

General

The estimated parameters for live weight, daily feed intake, and daily gain have to be interpreted while keeping in mind that animals were kept under a restricted feeding regime. Although pigs were kept under a restricted feeding regime, in reality only 25% of the animals ate all their allowed feed in a week, the other 75% did not eat all of their allowed feed.

Estimates of the genetic correlation between live weight, daily feed intake and daily recorded at 124 d of age and 173 d of age varied from 0.64 for live weight to 0.79 for daily gain (Tables 2, 3, and 4) indicating that these three traits cannot be considered to be the same trait throughout this relatively short test period. Extrapolation of these estimates to a larger interval between measurements will most probably result in lower genetic correlations, which implies that it is possible to change trait patterns over varying ages through selection.

Parameters and variances estimated with the random regression model were about similar to the multivariate estimates presented by Huisman et al. (2002b) who used the same data. Parameters estimated with the random regression model were smoother over the age

trajectory in comparison to the eight weekly measurements of the multivariate analysis. Variance estimates were similar for both approaches. In this analysis spline functions were used instead of polynomials: in contrast to polynomials, applying spline functions in a random regression model yields fewer parameters to be estimated, resulting in a more robust random regression model (Verbyla et al., 1999; White et al., 1999). When comparing estimated variances at any age *t*, estimated with a polynomial or a spline random regression model there was no difference between the variance estimates at any age *t* (results not shown).

Live weight

Huisman et al. (2002a) fitted various random regression models to weight data of ad libitum fed growing pigs using a sire model. Heritability estimates presented in this study were higher than the heritabilities found by Huisman et al. (2002a), although heritability estimates for the later ages were more similar to heritability estimates in this study. Differences between the results of Huisman et al. (2002a) and the results presented in this study, could be explained by use of genetic model, a sire versus an animal model, or by the feeding regime under which the animals were kept. Estimates for genetic and phenotypic correlations were similar in both studies.

Daily feed intake

Phenotypic correlations between daily feed intake at different ages obtained with a random regression model were similar to phenotypic correlations estimated with a multivariate model on the same data. Heritability estimates were higher in this study compared to the multivariate analysis. In the multivariate analysis, different weeks on test were treated as different traits, towards the end of test on average pigs did not eat their allowed food (no increments of 100g each week, Table 1), which means that animals were less restricted towards end of test. That could explain the increase in heritability towards the end of test, heritability of ad libitum feed intake is expected to be higher than the heritability of restricted feed intake (Hermesch et al. 1999). In the random regression analysis daily feed intake was modeled as function of age, and the less restricted feeding towards end of test does not show in the heritability estimates.

Estimated heritabilities for average feed intake per day over a certain test period ranged from 0.16 to 0.43 (Mrode and Kennedy, 1993; Schulze et al., 2001). Hermesch et al. (1999) estimated a heritability of 0.16 for average daily feed intake under restriction.

Phenotypic variance for average daily feed intake estimated by Hermesch et al. (1999) was a factor 10 lower (approx. 7000 animals tested over a 5-week period) than the total variance for actual daily feed intake. The trait in question was average daily feed intake, by taking the average of daily feed intake a lot of variation in daily feed intake disappears. Von Felde et al. (1996) estimated the heritabilities ranging from 0.16 to 0.30 for ad libitum daily feed intake over a 10-week period, which started at an age of approximately 100 d. Highest heritabilities were found after approximately 135d of age, in the same interval as we found the highest heritability. Hall et al. (2000) found an increasing heritability of daily feed intake over a 7-week test period for pigs with ad libitum access to feed, while Huisman and Van Arendonk (2002) found a decreasing heritability for daily feed intake over a 100 d test period of ad libitum fed growing gilts.

The lower heritability estimates in this study were due to the restricted feeding regime, Hermesch et al. (1999) estimated the heritability for average daily feed intake under ad libitum and restricted feed and found that the heritability under restricted feeding was significantly lower. As far as correlations were presented for daily feed intake over a certain period (Von Felde et al., 1996; Hall et al., 2000; Huisman and Van Arendonk, 2002), they all follow similar patterns as the correlations presented in Table 3.

Daily gain

Estimated heritabilities for classic ADG, where classic ADG stands for weight gain over a certain period divided by the length of that period, on test under a restricted feeding regime range from 0.14 to 0.76 (Clutter and Brascamp, 1998). Estimated heritability for classic ADG in this data set, where ADG was a linear regression through all weight records, was 0.20±0.06. Hermesch et al. (1999) found no difference in heritability of ADG on test for ad libitum and restricted fed pigs. Values for heritability found in this study were on the lower side of the literature estimates, which could be explained by the fact that estimates were for actual daily gain instead of classic ADG over a certain period, although Hermesch et al. (1999) found similar values for classic ADG. Genetic correlation estimated by Knol (personal communication) between classic ADG first 8 wk on test and classic ADG last 8 wk on test was 0.50, while the phenotypic correlation was negative (-0.04). In beef cattle, Koots et al. (1994) found the genetic correlation between gain from birth to weaning and gain from weaning to yearling weight to be 0.47, while phenotypic correlation was 0.24.

Live weight and daily feed intake

Huisman et al. (2002b) estimated the phenotypic correlation between live weight and daily feed intake in the same data set using a multivariate model to be 0.21 in all test weeks, while here phenotypic correlation between live weight and daily feed intake recorded at the same age was increasing with age. The estimated genetic correlations increased from 0.25 to 0.51 over week of test in their study, genetic correlations found in this study are higher and slightly decreasing with age. Veerkamp and Thompson (1999) estimated parameters for feed intake, live weight, and milk yield over lactation for dairy cattle with a multivariate random regression model. They found that DMI and live weight were highly genetically correlated over the whole lactation, with highest correlations found in mid-lactation. We also found high genetic correlations between daily feed intake and live weight. The correlations we found were higher than the estimates of Veerkamp and Thompson (1999), but our data consisted of growing animals instead of lactating animals which undergo only relatively minor changes in weight, which might have an impact on the estimates.

The estimated genetic correlation of approximately 0.8 between live weight and daily feed intake indicates that when selection is on live weight, daily feed intake is increasing as well. Genetic correlation between live weight and daily feed intake at higher ages was not as high as the genetic correlation at lower ages, which indicates that when animals are tested on higher ages, daily feed intake will not increase in the same way as when animals are tested on lower ages.

Live weight and daily gain

In beef cattle, Koots et al. (1994) published high correlations - both genetic and phenotypic - between live weight measurements (birth weight, weaning weight and yearling weight) and classic ADG measurements (from birth to weaning, and from weaning to yearling weight). Archer et al. (1998) found a small negative value for the genetic correlation between weaning weight and ADG in mature mice, indicating that a high weaning weight is more of an effect of the dam, than it is expressing the ability of an animal to grow fast. In our study, live weight at the start of test did not tell much about daily gain later on in the test. Live weight at older ages, from approximately 150 d onwards, has a high genetic correlation with daily gain at all ages (Table 6). Which means that an animal that has a high breeding value for live weight at the end of test, has a high breeding value for growth

rate at all previous ages. From this it is clear that high breeding values for gain at preceding ages are necessary to reach a high breeding value for weight at later ages, in other words an animal cannot reach a high weight at the end of test without fast growth during test.

Daily feed intake and daily gain

Several studies have estimated heritabilities and correlations, both genetic and phenotypic, for daily feed intake and classic ADG. Genetic correlations between classic ADG and daily feed intake are positive and generally high, but lower in restricted fed pigs (Clutter and Brascamp, 1998). Phenotypic correlations between classic ADG and daily feed intake are also positive and estimates range from 0.4 (Hall et al., 1999) to 0.74 (Mrode and Kennedy, 1993). Several studies estimated the genetic correlation between classic ADG and daily feed intake over a certain test period (Von Felde et al., 1996: test period of 10 weeks divided in five periods; Hall et al., 1999 and 2000: test period of eight weeks; Schulze et al., 2002: test period of nine weeks) all in approximately the same age range. Estimates of genetic correlation between daily feed intake at different time periods and classic ADG varied from 0.45 to 0.6, where the genetic correlations estimated by Von Felde et al. (1996) and Hall et al. (1999 and 2000) were stable over test, while Schulze et al. (2002) found that genetic correlation decreased towards end of test. Phenotypic correlations between daily feed intake at different times and classic ADG varied from 0.25 to 0.40.

Roehe et al. (1994) showed that pigs with a high EBV for classic ADG had higher EBV's for daily feed intake over the whole test, pigs with a low EBV for classic ADG had lower EBV's for daily feed intake over the whole test. Genetic correlations between daily gain and daily feed intake found in this study were approximately 0.35 for the whole age range, while the phenotypic correlations found in this study averaged 0.10 (Table 7). Indicating that it is possible to increase efficiency of growing pigs over this age trajectory, i.e. increasing daily gain without increasing daily feed intake at ages of interest.

Implications

Live weight, daily feed intake, and daily gain recorded in this age trajectory cannot be considered to be the same trait with equal variance and heritability over this trajectory. Extrapolating estimates yields lower genetic correlations between ages in the same trait,

which indicates that bending curves through selection is a viable option. Genetic and phenotypic correlations between live weight and daily feed intake at different ages were basically the same for all age combinations. Live weight at later ages had a high genetic correlation with daily gain at all ages. Correlations between daily feed intake and daily gain at different ages were basically the same for all age combinations. Pigs were given one week to adjust to new pen(-mate)s and the electronic feeders, results show that this adjustment week can be included in the test. The estimated genetic correlation of approximately 0.35 between daily gain and restricted daily feed intake indicates that it is possible to increase daily gain through selection without increasing daily feed intake.

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Chapter 5

Application of random regression models when selection is on part of a curve, a simulation study

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Abstract

Objective was to investigate the possibilities to alter the growth curve of pigs through selection. The impact of genetic correlation structure, measurement design, and missing records on achieved changes in growth curve and the accuracy of breeding value estimation have been investigated using simulation. Phenotypes of animals were simulated and subsequently breeding values were estimated using a random regression model. The best animals were selected and used to produce the next generation. This selection process was repeated for three generations. Animals were mated at random with no restrictions on inbreeding. The presented results were the average of 100 replicates. Traits of interest were early growth, intermediate growth, late growth and total growth. Phenotypes of animals over an age-period of 100 days were simulated for two genetic correlation structures. Structure one had high genetic correlations between days of age, for structure two the genetic correlation between days of age decreased more rapidly. A number of recording strategies that differed in interval between subsequent measurements were applied. For correlation structure one the interval between subsequent measurements could be increased to 25 d without substantial loss in achieved genetic gain, while for correlation structure two achieved genetic gain already dropped when the interval was increased to 10 d. A number of sampling strategies were investigated, these sampling strategies differed in number of measurements per animal and length of test period. In general it can be stated that fewer measurements equals lower genetic gain. When fewer phenotypes were recorded the accuracy of estimated breeding values diminished. Main conclusion from this study is that it is possible to change patterns through selection, the magnitude of change dependents on the underlying genetic structure. Recording extra weights will result in higher genetic gain; increments up to about 10% are possible.

Key Words: Simulation, Pigs, Regression, and Performance.

Introduction

An animal changes with age; these changes with age differ between animals and are partly caused by the genetic make up of the animal (Atchley et al., 1997). Interest is in genetic parameters that describe these changes with age, and in ways we have to measure animals to get accurate estimates of these parameters. Genetic parameters that describe these changes with age can be obtained using a random regression model, where the genetic and the non-genetic animal effect are modeled as a function of age. A number of people have done such analyses to obtain genetic parameters for milk production (e.g. Kirkpatrick et al., 1994; Van der Werf et al., 1998), for beef production (e.g. Meyer, 1999), for growth in pigs (e.g. Huisman et al., 2002). In pig breeding, selection is usually on weight at a certain age. However the desired weight and/or age at slaughter differs between markets. Pigs destined for the bacon market are slaughtered at a lower weight than pigs destined for the production of fresh pork. While other pigs are used for the production of Parma ham, these pigs have to be at least 9 months old and must have reached a live weight of 150 kg or more before slaughter. Common recording strategies can be defined as one weight measurement at the end of a certain test period. This creates an interesting dilemma for pig breeding organizations: Is it possible to alter the growth pattern in order to meet the range of market weights, and how do recording strategies have to change to achieve this?

Objective is to investigate the possibilities to change (part of) the growth curve of pigs through selection. What is the impact of genetic correlation structure, recording strategy, and missing records on achieved changes in growth curve and the accuracy of breeding value estimation making use of simulation.

Material and Methods

Simulation of animals

First a base population of animals was simulated. From this base population, animals were randomly selected to produce the base generation (generation 0). From this base

generation, the best animals were selected based on estimated breeding value and these animals were used to produce the next generation. Selection was based on what we called growth, but it could be any trait measured over a trajectory. This selection process was repeated for 3 generations. Animals were mated at random without restrictions on inbreeding. The presented results are the average of 100 replicates. Phenotypes of animals over an age-period of 100 days were simulated for two genetic correlation structures. The first genetic correlation structure was tighth correlation structure, genetic correlation decreased linear when the gap between ages increased, reaching a minimum of 0.5 when the age-difference was 99d:

$$\rho^{1}_{i,j} = 1 - (\tfrac{1}{200}|i - j|) \quad [1]$$

where $\rho_{i,j}^{1}$ is the genetic correlation between ages *i* and *j* for this genetic correlation structure, *i* and *j* are ranging from 1d through 100d of age.

The second genetic correlation structure was a more loose correlation structure. The correlation between days decreased more rapidly when the age difference increased and eventually dropped to zero when the age-difference became 99d:

$$\rho^{2}_{i,j} = \frac{(99 - |i - j|)^{2}}{99^{2}} \quad [2]$$

where $\rho_{i,j}^{2}$ is the genetic correlation between ages *i* and *j* for this genetic correlation structure, *i* and *j* are ranging from 1d through 100d of age.

A permanent environmental correlation structure was simulated to account for repeated measurements on the same animal. For both genetic correlation structures the permanent environmental correlation, $\rho_{i,j}^{pe}$, was the same, and equaled:

$$\rho^{pe}_{i,j} = 0.97^{|i-j|} \quad [3]$$

In [1], [2] and [3], *i* and *j* are ranging from 1 to 100, were 1 is the minimum age of an animal, and 100 is the maximum age in days. Phenotypic variance was the same for both cases and was simulated according:

$$\sigma^{2}_{i} = 10 + 0.5i - 0.025i^{2} \quad [4]$$

where *i* is ranging from 1 to 100 days. Variance was increasing until day 80, then flattened out.

Heritability was assumed constant over the whole age-range and heritability had a value of 0.33.

Table 1. Description of sampling strategies.

Strategy	All animals	50 % of the animals
100 100	Are measured through 100d	Not applicable
100 25	Are measured through 25d	Are measured through 100d
75 75	Are measured through 75d	Not applicable
75 25	Are measured through 25d	Are measured through 75d
50 50	Are measured through 50d	Not applicable
50 25	Are measured through 25d	Are measured through 50d
25 25	Are measured through 25d	Not applicable
75-1	Are measured on 75d	Not applicable

Recording strategies

Different recording strategies were applied to investigate the effects of number of measurements on accuracy of breeding value estimation and genetic gain. In all cases, measurements were taken until 100 days of age were reached. First measurement was taken as soon as the animal reached a phenotypic value of 25, which all animals reached in the first 10 days of age. The six strategies were IV01; all animals were measured each day on test, maximum of 100 observations per animal. IV05; all animals were measured every five days on test, maximum of 20 observations per animal. IV10; all animals were measured every 10 days on test, maximum of 10 observations per animal. IV25; all animals were measured every 25 days on test, maximum of 4 observations per animal. IV45; all animals were measured every 45 days on test; and 75-1 where all animals were only measured at day 75 on test. The number of measurements ranged from 1 measurements per animal to a maximum of 100 measurements per animal.

Effect of missing records

To study the effect of missing records on the accuracy of estimates of breeding values for a part of the curve, records in certain age periods were deleted (Table 1). In all cases, the situation with all records, which is sampling strategy 100 100, was used as a reference for the cases with missing records. Measurements were taken on four offspring per sire-dam combination. In case of sampling strategy 100 100, all four full sibs were measured from beginning to end of the age period (100d). Average simulated phenotypic value at day

Table 2. Description of pedigree designs[1]

Design	Sires	Dams per sire
S02	2	64
S04	4	32
S08	8	16
S16	16	8
S32	32	4
S64	64	2

[1] in all designs 4 offspring per sire-dam combination are produced

1 was 25 (S.D.=3.28). In case of sampling strategy 100 25, two randomly chosen full sibs were measured over the whole age period and the other two full sibs were measured through 25d of age. In case of sampling strategy 75-1, all four full sibs were measured once at 75d of age.

Pedigree designs

Different number of sires and dams per sire were applied to study the effect of population structure on the estimation of breeding value patterns (Table 2). In all designs, 512 offspring were produced per generation but the number of sires and dams were varied. In all designs the number of offspring per sire-dam combination was four. The dams were only mated once. For example, in design S02 there are 2 sires and each sire is mated with 64 dams resulting in 2 male and 128 female parents, 130 parents in total. The sires and dams for the next generation were selected from these 512 offspring. The same number of parents was used to produce the base generation; those parents were randomly selected from the unselected base population.

Traits under selection

Four different traits were defined to enable selection on growth in different parts of the curve, i.e. early growth (1 through 30d), intermediate growth (31 through 80d), late growth (61 through 100d) and total growth (1 through 100d). The four selection criteria were:

- Early growth (**EG**): defined as the sum of breeding values at the ages 1 through 30d
- Intermediate growth (**MG**): defined as the sum of breeding values at the ages 31 through 80d.

- Late growth (**LG**): defined as the sum of breeding values at the ages 61 through 100d.
- Total growth (**TG**): defined as the sum of breeding values at the ages 1 through 100d.

Breeding values for these four traits were calculated from the estimated breeding values for each day during the age period. Details on how these daily breeding values were estimated are given in the next section.

Breeding value estimation

Breeding value estimation for the two genetic correlation structures was done using the following model (Huisman et al., 2002):

$$y_{ij} = \mu_0 + \mu_1 t_{ij} + \sum_{l=2}^{4} \mu_l z_l\left(t_{ij}\right) + a_{i0} + a_{i1} t_{ij} + \sum_{l=2}^{4} a_{il} z_l(t_{ij}) + p_{i0} + p_{i1} t_{ij} + e \quad [5]$$

where y_{ij} is the phenotypic value of animal i at age j, the μ's are the coefficients for the average curve, t_{ij} is age j of animal i in days, $z_l(t_{ij})$ is the spline coefficient for knot l at age t_{ij}. And a_{i0} is the intercept for animal i, a_{i1} is the slope for animal i, and a_{il} is the estimate for animal i at knot-point l. And p_{i0} is the intercept for permanent environment i, a_{i1} is the slope for permanent environment i. The permanent environment part of the model was included to account for covariance's between repeated records on the same animal. A more correct term for this permanent environment would be non-genetic animal effect. Breeding value estimation was done with ASREML (Gilmour et al., 2000). Applying the model resulted in 5 breeding values per animal, because of the 5 random coefficients in the model. With the 5 estimated breeding values, breeding values for all 100 days of age were calculated as

$$\mathbf{EBV}_{\mathbf{pattern},x} = \mathbf{Z}_{\mathbf{spline}} \cdot \mathbf{A}_x \quad [6]$$

where $\mathbf{EBV}_{\mathbf{pattern},x}$ is a 100×1 vector containing the estimated breeding values for all 100 days for animal x, $\mathbf{Z}_{\mathbf{spline}}$ is a 100×5 matrix containing the spline coefficients for all ages, and $\mathbf{A}_x$ is a 5×1 vector containing the five estimated breeding values of animal x.

Results

Table 3 shows achieved genetic gain (SD units) after 3 generations of selection for the different measurement designs and correlation structures. Both correlation structures did not show a significant difference between measurement designs IV01 and IV05.

Table 3. Achieved genetic gain in SD units after 3 generations of selection for the different measurement designs for both genetic correlation structures [A].

		correlation structure 1		
design	selection on EG	selection on MG	selection on LG	selection on TG
IV01	1.48	1.53	1.55	1.59
IV05	1.46	1.54	1.51	1.57
IV10	1.49	1.53	1.54	1.56
IV25	1.44	1.50	1.50	1.52
IV45	1.32	1.44	1.52	1.52
75-1	1.04	1.38	1.41	1.42
		correlation structure 2		
design	Selection on EG	selection on MG	selection on LG	selection on TG
IV01	1.36	1.43	1.43	1.45
IV05	1.34	1.40	1.41	1.40
IV10	1.29	1.42	1.43	1.40
IV25	1.14	1.36	1.34	1.38
IV45	0.81	1.20	1.32	1.32
75-1	0.37	1.15	1.28	1.22

[A] pedigree design: S08

For correlation structure one, no significant differences in achieved genetic gain between measurement designs IV01, IV05 and IV10 for all traits were found. For EG IV45 achieved around 10% less genetic gain compared to the other designs, while recording strategy 75-1 achieved about 30% less genetic gain than strategies IV01, IV05 and IV10. Also for MG the biggest difference in recording strategies was found between IV45, 75-1 and the other measurement designs (Table 3). For LG only recording strategy 75-1 showed a decrease of about 10% in achieved genetic gain compared to the other strategies. For TG, recording strategies IV25 and IV45 achieved a 5% lower genetic gain than recording strategies IV01, IV05 and IV10. While 75-1 showed a decrease of 10% in genetic gain compared to strategies IV01, IV05 and IV10 (Table 3).

For correlation structure two, there was no difference in achieved genetic gain between measurement designs IV01 and IV05. The differences in achieved genetic gain between the recording strategies were bigger than for correlation structure one. For EG,

recording strategy IV10 achieved about 5% lower genetic gain than recording strategies IV01 and IV05. Recording strategy IV25 achieved about 15% lower genetic gain than recording strategies IV01 and IV05. Recording strategy IV45 achieved about 40% lower genetic gain than recording strategies IV01 and IV05, and recording strategy 75-1 achieved about 75% lower genetic gain than recording strategies IV01 and IV05. For MG, recording strategy IV25 achieved about 5% lower genetic gain than sampling strategies IV01, IV05 and IV10; recording strategy IV45 achieved about 15% lower genetic gain than sampling strategies IV01, IV05 and IV10; recording strategy 75-1 achieved about 20% lower genetic gain than sampling strategies IV01, IV05 and IV10. For LG, recording strategy IV25 achieved about 5% lower genetic gain than sampling strategies IV01, IV05 and IV10; recording strategy IV45 achieved about 10% lower genetic gain than sampling strategies IV01, IV05 and IV10; recording strategy 75-1 achieved about 10% lower genetic gain than sampling strategies IV01, IV05 and IV10. For TG, recording strategy IV25 achieved about 5% lower genetic gain than sampling strategies IV01, IV05 and IV10; recording strategy IV45 achieved about 10% lower genetic gain than sampling strategies IV01, IV05 and IV10; recording strategy 75-1 achieved about 15% lower genetic gain than sampling strategies IV01, IV05 and IV10. The realized genetic gains after 3 generations of selection were also reflected in Figure 1, were the correlation between true and estimated breeding value over the 100d period were shown. It can be seen that when the correlation structure was tight, e.g. correlation structure 1, the correlation between true and estimated breeding value was almost constant over time. The points at which measurements were taken, was not of importance, as long as there were some over the whole range. While when the correlation structure was looser, the correlation between true and estimated breeding value was highest at the point at which measurements were done.

In Table 4 achieved genetic gain after 3 generations of selection for the different sampling strategies were shown. The achieved genetic gain of all sampling strategies other than sampling strategy 100 100 were expressed as percentage of the achieved genetic gain of sampling strategy 100 100.

Under the assumption of correlation structure one, the same genetic gain could be achieved for EG with all sampling strategies. Except for sampling strategy 75-1, with which about 30% of the genetic gain was lost compared to the other sampling strategies. For MG there were more differences in achieved genetic gain, in general the fewer data is used the lower genetic gain is achieved. The exception being sampling strategy 75-1 which has one

Table 4. Achieved genetic gain after 3 generations of selection relative to sampling strategy 100 100[A].

	100 100	100 25	75 75	75 25	50 50	50 25	25 25	75-1
			correlation structure 1					
EG	1.46	100%	99%	101%	101%	99%	96%	71%
MG	1.42	93%	96%	91%	90%	87%	81%	90%
LG	1.28	90%	95%	87%	84%	75%	75%	94%
TG	1.44	94%	97%	91%	90%	87%	81%	90%
			correlation structure 2					
EG	1.34	101%	98%	102%	99%	101%	102%	28%
MG	0.98	85%	101%	85%	87%	75%	55%	82%
LG	0.56	74%	86%	66%	54%	45%	29%	91%
TG	0.98	85%	94%	82%	79%	69%	60%	87%

[A] Pedigree design: S08, Measurement design: IV05, standard error of achieved genetic gain was about 0.26 for all sampling strategies.

measurement in the trajectory for this trait, compared to sampling strategy 25 25 which has none. For LG, sampling strategies 75 75, and 75-1 did not differ in achieved genetic gain compared to sampling strategy 100 100. For the other sampling strategies the achieved genetic gain decreased with a decrease in amount of data available. For TG, sampling strategies 100 25 and 75 75 did not differ in achieved genetic gain from sampling strategy 100 100. For the other sampling strategies the achieved genetic gain decreased with the amount of data available.

Under the assumption of correlation structure two, most sampling strategies did not differ in achieved genetic gain for EG from sampling strategy 100 100. The exception was sampling strategy 75-1, which has no observations available in this age period and genetic gain was 70% less than genetic gain achieved with sampling strategy 100 100. Sampling strategies 100 100 and 75 75 achieved the same genetic gain for MG, for the other sampling strategies applies the fewer data, the lower genetic gain. Especially if for a specific sampling strategy no observations were sampled in the trajectory in which the trait is defined. For LG, achieved genetic gain is different for all sampling strategies, except for sampling strategies 75 75 and 75-1 and sampling strategies 100 25 and 75 25 which achieve the same genetic gain for LG. For TG applies the same as for MG, the fewer data sampled, the lower genetic

Table 5. Achieved genetic gain in EG, MG, LG and TG when selection is on only one of the aforementioned traits [A].

		correlation structure 1			
			selection on		
		EG	MG	LG	TG
response in	EG	100%	84%	73%	84%
	MG	92%	100%	92%	100%
	LG	85%	102%	100%	103%
	TG	92%	99%	94%	100%
		correlation structure 2			
			selection on		
		EG	MG	LG	TG
response in	EG	100%	49%	26%	52%
	MG	70%	100%	85%	97%
	LG	40%	93%	100%	96%
	TG	70%	99%	92%	100%

[A] Pedigree design: S08, Measurement design: IV05

gain achieved. In Figure 2 are the correlations between true and estimated breeding values of some of the sampling strategies, clear is that -for both correlation structures- when there was no information available the correlation between true and estimated breeding value decreased. Although the decrements in correlation between true and estimated breeding values were lower for genetic correlation structure one, where the genetic correlation structure was tighter.

In Figure 3, true breeding values are plotted for both genetic correlation structures and the four traits. What attracts attention is that for both correlation structures there is little difference in shape of the patterns for MG and TG. When comparing the patterns for EG and LG, a clear difference is visible.

For correlation structure one, selection on EG resulted in the highest genetic gain for this trait; correlated responses in MG and TG were higher than the correlated response in LG. Selection on MG resulted in high correlated responses for LG and TG, while the correlated response in EG was about 15% lower than response of direct selection on EG. Selection on LG resulted in highest response in LG, while correlated response in MG and

TG was about 5% lower than direct response in MG and TG, the correlated response in EG was some 25% lower. Selection on TG resulted in equal responses in MG and LG as directly selecting on both traits. Correlated response in EG was about 15% lower than direct response (Table 5).

For correlation structure two, selection on EG resulted in the highest genetic gain for this trait; correlated responses in MG and TG were higher than the correlated response in LG. Selection on MG resulted in high correlated responses for LG and TG, while the correlated response in EG was about 50% lower than the direct response in EG. Selection on LG resulted in highest response in LG, while correlated responses in MG and TG were somewhat lower than the direct responses in both traits, the correlated response in EG was about 75% lower. Selection on TG resulted in roughly equal responses in MG and LG as direct responses in both traits. Correlated response in EG was about 50% lower than direct response (Table 5).

Discussion

Several studies have investigated the effect of selection on different species and different traits. Atchley et al. (1997) selected mice for 14 generations on a restricted index, on growth rate from birth to 10d of age, and on growth rate from 28d through 56d of age. Which resulted in mice with different growth patterns. Atchley (1998) showed that different selection pathways could lead to different individual growth patterns in mice. Another example is in broilers; where Mignon-Grasteau et al. (2000) selected broilers on bodyweight at 8wk of age, and on bodyweight at 36wk of age. Broilers selected on bodyweight at 8wk of age had higher maturation rates, while broilers selected on bodyweight at 36wk of age had higher asymptotic weights. The age difference between 8wk and 36wk is about 100d, Mignon-Grasteau (2000) clearly demonstrated that it is possible to change growth patterns in broilers. Oksbjerg et al. (2000) compared the current form of the Danish Landrace pig with the Danish Landrace pig of 25 years ago to study the effect of selection. Twenty-five years ago, Danish Landrace pigs grew slower, also a change in growth patterns. In her research in beef cattle Meyer (1999) concludes that weight of adult cows throughout their lives cannot be regarded as repeated measurements of a single trait with constant variance and heritability. Knap (2000) states that over the past decades, body protein mass, and

growth rate are increased, while mature body weight of pigs has decreased. Fast growing pigs put on more fat than slow growing pigs, faster growing pigs have a higher average daily gain and a higher average daily feed intake (Woltmann et al., 1992). It could be possible to change carcass characteristics through selection on growth and feed intake patterns.

Pool (2000) showed for lactation records of dairy cows that when interval between milk-recordings increased it is harder to predict daily milk yield. Pool (2000) also found that it is important to include information about test-day records at the end of lactation period, in order to get accurately estimated parameters for the whole trajectory. This is in line with our study, information over the whole period is necessary to be able to estimate accurate breeding values. From Figure 2 it is clear that when there is no information, correlation between true and estimated breeding values drops quickly. Which is reflected in Table 3, when genetic correlation between days of age was high, the interval between measurements could be increased without loss of information. There was no difference in achieved genetic gain between recording strategies IV01, IV05 and IV10, and started to decrease with recording strategy IV25. However when the genetic correlation between days of age was decreasing more rapidly, the cost of increasing the interval between measurements was higher (Table 3). The length of the test period could be reduced depending on the trait of interest and the underlying genetic correlation assumed (Table 4).

A constant heritability of 0.33 over the whole age-range was assumed. Huisman et al. (2002) estimated a heritability of around 0.17 for body weight of pigs for the age trajectory 50d through 225d of age using random regression models, the genetic correlation structure in this data set was similar to correlation structure one. Although the genetic correlations in correlation structure one were high, there still was half a genetic standard deviation difference between EG and LG at day 1 (Figure 3). These differences will be smaller when heritabilities are lower.

From the two assumed genetic correlation structures, correlation structure one is probably the most realistic structure. But even under the assumption of correlation structure one some extra genetic gain is achievable. Assuming that common practice in pig breeding world is recording strategy 75-1 and in an advantageous situation strategy IV45. Moving from strategy 75-1 to IV45 for TG results in an extra 6-7% genetic gain after 3 generations. Moving to a strategy where even more measurements are taken could result in a 12% increase in genetic gain.

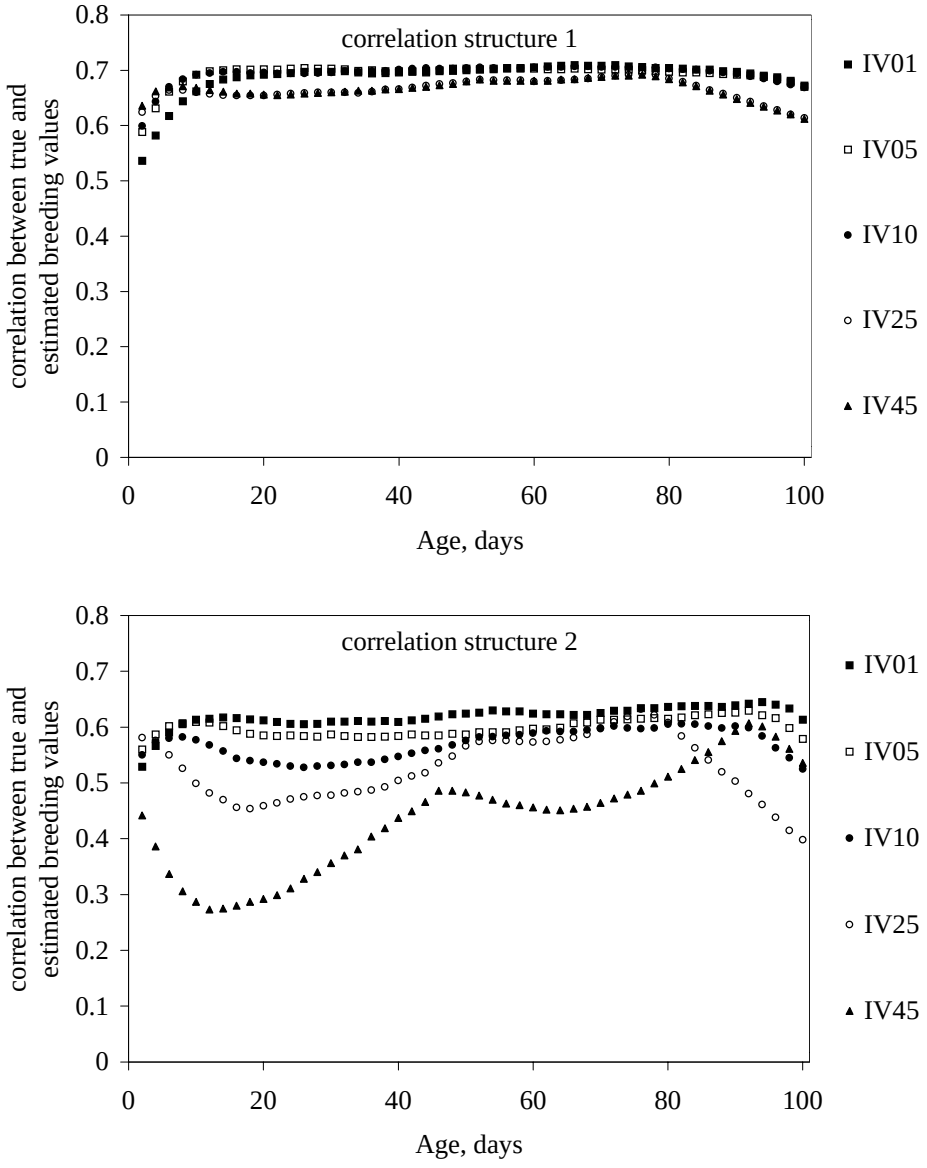

Figure 1. Correlation between true and estimated breeding value at all ages for different measurement designs and both genetic correlation structures (pedigree design: S08).

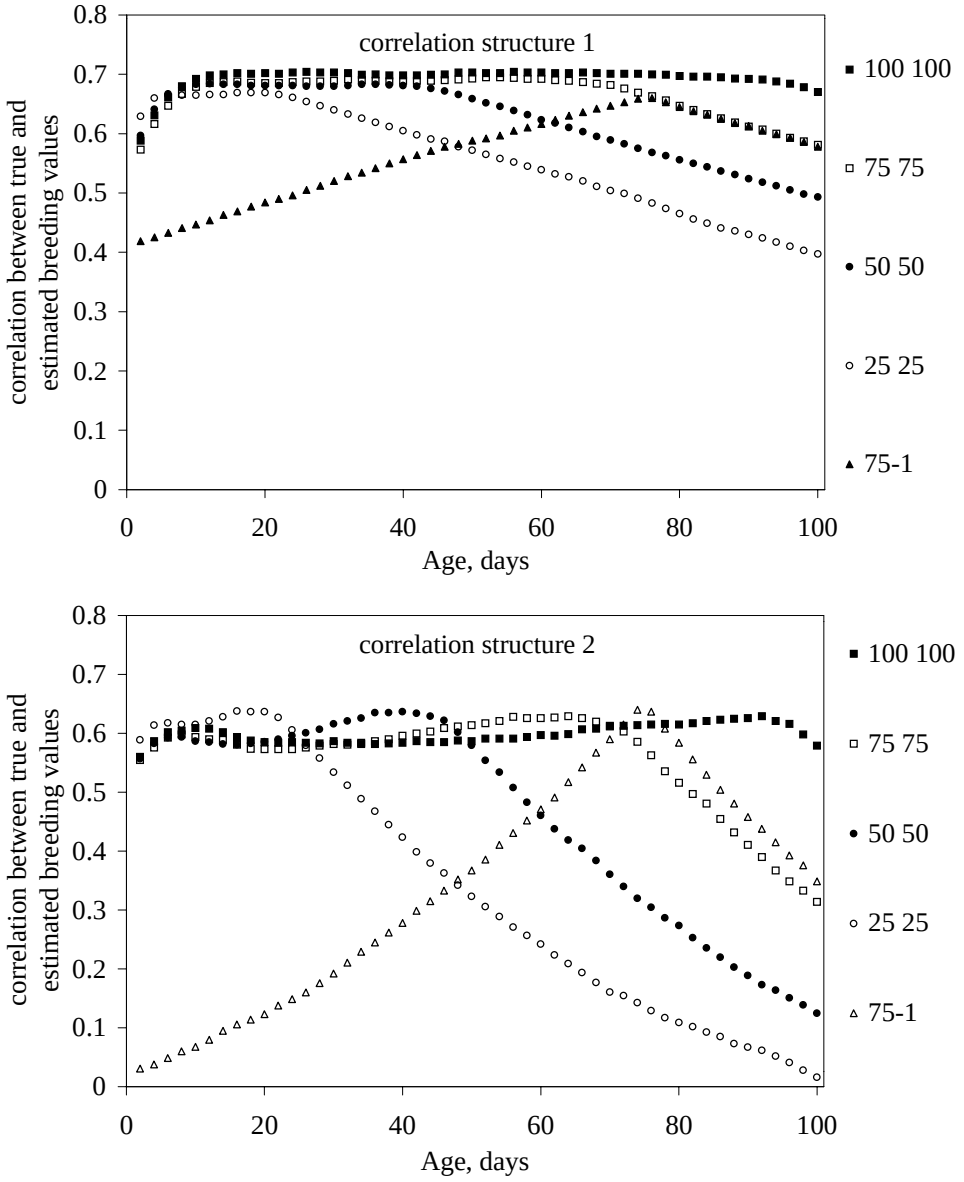

Figure 2. Correlation between true and estimated breeding value at all ages for all sampling strategies and both genetic correlation structures (pedigree design: S08, measurement design: IV05).

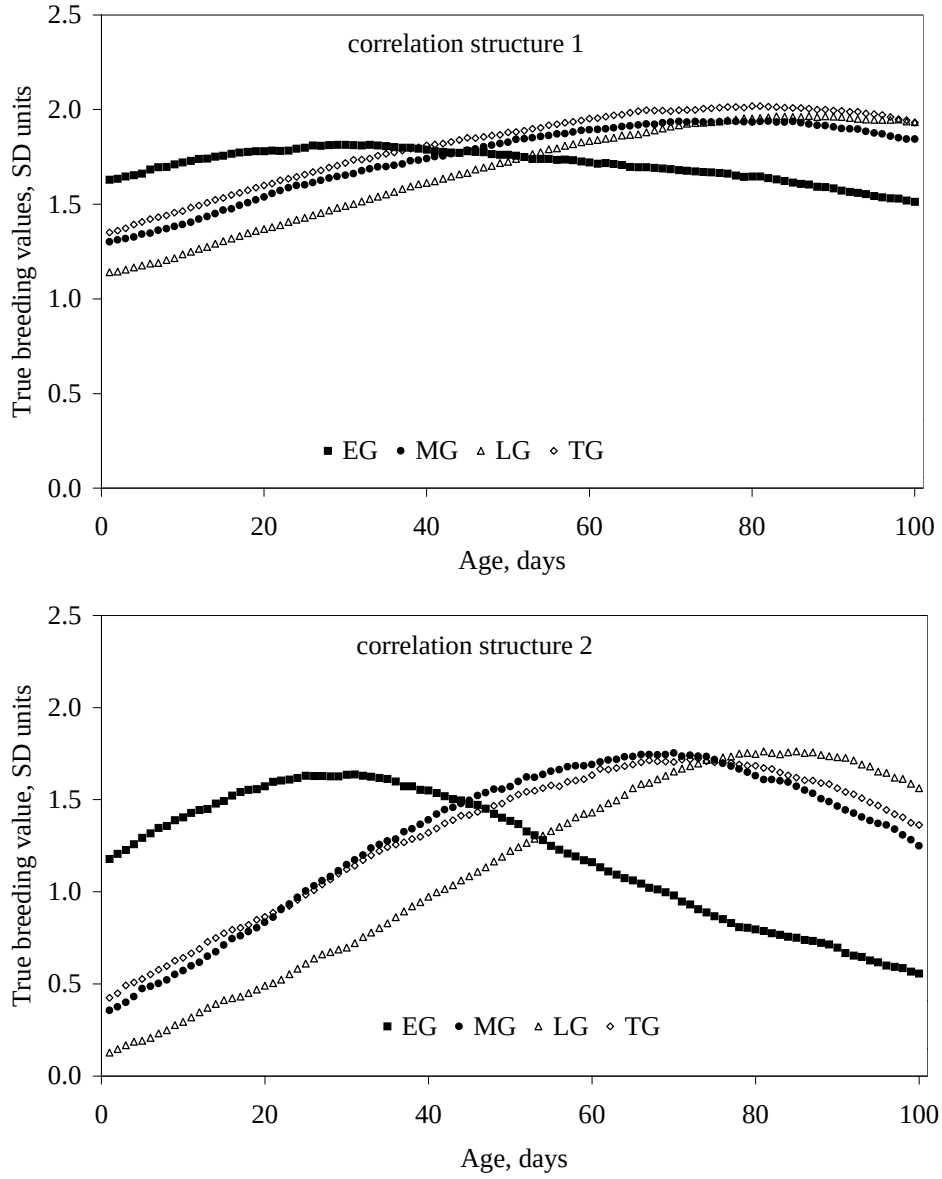

Figure 3. Breeding value patterns after 3 generations of selection for EG, MG, LG and TG (in SD units, pedigree design: S08, measurement design: IV05).

Implications

When selection is on part of a curve it is necessary to have measurements in that age period. Depending on the genetic correlation structure it is possible to enlarge the age gap between subsequent measurements and achieve about the same genetic gain as with smaller intervals between subsequent measurements. When the genetic correlation decreases more rapidly between adjacent ages the interval between subsequent measurements must not become to big. When fewer phenotypes were recorded the correlation between true and estimated breeding values drops immediately. Main conclusion from this study is that it is possible to change patterns through selection, the level of change is highly dependent on the underlying genetic structure. With lower genetic correlations between days of age, opportunities to change part of a performance pattern are more likely. Doing more measurements resulted in higher genetic gain; increments up to approximately 10% in genetic gain are possible.

Acknowledgements

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Chapter 6

Multivariate random regression to describe daily gain, daily feed intake and feed efficiency as function of weight in growing pigs

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To be submitted

Abstract

Objectives of this study were to describe daily gain and feed intake as a function of weight using random regression models, and to derive variance components for feed efficiency at different weights from the estimated variance components of daily gain and daily feed intake. Data were boars tested for a 7-week period, with an adjustment period one week prior to test. Pigs entered the test at an average live weight of 71.3 kg ± 9 kg. Pigs were fed restricted by scale-equiped electronic feeders. Individual feeder visits of each pig were used to derive daily records. Only pigs that had at least 10 weight records were kept to fit a quadratic curve of weight over age, daily gain was derived from this curve. In the random regression analysis daily gain and daily feed intake were modeled as a function of live weight using spline functions. When variances and covariances of daily gain and daily feed intake are known for all weights, it is possible to approximate variances for feed efficiency, which is defined as gain divided by feed intake. Genetic correlations between daily gain at different weights were not different from one. However, genetic variance and heritability differed between weights. Phenotypic correlations between daily gain at different weights decreased with an increase in weight interval. Heritability of daily gain was highest (0.18) between 105 and 110 kg. Genetic correlations between daily feed intake at different weights decreased with increase in weight interval, phenotypic correlations between daily feed intake at different weights were low. Highest heritability (0.18) of daily feed intake was found between 80 and 90 kg. Highest heritability (0.18) for feed efficiency was found between 100 and 115 kg. Genetic correlation between daily gain and feed efficiency increased with weight, phenotypic correlations decreased slightly. Genetic and phenotypic correlations between daily feed intake and feed efficiency were fairly constant for this weight trajectory, phenotypic correlation decreased slightly at end of weight trajectory. In general, variance components for all three traits decreased with increased weights. In this evaluation system, where pigs have restricted access to feed, when selection is on daily gain, daily feed intake will decrease.

Keywords: body weight, regression, feed intake, weight gain, efficiency.

Introduction

An important goal in pig breeding is to breed pigs that grow much lean meat in a short amount of time, preferably with low feed consumption. To select pigs for this breeding goal, pigs usually are tested over a fixed weight- or age trajectory, under the assumption that traits, like gain and feed intake, are genetically the same and that parameters do not change over the test period. Although this is likely to be true for short test periods, for longer test periods this does not hold (e.g. Huisman et al., 2002a and 2002b). Growth and voluntary feed intake do change genetically during the lifetime of a pig (Huisman et al. 2002b). Growth rate depends on age and size of the animal (Emmans and Kyriazakis, 1998). When pigs are able to express their full growth potential, growth rate follows a parabolic curve. Growth rate increases with increasing live weight until maximum growth rate is achieved, after which growth rate decreases. Daily feed intake is increasing with live weight, maximum feed intake will be achieved when a pig reaches about one half of its mature size (Emmans, 1995), after which voluntary feed intake decreases until mature weight is reached and voluntary feed intake stabilises. Feed efficiency, which is defined as the ratio of gain and feed intake, decreases with increasing live weight until an approximate constant feed efficiency is reached.

It has been shown that genetic parameters for daily feed intake and daily gain vary with age, and thus can these traits not be considered as same trait over a certain test period (e.g. Huisman et al., 2002b). When daily gain and daily feed intake are analysed in multivariate way, estimated covariances between daily gain and daily feed intake are also available, that makes it possible to derive variances for feed efficiency at different weights as well. Estimating genetic parameters for daily gain and daily feed intake as function of weight using random regression models has not been done before; it may lead to new insights regarding weight range and length of test period.

Objectives of this study were to describe daily gain and feed intake as a function of weight using random regression models, and to derive variance components for feed efficiency at different weights from the estimated variance components of daily gain and daily feed intake.

Material and Methods

General

QAF Meat Industries routinely records live weight and daily feed intake during test using scale equipped electronic feeder stations. With this data it is possible to study patterns in growth and feed intake and how growth and feed intake interact during the test period. Boars were tested for a 7-week period, with the week prior to test being an adjustment period to their new environment. All eight weeks were included in the analysis. Pigs entered the test at an average live weight of 71.3 kg ± 9 kg. Based on their weight at start of test pigs were assigned to a certain feeding level (target was 80% of ad libitum intake). Feeding levels were increased by 100 g each week. If an animal did not completely eat its daily allowed amount of feed; it was allowed to eat it the next days. Once a week, when feeding levels were increased, the amount of feed that was not eaten was discarded. Energy content of the diet was 13.5 MJ/kg ME. Pigs were of three sire lines with different genetic backgrounds. Pigs were tested in 29 batches of about 60 pigs each. Pigs of each batch were evenly distributed over two pens. Every week a new batch of pigs entered the test. Each pen contained three electronic feeder stations of which at least one was equipped with a weight scale. For a detailed description of the feeder stations see, McSweeny et al. (2001). Data were collected between February 2001 and October 2001. Of each pig daily feed intake was determined by accumulating the records of each visit to the feeder station per pig per day on test. Individual daily live weight was determined by averaging the individual weight records of per pig per day on test. For live weight measured on subsequent test days, measurements that were 5 kg or more below or above the previous measurement were considered outliers, and excluded from the analysis. Only pigs that had at least 10 daily live weight records were kept in the data set to fit a quadratic curve of live weight over age. Daily gain for each weight measurement was derived from this curve. Only feed intake records that also had a live weight measurement at the same day were kept. All records with live weight lower than 60 kg or greater than 120 kg were excluded from the analysis. After editing, the data set contained 1581 pigs with approximately 33 daily gain and daily feed intake records per animal.

Random regression model

In the random regression analysis daily gain and daily feed intake were modeled as a function of live weight using spline functions. The program ASREML (Gilmour et al., 2001) fits splines as described by Verbyla et al. (1999). This resulted in the following model:

$$y_{ijk} = Fixed + u_{i0} + u_{i1} + \sum_{l=2}^{q-1} u_{il} z_l(t_{ij}) + p_{i0} + p_{i1} + \sum_{l=2}^{q-1} p_{il} z_l(t_{ij}) + e_{ik} \quad [1]$$

where y_{ijk} is the trait (daily gain or daily feed intake) recorded for animal i at age j and week k, *Fixed* represents the fixed effects for each trait as described under the heading Fixed effects, u_{i0} represents the intercept for animal i, u_{i1} represents the slope for animal i, and u_{il} represent the random regression coefficient for animal i at knot l. The p_{i0} represents the intercept for permanent environment i, p_{i1} represents the slope for permanent environment i and p_{il} represents the random regression coefficient for permanent environment i at knot l. Permanent environment i is equal to the non-genetic individual animal effect. The $z_l(t_{ij})$ represent the spline coefficients for age t_{ij} and q represents an index number for the knotpoints. For the error term, records were divided in 12 weight ranges of 5 kg each, which was denoted by e_{ik}, for an observation at animal and permanent environment i in weight range k. In matrix notation [1] can be written as:

$$\mathbf{y} = \mathbf{X\beta} + \mathbf{Z_s u} + \mathbf{Z_s p} + \mathbf{e} \quad [2]$$

where **y** is a vector containing the observations, **β** is the vector containing the fixed effects, **u** is a vector containing the estimates for genetic spline effects and **p** is a vector containing the estimates for permanent environmental spline effects and **e** is the vector with error terms. **X**, and $\mathbf{Z_s}$ are incidence matrices relating **y** to **β**, **u**, and **p**. $\mathbf{Z_s}$ is an incidence matrix that contains the random regression coefficients, the spline coefficients for each observation in blocks of animals.

Fixed effects

Spline functions were also used to model the fixed effects. For daily gain and daily feed intake the same used fixed effect model was used. Two average curves were fitted for both traits, one as a spline function of live weight, and one as a spline function of age. Both average curves were spline functions with 12 evenly distributed knotpoints, corresponding to the 12 error terms. Other fixed effects were line, week of test, feeding level and

management group, the interaction between pen and batch. For all the latter fixed effects a spline function with six knotpoints was used. The knotpoints were evenly spread over the trajectories for all spline functions.

Derivation of feed efficiency

When variances and covariances of daily gain and daily feed intake are known for all weights, it is possible to approximate variances for feed conversion ratio and feed efficiency, both are ratios of gain and feed intake. The delta method yields a good approximation for the variance of a ratio (Stuart and Ord, 1994). The variance of feed efficiency (daily gain divided by daily feed intake) at any given weight can be approximated by:

$$\sigma^2\left(\frac{DG}{DFI}\right) \cong \left(\frac{\mu_{DG}}{\mu_{DFI}}\right)^2 \left(\frac{\sigma^2_{DG}}{\mu^2_{DG}} + \frac{\sigma^2_{DFI}}{\mu^2_{DFI}} - \frac{\sigma_{DG,DFI}}{\mu_{DG}\mu_{DFI}}\right) \quad [3]$$

where $\sigma^2\left(\frac{DG}{DFI}\right)$ is the variance of feed efficiency, μ_{DG} is the average daily gain, μ_{DFI} is the average daily feed intake, σ^2_{DG} is the variance of daily gain, σ^2_{DFI} is the variance of daily feed intake and $\sigma_{DG,DFI}$ is the covariance between daily gain and daily feed intake. The phenotypic correlations between feed efficiency and daily gain at any weight can be approximated by (Gunsett, 1984):

$$r_{FE,DG} \cong \frac{C^2_{DG} - r_{DG,DFI} C_{DG} C_{DFI}}{C_{DG}\sqrt{C^2_{DG} + C^2_{DFI} - 2r_{DG,DFI} C_{DG} C_{DFI}}} \quad [4]$$

where C_x (σ_x / μ_x) was the coefficient of variation of trait *x*, and $r_{DG,DFI}$ the correlation between daily gain and daily feed intake. The phenotypic correlations between feed efficiency and daily feed intake at any given weight were derived using the same approximation methods. Genetic correlations between feed efficiency and daily feed intake at any weight can be approximated by (Gunsett, 1984):

$$r_{G:FE,DFI} \cong \frac{r_{G:DG,DFI} h_{DG} C_{DG} h_{DFI} C_{DFI} - h^2_{DFI} C^2_{DFI}}{h_{DFI} C_{DFI}\sqrt{h^2_{DG} C^2_{DG} + h^2_{DFI} C^2_{DFI} - 2r_{G:DG,DFI} h_{DG} C_{DG} h_{DFI} C_{DFI}}} \quad [5]$$

where C_x was as before, $r_{G:DG,DFI}$ was the estimated genetic correlation between feed efficiency and daily feed intake, h^2 was the estimated heritability for daily gain or daily feed

intake at any given weight. Genetic correlation between feed efficiency and daily gain at any weight can be derived using the same approximation method.

Table 1. Means and standard deviation of daily gain, daily feed intake and feed efficiency for different weight ranges.

	Daily gain (kg/d)		Daily feed intake (kg/d)		Feed efficiency	
Weight range	Mean	STD	Mean	STD	Mean	STD
60-65kg	0.79	0.26	1.56	0.56	0.51	0.28
65-70kg	0.79	0.26	1.72	0.53	0.46	0.23
70-75kg	0.78	0.24	1.84	0.49	0.43	0.20
75-80kg	0.77	0.24	1.93	0.48	0.40	0.17
80-85kg	0.76	0.22	2.03	0.46	0.38	0.15
85-90kg	0.77	0.20	2.11	0.46	0.36	0.14
90-95kg	0.77	0.18	2.20	0.45	0.35	0.12
95-100kg	0.78	0.18	2.25	0.46	0.35	0.12
100-105kg	0.80	0.16	2.31	0.47	0.35	0.11
105-110kg	0.82	0.15	2.40	0.48	0.34	0.11
110-115kg	0.84	0.16	2.46	0.47	0.35	0.11
115-120kg	0.87	0.15	2.50	0.50	0.35	0.11

Results

Raw means for daily gain, daily feed intake and feed efficiency in different weight ranges are in Table 1. Lowest value for daily gain was between 80 and 85 kg. From 85 kg on daily gain was increasing from 0.76 kg/d to 0.87 kg/d. Standard deviation for daily gain decreased with increasing live weight. Daily feed intake increased from 1.56 kg/d at a live weight of 60 to 65 kg to 2.50 kg/d at a live weight of 115 to 120 kg. Standard deviation decreased with increasing live weight to reach a minimum between 90 and 95 kg. After 95 kg standard deviation for daily feed intake increased again. Feed efficiency decreased with increasing live weight, from approximately 0.5 at start of the weight trajectory to 0.35 at 90

Table 2. Variance component and heritability estimates for daily gain, daily feed intake and feed efficiency at different weights [A].

Weight (kg)	Daily gain (kg/d)^2			Daily feed intake (kg/d)^2			Feed efficiency		
	$\sigma_A^{2\,B}$	$\sigma_{PE}^{2\,B}$	h^2	$\sigma_A^{2\,B}$	$\sigma_{PE}^{2\,B}$	h^2	$\sigma_A^{2\,B}$	$\sigma_{PE}^{2\,B}$	h^2
62.5	5.7	114.1	0.05	44.6	50.6	0.15	6.8	52.1	0.09
67.5	5.7	96.1	0.06	40.7	28.7	0.15	4.9	35.2	0.09
72.5	5.8	80.9	0.07	39.7	21.0	0.17	3.9	25.0	0.10
77.5	5.8	68.0	0.08	40.5	22.6	0.17	3.3	18.6	0.11
82.5	5.9	57.0	0.09	41.6	26.6	0.18	3.0	14.2	0.13
87.5	6.0	47.9	0.11	41.9	28.6	0.18	2.7	10.9	0.14
92.5	6.1	40.4	0.13	41.6	28.8	0.17	2.5	8.7	0.16
97.5	6.1	34.7	0.15	40.7	27.4	0.17	2.3	7.1	0.17
102.5	6.1	30.7	0.17	39.1	23.9	0.17	2.2	6.0	0.18
107.5	6.2	28.7	0.18	37.8	22.9	0.15	2.0	5.4	0.18
112.5	6.3	29.1	0.17	38.2	31.1	0.15	2.0	5.6	0.18
117.5	6.4	32.1	0.17	41.6	53.6	0.14	2.0	6.5	0.16

[A] where σ_A^2 is the additive genetic variance; σ_{PE}^2 is the permanent environmental variance, due to the non-genetic animal effect; and h^2 is the estimate of the heritability.
[B] estimated variance components $\times 10^{-3}$

kg of live weight. After 90 kg of live weight was reached, feed efficiency was fairly constant. Standard deviation for feed efficiency followed a similar pattern.

With increasing weight genetic variance of daily gain increased slightly and permanent environmental variance of daily gain decreased (Table 2). Total variance of daily gain decreased with an increase in weight, and was lowest around 105-110 kg. Heritability of daily gain was highest for the weight range 105-110 kg (0.18), and lowest around start of the weight trajectory (0.05) (Table 2). Genetic correlations between daily gain at different weight were almost equal to one, indicating that an animal with a high breeding value for gain measured at lower weights is expected to have a high breeding value for gain measured at later weights as well, while phenotypic correlations between daily gain at different weights decreased with an increasing interval between weights (Table 3). The phenotypic

Table 3. Estimates of genetic and phenotypic correlations for daily gain at different weights[A].

		Weight (kg)											
		62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5	102.5	107.5	112.5	117.5
Weight (kg)	62.5	-	1.00	0.99	0.99	0.98	0.98	0.98	0.98	0.98	0.99	0.99	0.99
	67.5	1.00	-	1.00	1.00	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	72.5	0.98	0.99	-	1.00	1.00	1.00	0.99	0.99	0.99	0.99	0.99	0.99
	77.5	0.97	0.98	0.99	-	1.00	1.00	1.00	1.00	1.00	0.99	0.99	0.99
	82.5	0.94	0.96	0.98	0.99	-	1.00	1.00	1.00	1.00	0.99	0.99	0.98
	87.5	0.90	0.93	0.95	0.97	0.99	-	1.00	1.00	1.00	0.99	0.99	0.98
	92.5	0.85	0.88	0.91	0.94	0.97	0.98	-	1.00	1.00	1.00	0.99	0.98
	97.5	0.77	0.81	0.85	0.89	0.92	0.96	0.98	-	1.00	1.00	0.99	0.98
	102.5	0.68	0.73	0.77	0.81	0.86	0.91	0.95	0.98	-	1.00	1.00	0.99
	107.5	0.57	0.61	0.66	0.71	0.77	0.82	0.88	0.94	0.98	-	1.00	0.99
	112.5	0.43	0.48	0.53	0.58	0.64	0.71	0.78	0.85	0.92	0.97	-	1.00
	117.5	0.29	0.34	0.38	0.44	0.50	0.58	0.66	0.75	0.84	0.92	0.97	-

[A] Estimates for genetic and phenotypic correlations are respectively above and below the diagonal

correlations between lower weights seemed to be somewhat stronger than the phenotypic correlations between higher weights.

Genetic variance of daily feed intake at different weights seems to be rather constant over this weight trajectory (Table 2). Variance due to the permanent environment (the non-genetic animal effect) was highest at both ends of the trajectory, and fairly constant in between (Table 2). Heritability of daily feed intake was highest between approximately 80 and 90 kg of live weight, and lower towards both ends of the trajectory (Table 2). Genetic correlations between daily feed intake at different weights decreased with an increasing interval between weights, lowest genetic correlations between daily feed intake at different weights were found for the weight range 80 to 100 kg with both ends of the weight

Table 4. Estimates of genetic and phenotypic correlations for daily feed intake at different weights [A].

		Weight (kg)											
		62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5	102.5	107.5	112.5	117.5
Weight (kg)	62.5	-	0.98	0.93	0.87	0.82	0.79	0.78	0.79	0.82	0.86	0.88	0.87
	67.5	0.28	-	0.98	0.95	0.91	0.88	0.87	0.87	0.88	0.90	0.90	0.88
	72.5	0.23	0.24	-	0.99	0.97	0.95	0.93	0.92	0.92	0.92	0.90	0.85
	77.5	0.18	0.21	0.25	-	0.99	0.98	0.96	0.95	0.94	0.92	0.88	0.81
	82.5	0.13	0.18	0.24	0.27	-	1.00	0.98	0.96	0.95	0.92	0.87	0.78
	87.5	0.10	0.16	0.22	0.26	0.29	-	0.99	0.98	0.96	0.93	0.87	0.77
	92.5	0.08	0.13	0.19	0.23	0.27	0.29	-	1.00	0.98	0.95	0.88	0.78
	97.5	0.07	0.12	0.17	0.21	0.24	0.27	0.29	-	0.99	0.97	0.91	0.81
	102.5	0.07	0.11	0.14	0.17	0.21	0.24	0.26	0.27	-	0.99	0.94	0.86
	107.5	0.08	0.10	0.12	0.14	0.16	0.19	0.21	0.23	0.25	-	0.98	0.93
	112.5	0.10	0.10	0.10	0.11	0.12	0.14	0.16	0.19	0.22	0.25	-	0.98
	117.5	0.10	0.09	0.08	0.07	0.07	0.08	0.10	0.13	0.17	0.23	0.28	-

[A] Estimates for genetic and phenotypic correlations are respectively above and below the diagonal

trajectory (Table 4). Phenotypic correlations between daily feed intake at different weights were low and rapidly decreasing when the interval between weights became larger (Table 4).

The genetic correlation between daily gain and daily feed intake decreased with increasing weight (Figure 1). Phenotypic correlations between daily gain and daily feed intake were highest between daily gain at lower weights and daily feed intake at higher weights and between daily feed intake at lower weights and daily gain at higher weights.

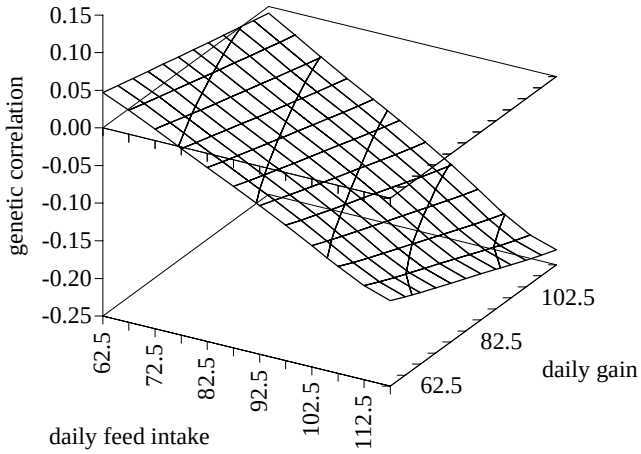

Figure 1. Estimates of the genetic correlation between daily gain and daily feed intake at different weights.

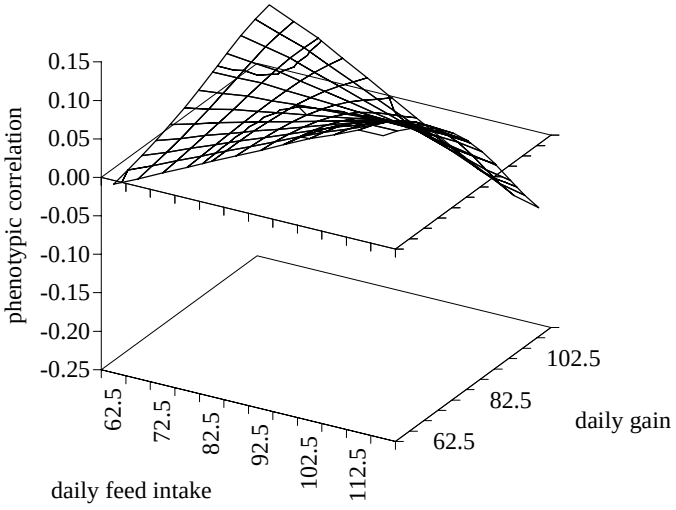

Figure 2. Estimates of the phenotypic correlation between daily gain and daily feed intake at different weights.

Table 5. Derived genetic (r_g) and phenotypic (r_p) correlations between daily gain, daily feed intake and feed efficiency at different weights.

Weight (kg)	Daily gain and feed efficiency		Daily feed intake and feed efficiency	
	r_g	r_p	r_g	r_p
62.5	0.55	0.79	-0.81	-0.62
67.5	0.62	0.80	-0.77	-0.59
72.5	0.66	0.81	-0.75	-0.56
77.5	0.70	0.80	-0.73	-0.56
82.5	0.72	0.80	-0.72	-0.56
87.5	0.74	0.78	-0.72	-0.58
92.5	0.76	0.77	-0.72	-0.60
97.5	0.78	0.76	-0.72	-0.62
102.5	0.80	0.75	-0.72	-0.65
107.5	0.81	0.74	-0.73	-0.68
112.5	0.82	0.76	-0.74	-0.70
117.5	0.81	0.75	-0.76	-0.73

Phenotypic correlation between daily gain and daily feed intake at the same weight decreased with an increase in weight (Figure 2).

Variance components for feed efficiency decreased with weight; permanent environmental variance decreased a lot faster than the genetic variance (Table 2). Heritability of feed efficiency increased with increasing weight and reached a maximum somewhere in the weight range 100-115 kg (Table 2), which was approximately in the same weight range as where highest heritability for daily gain was found.

Derived correlations between feed efficiency and daily gain at all weights and between feed efficiency and daily feed intake at all weights are in Table 5. Genetic correlations between feed efficiency and daily gain at a weight were positive and increased with an increase in weight. Phenotypic correlations between feed efficiency and daily gain at a given weight were fairly constant over the weight trajectory, but slightly decreasing towards the end of the weight trajectory. The correlations between feed efficiency and daily

feed intake were negative at all weights. Genetic correlations were fairly constant over the weight trajectory, phenotypic correlations decreased with an increase in weight.

Discussion

Daily gain seemed to be genetically constant throughout the weight trajectory, genetic correlation did not go under 0.98, while the estimated variances decreased with weight (Tables 2 and 3). Huisman et al. (2002b) described daily gain as function of age and found that heritability of daily gain as function of age was highest (at a value of 0.17) somewhere between 145 d and 152 d of age, which corresponded with a live weight of approximately 90 kg. However, when daily gain was modeled as function of weight, highest heritability was found somewhere between 105 kg and 110 kg of live weight. Because the data used in this study and in Huisman et al. (2002b) was practically the same, the difference should be explained by the difference in used models. In this study an average curve was fitted for both weight and age, while all other fixed effects where modeled as functions of weight. Huisman et al. (2002b) only fitted fixed effects as functions of age. Heritabilities found in this study and heritabilities presented by Huisman et al. (2002b) were of similar magnitude. The correlations, both genetically and phenotypically, between daily gain at different weights appear to be somewhat higher than between daily gain at different ages.

Voluntary feed intake is depending on a lot of factors; such as body weight, breed, sex, and temperature (Quiniou et al., 2000), while restricted feed intake is mainly based on the level of restriction. Hermesch et al. (1999) estimated genetic parameters for performance traits of pigs recorded under an ad libitum and a restricted feeding regime, there was a genotype by feeding regime interaction for feed intake and feed conversion ratio, while no genotype by feeding regime was found for two different measures of average daily gain. The estimated variance components were reduced under the restricted feeding regime. The raw means of daily feed intake show an increase of approximately 100 g each weight range, except between 90 and 105 kg, where the increase in average daily feed intake is somewhat lower. Irgang et al. (1992) showed that gilts of various pig breeds almost all reached puberty somewhere between 90 and 100 kg of live weight. It could be that the boars in this study reached puberty at about the same weight range and therefore ate less. Heritabilities for

daily feed intake were somewhat higher when daily feed intake was modeled as function of weight instead of age, as in the study of Huisman et al. (2002b). Heritability for daily feed intake was highest between 80 and 90 kg, at an age of approximately 140 d., Huisman et al. (2002b) found that heritability of daily feed intake was highest between 131 and 138 d of age, which corresponded to a live weight of approximately 80 kg. Kalm et al. (1996) split the test trajectory in five periods of two weeks and found that the heritability of daily feed intake was highest between 77 and 91 kg live weight. Both were roughly equal to the findings in this study. Von Felde et al. (1996) estimated genetic parameters for daily feed intake of ad libitum fed pigs during a 10 wk test period, and found that heritability of daily feed intake increased until about mid-test and decreased afterwards. A similar pattern as was found in this study, however the heritability estimates by Von Felde et al. (1996) were somewhat higher than the estimates presented in this study. A possible explanation for the lower heritabilities at beginning of the weight trajectory (Table 2) could be that at start of test pigs did not know how to get feed out of the feeders and restrict themselves.

Schulze et al. (2001) estimated genetic parameters for daily gain and daily feed intake in ad libitum fed pigs. Genetic correlation between daily gain and daily feed intake were about 0.5 for all weeks (tested over 10 weeks). Schulze et al. (2002) found in pigs with ad libitum access to feed that the genetic correlation between average daily gain and daily feed intake (measured in 10 weeks) was low (±0.1) in the first week and about 0.6 in the other weeks, slightly decreasing towards end of test. Huisman et al. (2002b) found that the genetic correlation between daily gain and daily feed intake at different ages was fairly constant at about 0.3, while phenotypic correlation was at its highest (0.14) around 150d. In this study the genetic correlation between daily gain and daily feed intake was decreasing with weight. Estimates for genetic correlations were small and ranged from –0.23 to 0.05. This indicates that animals that have a high breeding value for daily gain at lower weights tend to have a 'low' breeding value for daily feed intake at higher weights. This could mean that in this evaluation setting faster growing animals had a more restricted access to feed than slower growing animals towards the end of the weight trajectory. Figure 3 demonstrated that when selection is on average daily gain in this evaluation system, daily feed intake would reduce with increasing weight. If animals were selected on average daily feed intake, daily feed intake would increase, while daily gain at higher weights would slightly decrease.

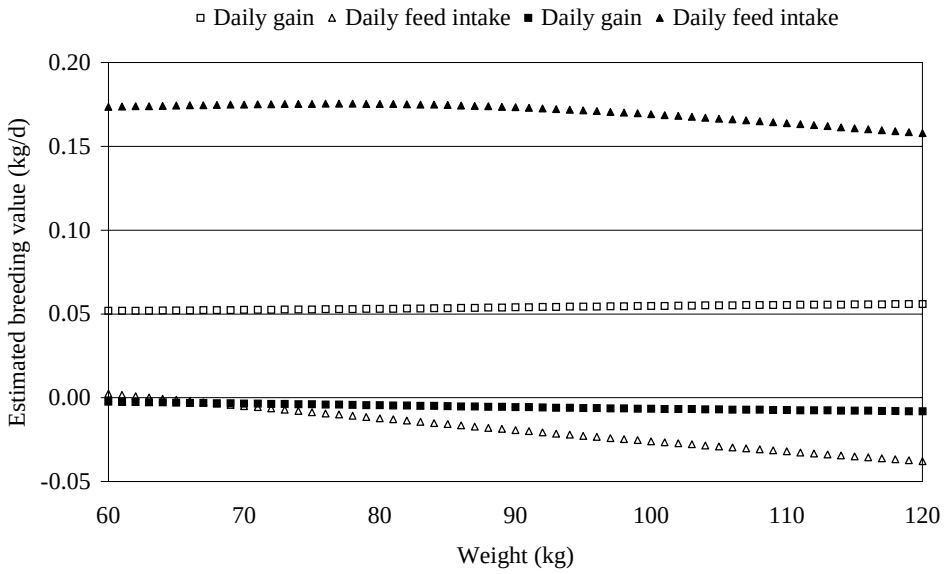

Figure 3. Estimated breeding values for the 10% highest-ranking animals for average daily gain (open symbols) and for average daily feed intake (closed symbols).

Average feed efficiency decreased with increasing weight and age. Flipot et al. (1992) stated that feed efficiency was not significantly affected by feeding level. Others (Chiba et al., 2002) state that efficiency is depending on the offered diet. Roehe et al. (1994) showed that heritability of feed conversion ratio was highest at about 120 d of age, while in this study heritability of feed efficiency was highest between 100 and 115 kg of live weight, roughly equal to an age of 160 to 165 d. Schulze et al. (2001) found that the heritability of feed conversion ratio was highest mid test, at an approximate weight of 70 kg. Kanis and Koops (1990) modeled phenotypic feed efficiency as function of weight and did not find differences in feed efficiency values between restricted and ad libitum fed pigs, except for the higher weights (100 kg), where the restricted fed pigs were somewhat more efficient. Hermesch et al. (1999) found no significant difference in heritability between feed conversion ratio (which is the inverse of feed efficiency) under an ad libitum feeding and a restricted feeding regime. The differences in parameters found between this study and the

studies of Roehe et al. (1994) and Schulze et al. (2001) could very well be explained by the method used to derive variance components for feed efficiency.

The high correlations, both genetic and phenotypic, between feed efficiency and daily gain and between feed efficiency and daily feed intake were due to high overlap that exists between feed efficiency and its component traits. Clutter and Brascamp (1998) reported an average genetic correlation of –1.0 between average daily gain and feed conversion ratio over test in pigs restricted with access to feed. Which would translate to an average genetic correlation of 1.0 between average daily gain and feed efficiency over test, since feed conversion ratio and feed efficiency are opposites of each other. Schulze et al. (2001) found, in pigs with ad libitum access to feed, that genetic correlation between feed conversion ratio and daily gain was lowest in the first week of test (-0.82), increased in the third week to -0.32 after which it decreased again to -0.51 in the ninth week. We found that the genetic correlation between daily gain and feed efficiency increased with weight, that indicates that faster growing pigs used their feed more efficient. This means that in this evaluation system the pigs with the higher growth rates were also the more efficient pigs.

Von Felde et al. (1996) found that genetic correlations between daily feed intake measured in 10 weeks and feed conversion ratio over test were about zero, slightly negative at start of test and slightly positive at end of test. Phenotypic correlations were decreasing over test. Hall et al. (1999) estimated correlations between feed intake measured in four biweekly periods and feed conversion ratio over test in pigs. The genetic correlation between the four periods and feed conversion ratio was fairly constant (0.6); phenotypic correlation was highest in the third period (0.24), roughly equal to a live weight range of 60 to 80 kg. Schulze et al. (2001) estimated genetic correlations, in pigs with ad libitum access to feed, between daily feed intake and feed conversion in different weeks on test, genetic correlation was negative in the first week, and about 0.5~0.6 in the other weeks. Genetic correlations between daily feed intake and feed efficiency that were estimated in our study were high and fairly constant over the whole weight trajectory.

Variance components for feed efficiency at different weights were derived from the estimated variance components for daily gain and daily feed intake at different weights using formula [3]. Gunsett (1987) showed that formula [3] leads to over- and underestimated heritabilities, depending on selection intensities estimated heritability could deviate as far as 15% from the simulated heritability. This demonstrates that formula [3] can only be used as an approximation of the true variance components. The heritability of a

quotient trait is expected to decrease with an increase in the phenotypic correlation between the original trait (Krieter and Presuhn, 1997), here we find that heritability of feed efficiency is increasing towards the higher weights, when phenotypic correlation is also decreasing (Figure 2). The genetic parameters of the ratio are determined from the numerator. For feed efficiency the numerator is daily gain, the estimated heritabilities for feed efficiency followed a similar pattern, and were of similar magnitude as heritabilities estimated for daily gain (Table 2).

Implications

Daily gain at lower weights were a good genetic predictor of daily gain at higher weights. Heritability of daily gain and feed efficiency was highest between 105 and 110 kg. Highest heritability of daily feed intake was found between 80 and 90 kg. In general, largest heritabilities for all three traits were estimated for the higher weight ranges. Permanent environmental variance components of daily gain, daily feed intake and feed efficiency were lowest for the higher weight ranges. Genetic correlations between daily gain and daily feed intake decreased with weight. Genetic correlations between feed efficiency and daily gain and feed efficiency and daily feed intake were high at all weights. In this evaluation system, where pigs have restricted access to feed, when selection is on daily gain, daily feed intake will decrease. Therefore this evaluation system will result in more efficient pigs through reduced feed intake.

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Chapter 7

General Discussion

Random regression models

General

In conventional animal breeding, both a repeatability model and a multivariate model have been applied to analyze traits that are measured over a trajectory. A repeatability model assumes genetic correlations of one between subsequent observations and a constant variance at all observations. A multivariate model assumes subsequent observations to be separate traits. Meyer (1999) concludes that weight of adult cows throughout their lives cannot be regarded as repeated measurements of a single trait with constant variance and heritability. A better way of dealing with traits that are measured over a trajectory is to fit a set of random coefficients of time or weight for each individual to allow for individual variation in the course of the trajectory (Meyer, 1998). These models are referred to as random regression models or covariance functions. The terms random regression model and covariance function are interchangeable (Van der Werf et al., 1998), i.e. these two terms are used to describe the same kind of model. In this thesis the term random regression model is used predominantly.

Several advantages of the use of random regression models are mentioned in the literature (Kirkpatrick and Heckman, 1989). Random regression models facilitate more accurate modeling of the variance-covariance structure of traits that change and/or are measured over a trajectory. Random regression models are able to predict covariance structures at any point along a continuous scale e.g. age or weight. With random regression models it is not necessary to correct towards certain landmark ages. As is the case when selection is on weight at a certain age, weights that are not recorded exactly at that age have to be corrected towards that age to allow for a better comparison between animals. Random regression models will make more efficient use of the available data. In addition random regression models will need fewer parameters to describe longitudinal data compared to a multivariate model. In comparison to a multivariate model, a random regression model estimates variances and covariances smoother and with less bias (Kirkpatrick et al., 1990). Main disadvantage of the use of a random regression model is the difficulty to extrapolate outside the trajectory in which parameters are estimated.

Animal breeders are interested in genetic parameters that describe the shape of curves that describe traits that are measured over a trajectory. Such parameters might give information on whether and how desirable changes in the course of such traits can be achieved. Random regression models provide a method for analyzing longitudinal records in animal breeding that reveal specific patterns of change over a trajectory (Kirkpatrick et al., 1990). Because the use of random regression models will lead to more accurate prediction of breeding values, a higher genetic progress should be possible. Schenkel et al. (2002) found no proof that random regression models would bring higher genetic progress. Although it was suggested that higher genetic progress could be achieved when random regression models were applied (Schenkel et al., 2002), because a random regression model allowed for a theoretically more complete model as well as for non-linear changes in daily gain. In the next section examples are given of the benefits of applying random regression models. The first two examples will deal with the effect of random regression models on accuracy of selection, while the third example will deal with the possibility to select on genetic differences in performance patterns.

Examples

Applying random regression models is expected to result in an increase in accuracy of selection compared to a multiple trait selection program. This is illustrated using parameters for live weight of growing pigs estimated by Huisman et al. (2002a). Estimates of variances, heritabilities and correlations can be found in Huisman et al. (2002a). The computer program SelAction (Bijma and Rutten, 2002) was used to calculate accuracy of selection on various indices. Breeding goal was weight at 190 days of age. Selection indices varied in number of measurements included per animal. Base selection index was the multivariate scenario where weight was measured at beginning (at 73±8.5 days of age) and end (at 190±8.7 days of age) of test. In the multivariate scenario weights were not exactly recorded on ages of interest. The range of age at measurement was approximately 50 days (Huisman et al., 2002a), whereas in the random regression scenario estimated breeding values for weight were available at all ages in the trajectory, using the same observations. In case of W1, which is weight recorded at an average age of 70 days, some animals had their weight recorded at 55 days of age and other animals had their weight recorded at 95 days of age. The same holds for traits W2 and W3. The weights W1, W2 and W3 were not corrected for age. Results in Table 1 show that accuracy of selection is improved when a random regression model is applied instead of a multivariate scenario. Largest increase in accuracy

Table 1. Accuracy of selection (r_{IH}) using various selection indices when the breeding goal is weight at 190 d of age [A].

Information in the index [B]						
Multivariate scenario						
W1		W2		W3	r_{IH}	Δr_{IH} [C]
✓				✓	0.466	-
✓		✓		✓	0.478	3%
random regression scenario						
W070	W100	W130	W160	W190	r_{IH}	Δr_{IH} [C]
✓				✓	0.497	7%
✓		✓		✓	0.523	12%
✓	✓	✓	✓	✓	0.526	13%

[A] Information sources were own performance, four full sibs and 45 half sibs, 10% of boars and 50% of sows were selected.

[B] W1 is first weight measurement at 73d±8.5d, W2 is second measurement at 134.7d±8.8d, and W3 is third measurement at 190.0d±8.7d for the multivariate scenario (Huisman et al. 2002), W070 represents weight at 70 d of age, W100 represents weight at 100 d, etc. for the random regression scenario.

[C] relative increase in accuracy of selection compared to index = W1 + W3.

of selection is achieved when a random regression model is applied and all weight measurements are included in the index. An increase in accuracy of selection will lead to higher genetic progress. When the whole population was weighed at beginning and end of age trajectory, i.e. at about 70 d and about 190 d of age, recording one extra weight at approximately 130 d of age improves accuracy of selection by about 2-3% for this example. However when these three weights are recorded and a random regression instead of a multivariate model is applied, the accuracy of selection increases from 3 % to 12 % above the base index for weight at 190 d (Table 1). Accuracy of selection in the multivariate scenario could be higher if weights were corrected for age. This shows that when weights are modeled as a function of age, weights do not have to be adjusted for age, and predictions are more accurate. Instead of measuring at exact ages, which is close to impossible in practice, random regression models can be applied to get more accurate estimates of breeding values for ages of interest. Weight gain can be calculated between the same ages for all animals, while it is not necessary to record weights at exact ages for all animals.

A second example is the inclusion of extra daily feed intake (DFI) measurements into a selection index, where the breeding goal is average DFI over test. Parameters estimated by Huisman and Van Arendonk (2002a) for DFI patterns were used. Genetic

parameter estimates are shown in Table 2. When measurements of actual daily feed intake at day five, day 50, and day 95 on test were included in the index. Accuracy of selection increased with 30% compared to an index with only average DFI over test in it. Average DFI can be calculated from the summed DFI at different days on test when animals are fed through electronic feeder stations. In this case DFI at almost all days on test is available for tested animals, it is useful and possible to include this information to get more accurate estimated breeding values, not only for average DFI but also for the shape of the DFI curve.

Table 2. Heritabilities (on diagonal) and correlations (below diagonal) and between derived traits for the model with four knotpoints for both random effects. (Taken from Huisman and Van Arendonk, 2002a).

	DFI_average	DFI05	DFI50	DFI95
DFI_average	0.22			
DFI05	0.66	0.53		
DFI50	0.89	0.37	0.28	
DFI95	0.59	0.30	0.29	0.24

A third example is on the differences in genetic performance patterns. Heritability of actual DFI decreased over test, while genetic variance was fairly constant over test period of 100 days, permanent environmental and error variances both increased with increasing number of test days (Huisman and Van Arendonk, 2002a). This indicates that when selection is on average DFI, actual DFI at start of test will increase more than actual DFI at end of test. To capture genetic differences in DFI patterns various DFI traits were defined by Huisman and van Arendonk (2002a). Three of these traits were average DFI on test and DFI at start and end of test. For a more detailed description see Huisman and Van Arendonk (2002a). For average DFI, DFI at start and DFI at end of test, the course of average estimated breeding values of the 10 highest ranking animals are plotted in Figure 1. The plots in Figure 1 represent average estimated breeding values for DFI at 100 different test days, which can be seen as estimated breeding values for 100 separate traits. DFI *x* is then defined as the estimated breeding value for DFI at day *x* on test. Figure 1 shows the existence of different genetic patterns for DFI over test. Depending on selection criteria, it is possible to change DFI patterns and not just DFI averages.

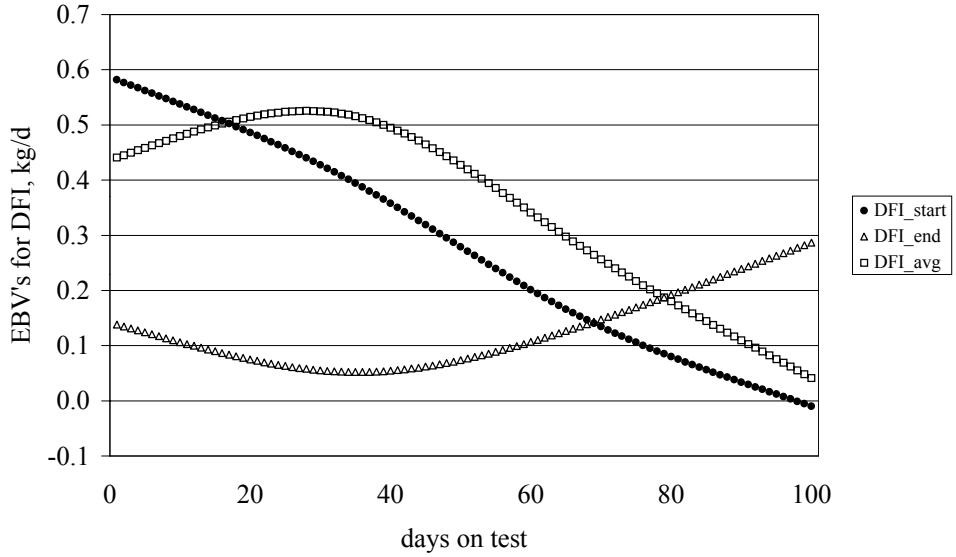

Figure 1. Estimated breeding values for DFI on different days on test for the 10 highest ranking animals for DFI_start, DFI_end, and DFI_avg

Conclusions

Random regression models provide a method to analyse longitudinal records in animal breeding that reveal specific patterns of change over a trajectory. Advantages, a higher accuracy of selection, the use of information of the course of traits, and the possibility to change the course of a trait through selection, of the application of random regression models were listed and illustrated with some examples.

Change of performance patterns in pigs through genetic selection

Literature

Since the start of domestication, man has changed animals by selection. In the last 50 years or so breeding companies started breeding programs, which resulted in fast genetic progress especially for production traits (Merks, 2000). The pig has a huge growth potential, growing to 100 kilograms live weight in less than six months. The mature weight of sows

was estimated to be somewhere between 260 and 285 kg (Solanes and Stern, 2001). It seems that domesticated pigs do not attain mature weight within the first three years of their life (Solanes and Stern, 2001). Modern European breeds have been selected for rapid weight gain and for high amounts of lean meat at the expense of adipose tissue in the carcass (Weiler et al., 1998). Large differences in growth curves between Wild boar, Meishan and Large White boars were found by Weiler et al. (1998).

Chadd et al. (1993) compared feed intake and performance of two pig genotypes grown to 120 kg live weight, genotypes consisted of offspring of a crossing between the same sire line and two different dam lines. The experiment was designed to study voluntary feed intake of two types of modern pigs when feed was offered ad libitum. No significant difference between voluntary feed intake, live weight gain and feed conversion ratio from 60 to 120 kg was found between the two genotypes, while the two genotypes showed significant differences in live weight gain and feed conversion ratio from 25 to 60 kg. This demonstrates that there are differences in growth and feed intake patterns between modern genotypes, even when they are as closely linked as the two genotypes in this study.

Mignon-Grasteau et al. (2000) concluded from genetic analysis of growth curve parameters that changing the shape of the growth curve in chickens is possible. Chickens were selected on body weight at 8 wk and/or 36 wk of age. Four selection lines were established: high 8 wk weight and low 36 wk weight, low 8 wk weight and high 36 wk weight, high 8 wk and 36 wk weight, and low 8 wk and 36 wk weight. The lines selected for a high 8 wk weight showed higher estimates of initial specific growth rate and maturation rate and lower estimates for age at inflection. Selection lines for a high 36 wk weight showed highest estimated values for mature weight.

Schnyder (2001) fitted a random regression model using second order polynomials to fit weekly averages of daily feed intake on age for growing pigs. Heritability estimates for the linear and the quadratic terms were close to zero, while the heritability estimate for the intercept (level/average) was moderate. Based on these findings, he concluded that changing the shape of feed intake curves by selection will be very difficult, and most probably not worth the extra effort. Schulze et al. (2002) also estimated heritabilities for the intercept, the linear and the quadratic term in polynomials that described feed intake over test. Estimated heritabilities for the linear and the quadratic term were both higher than the estimated heritability of the intercept of feed intake. Eissen (2000) estimated moderate heritabilities for intercept and slope when a linear regression was fitted on individual feed intake data of

pigs. Results from both Eissen (2000) and Schulze et al. (2002) indicate that there is genetic variation in feed intake patterns of pigs. Largest difference between the study of Schnyder (2001) and the studies of Eissen (2000) and Schulze et al. (2002) is that Schnyder (2001) used weekly averages of daily feed intake, while Eissen (2000) and Schulze et al. (2002) used actual daily feed intake in their analyses.

In the genetic size-scaling theory (Taylor, 1980), genetic size is considered as the major genetic factor that controls growth rate of an organism from its early embryonic stages to full maturity, and continues to determine rate and duration of life processes during the remaining part of life. Selection for improved growth rate is expected to increase mature size of an animal. It is not clear whether the scaling rules hold for genetic differences within breeds, and whether within breed selection does more than merely change body size (Taylor, 1985). The size scaled growth curve must change in shape and/or composition when more than body size is changed through selection. Knap (2000) analyzed Gompertz growth curve parameters over several decades, and found that maximum protein deposition and growth rate increased over these decades, while body lipid mass and lipid/protein ratio decreased over the same decades, accompanied with a somewhat lower mature weight. Knap (2000) concluded that selection on mature protein mass has not favored genotypes with larger mature sizes, but mainly decreased lipid mass. Short-term selection responses are mainly due to differences in genetic size. However, in the long term 'specific' genetic factors (factors other than genetic size) become more important and changes in shape of the growth curve are not only the result of scaling (Rauw et al., 2000). Thus, long-term selection probably does more than merely change mature sizes.

Results from this thesis

Huisman et al. (2002a) estimated genetic parameters for live weight of pigs, using random regression models. Random regression models performed better in the description of weight data of growing pigs and gave better estimates of genetic parameters compared to a multivariate model. When weight was fitted as a function of age in the random regression model, the fact that not all animals were weighed at the same age was taken into account. Daily feed intake increased from the start of the growing period, following a diminishing returns pattern. Total variance of DFI increased over test, while genetic variance was fairly constant. Heritability of DFI therefore decreased over test. Genetic correlations between DFI at different days on test varied from 0.3 to 1.0. Taken together these results indicate that DFI cannot be regarded as the same trait throughout test, with constant heritability and variance

(Huisman and Van Arendonk, 2002a). The interactions between weight, daily gain and DFI over an age trajectory were studied by Huisman et al. (2002b). Genetic and phenotypic correlations between live weight and DFI did not differ between age combinations for restricted fed pigs. Genetic correlations were 0.7-0.8 for all age combinations, and phenotypic correlations were 0.1-0.2 for all age combinations. Live weight at later ages had a high genetic correlation with daily gain at all ages, Genetic and phenotypic correlations between DFI and daily gain did not differ greatly between age combinations: genetic correlations were 0.3-0.4, and phenotypic correlations were 0.1 for all age combinations (Huisman et al., 2002b). When daily gain and DFI were modeled as function of weight, genetic correlations between daily gain at different weights were almost equal to unity, while genetic correlations between DFI at different weights were not equal to unity (Huisman et al., 2002c). Genetic correlation between daily gain and DFI at the same weight decreased with increasing weights, phenotypic correlation between daily gain and DFI at the same weight was highest around 80 to 90 kg of live weight (Huisman et al., 2002c).

Conclusions

Measurements of live weight and DFI over time cannot be regarded as measurements of the same trait. Literature and results from this thesis demonstrate that genetic correlation between live weight, daily gain, and DFI measured at different ages are not equal to one. The results from this thesis and from literature show that it should be possible to change patterns of weight, DFI and daily gain over an age or weight trajectory through genetic selection.

What is the desired direction of genetic change?

Change in what direction?

The pig industry is shifting towards integrated pyramids which serve specific needs of retailers (Webb, 2000; Walters, 2001). Breeding objectives are expected to shift from efficiency of production towards consumer appreciation. Product quality and production methods are getting increased attention (Webb, 2000; Merks, 2000). Literature reports indicate that feed intake of the modern pig is not in balance with the pig's potential to grow (Webb, 1998). According to Webb (1998) pigs eat too little prior to a body weight of 40 kg and too much after a body weight of 70 kg is reached. As a consequence pigs with ad

libitum access to feed become too fat later in their life. Challenge will be to identify pigs that eat more at the beginning of the growth period and use all this extra feed to grow more and produce lean meat instead of fat. One of the most important characteristics for slaughterhouses is uniformity in pigs that are delivered for slaughter for a specific market. Different markets require pigs with different weight and/or age at slaughter. Pigs destined for the bacon market are slaughtered at a lower weight than pigs destined for the production of fresh pork. Other pigs are used for the production of Parma ham. These pigs have to be at least nine months old and must have reached a live weight of 150 kg or more before slaughter. Nowadays, some animals are too lean for the bacon market. The fat content of pigs destined for the bacon market is directed by the choice of breeds that are used as (grand) parents of the slaughter animals. Random regression technology could be helpful here in identifying different growth patterns, and different lines of pgis could be set up for different markets. When using random regression models it is theoretically possible to breed an animal with the right properties for each market segment. The ultimate goal is a set of random regression models that include weight, daily feed intake, fat- and protein retention over the pig's life should be realised to select desired animals that are uniform at a slaughterweight and with a fat content of choice.

Ad libitum feed intake capacity of growing pigs is generally considered as a trait with an optimum with respect to feed efficiency. The linear-plateau model (Whittemore and Fawcett, 1976) is commonly used to describe the relation between energy intake and protein retention (Pr) and lipid retention (Lr). It is generally accepted that there is a linear effect of energy intake on Pr and Lr when energy intake is greater than the amount needed for maintenance and less than the amount required for maximizing protein retention. The economically optimum feed intake (or energy intake) is equal to the minimum level of intake to reach maximum protein retention (Eissen, 2000). Most efficient lean growth is achieved when pigs consume enough energy to achieve 95-100% of their lean growth potential (Schinckel and Richert, 2002). Eissen (2000) set up an experiment in which parameters related to the linear-plateau model were determined for different weight ranges, 25-65 kg, 65-95 kg, and 95-125 kg. Actual feed intake was studied in relation to optimum feed intake. Figure 2 is adapted from results of Eissen (2000). In this figure it is shown that feed intake capacity was higher than optimum feed intake for the weight ranges 65-95 kg, and 95-125 kg, while feed intake capacity was on average equal to optimum feed intake for the weight range 25-65 kg. Lean growth potential is expected to increase through selection

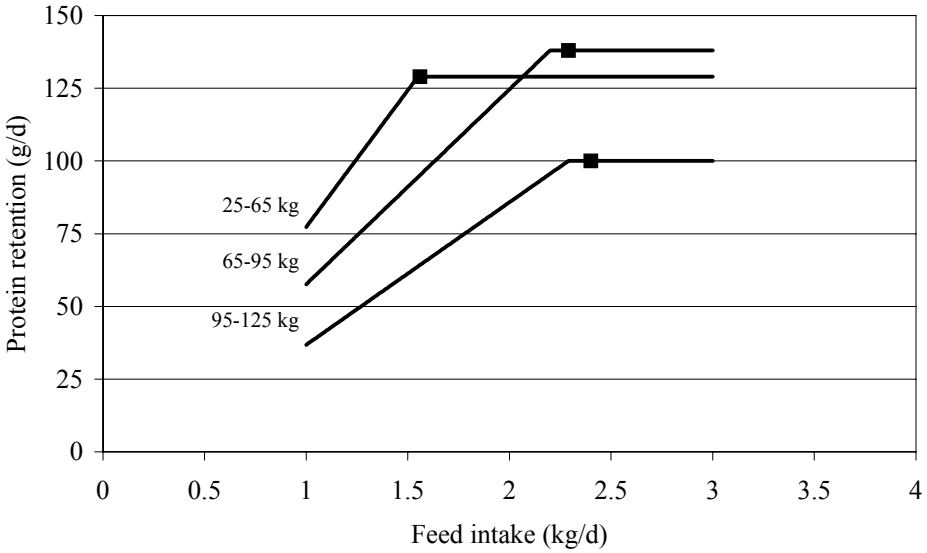

Figure 2. Relationship between protein retention and feed intake, the ■ represent average feed intake capacity. (Averages of five genotypes as estimated by Eissen (2000)).

and through better feeding strategies. Energy intake capacity is likely to become the limiting factor for more lean growth (Schinckel and De Lange, 1996). This means that feed intake is or may become lower than optimum and becomes a limiting factor for a further increase in lean growth rate during at least part of the growth period. Feed intake is more often lower than optimum for gilts and boars than for castrated males within genotypes (Eissen, 2000). Protein retention rate and lipid retention rate change with live weight. Genotypes with a higher protein retention rate maintain higher protein retention rates at heavier weights than low or average protein retention genotypes (Schinckel and De Lange, 1996). Protein retention decreases with live weight, whereas lipid retention increases with live weight. Maximum protein retention is reached at intermediate live weights (75-85 kg) (Emmans and Kyriazakis, 1997), and follows a curvilinear pattern (Whittemore et al., 1988). In the optimum situation, feed intake capacity would be equal to the inflection point of the protein retention curves (Figure 2). To achieve this, feed intake capacity has to decrease or maximum protein retention has to increase. Random regression models provide a method to gear feed intake capacity towards the optimum at all weights.

Conclusions

The desired pig should meet the requirements for the market for which it is destined in reasonable time. The entire animal has to be in balance, its feed intake capacity has to be in tune with the ability of the animal to retain protein during each day of the growth period. Random regression models are capable of identifying differences in growth and feed intake patterns. The ultimate goal is a set of random regression models for (lean) growth and feed intake, which facilitates the identification and fine-tuning of animals for different market segments.

How can we change performance patterns?

When the desired direction of change in performance patterns is clear, individual genetic performance patterns have to be identified. To identify individual genetic patterns, measurements have to be done in the trajectory of interest with regular intervals to get accurate estimates of the individual genetic patterns (Huisman and Van Arendonk, 2002b). In an optimal test system, live weight and DFI would be measured on a regular basis without influencing normal behaviour of the pig. Wolter et al. (2002) found that frequency of hand weighing did not affect growth performance or carcass characteristics of pigs. Others (Augspurger and Ellis, 2002) suggest that feed intake on day of weighing was reduced and feeding patterns were substantially altered on day of weighing. Schulze et al. (2001) compared a continuous feeding regime where pigs were fed using electronic feeding stations all weeks and a periodic feeding regime where pigs were fed using electronic feeding stations in the odd weeks and conventional feeders in the other weeks. Growth rate and backfat thickness were non-significantly different between feeding regimes, whereas daily feed intake and behavioural traits did show significant differences. A continuous feeding regime was recommended by Schulze et al. (2001), because repeated adaptation to electronic feeding stations is avoided, because of the more reliable information such a regime generates, and because of the more accurate prediction of feed intake capacity. When selection is for part of a curve it is necessary to have measurements in that particular trajectory. The maximum interval between subsequent measurements depends on the genetic correlation structure. A maximum of five days between subsequent measurements is possible for both loose and tight genetic correlation structures. With larger gaps between

subsequent measurements possible genetic gain is reduced (Huisman and Van Arendonk, 2002b).

Another way of analysing growth is the application of growth functions. A common characteristic of growth functions is that they each utilize biologically relevant parameters (Fitzhugh, 1976). Growth functions generally have some desired properties: weight tends to an asymptotic value with time, growth rate has a maximum at some intermediate weight or age, and relative growth rate decreases monotonically. Growth functions describe weight under the assumption that animals are kept in non-limiting environments. However, in practice not all animals achieve their potential to grow. A growth function has to be estimated for each individual, based on phenotypic observations. Precision of the estimates of growth curve parameter values varies where the frequency of live weight recording differs between animals. The use of these, less precise, parameters to characterize genetic merit between animals may for these reasons be problematic (Lewis et al. 2002). Random regression models have better properties for genetic evaluation. Random regression methodology offers a more powerful and flexible means than the growth functions approach to evaluate repeated live weight information to determine genetic merit (Lewis and Brotherstone, 2002). Random regression is more suitable to estimate individual deviations from an average growth curve; variation that is not picked up by growth functions will be picked up using random regression models. Pool (2000) concludes that statistical functions, such as random regressions, provide a better fit to lactation data in dairy cattle than biological functions. Usually, traits are only recorded for a short period of time. This makes it very difficult to get accurate estimates for growth functions, which are based on lifetime performance.

In conclusion, to estimate breeding values over a certain trajectory random regression models are preferred to growth functions. A set of multivariate random regression models can be set up, yielding estimated breeding values for traits of interest along a trajectory, e.g. a weight - or age trajectory. Those estimated breeding values should be used in an index, where most emphasis is put on that part of the trajectory that we want to change. Ad libitum access to feed is preferred to a restricted access to feed of tested animals. Ad libitum fed animals are able to show their full genetic potential for growth and feed intake. If animals have ad libitum access to feed, a multivariate random regression could tune ad libitum feed intake to an optimum to realize maximum lean growth at all points

along the trajectory of interest. Animals with these genetics should produce lean meat in a feed restricted environment as well.

Consequences of changing performance patterns

The current pig is different from the pig of decades ago. Selection for high lean growth rate may have consequences for the pig. A high lean growth rate might delay the onset of puberty in gilts (Patterson et al., 2002). Others suggest that selection for average lean tissue growth will lead towards heavier but less mature piglets at birth, which may affect piglet survival (Herpin et al., 1993). Selection for weight at a given age is predicted to result in greatly increased feed intake at all weights (Emmans and Kyriazakis, 2000), which could mean increasing feed intake with increasing weight. Mass selection on weight at 70d in pigs resulted in increased weight at 35d in the selection line (Kuhlers and Jungst, 1990), and thus a higher gain between 0 and 35d. There are indications that substantial indirect selection for preweaning growth does occur in populations subjected to selection for improved postweaning growth and/or minimum fat (Fredeen and Mikami, 1986). Large differences in blood parameters between Wild boar, Meishan and Large White boars were found by Weiler et al. (1998), indicating that selection influences the physiological state of an animal. Selection for increased growth rate or decreased back fat thickness is associated with changes in endocrine and metabolic status of the pig (Te Pas et al., 2001). Oksbjerg et al. (2000) compared a current genotype with an unimproved (unselected for 25yrs) genotype of Danish Landrace, and found that the unimproved genotype grew slower. It seemed that the improvement in growth performance was accompanied by degradation in muscle color and reduced tenderness. Knap (2000) investigated the time trends of Gompertz growth parameters in pigs. Over the years body protein mass, growth rate and maximum daily protein deposition increased. However, Knap (2000) also found that mature weight of the 'meat-type' pig is decreasing based on growth curve analysis, which is not in line with expected development in mature weight. Long-term selection on growth rate is more likely to result in higher mature weights.

Selection for improved lean growth may increase maintenance requirements (Kolstad and Vangen, 1996). Selection for feed conversion ratio – one of the most important traits of fattening pigs – may lead to reduction of voluntary feed intake (Von Felde et al., 1996). Some breeding programs, which put a lot of emphasis on efficiency, have led to a

reduction in daily feed consumption (Cameron and Curran, 1994). Responses to selection for fattening traits may be better visible in the mature these pigs. For example, selection for efficiency may lead to sows that do not have enough capacity to eat what they need during lactation, or are too lean to endure pregnancy and/or lactation (Ten Napel et al., 1995; Whittemore, 1996).

Random regression models could be helpful here to identify and select animals that do not show unwanted side effects of selection, e.g. animals that grow faster within a desired trajectory without increased feed intake in that same trajectory, or animals that show superior lean growth potential but not the increased maintenance requirements. Random regression models could help identify and select sows that are not too lean and do eat enough to lead a healthy and reproductive live.

Other applications of random regression models

Miscellaneous

Most traits of interest are modeled as a function of age. Interesting alternatives are modeling traits as a function of weight or feed intake. When feed intake is modeled as function of weight, feed efficiency measures can be derived. Huisman et al. (2002c) estimated genetic parameters for daily gain and daily feed intake using random regressions, where daily gain and daily feed intake were modeled as function of weight, from these variances and heritabilities for feed efficiency were derived. Other random coefficients are possible, for example Andersen and Pedersen (1996) used cumulative feed intake to describe weight-data of pigs, and weight to describe feed intake data. Apparent is that it is useful to take random coefficients that do vary over a certain trajectory.

Up to now, mainly random regression models in growing pigs were discussed. Random regression models could also be used for reproduction traits. Possible genetic differences in litter size or weight patterns could be identified using random regression models. Something like persistency in litter size or weight could be used to select breeding sows more efficient. Another trait that could be monitored and taken into account in breeding programs using random regression models is the change in fat depth of pregnant and lactating sows.

Application of random regression models in cattle and poultry

In beef cattle, selection is usually on weight at a certain age. In practice it is impossible to measure all animals at the same age, therefore weights are corrected towards certain landmark ages. Random regression provides a method which estimates breeding values for all ages of interest, without the need to correct phenotypic observations towards landmark ages. In dairy cattle, random regression models are widely used to model milk yield and related yield traits, such as fat- and protein yield. Canada was one of the first countries to implement a random regression model for the genetic evaluation of the national dairy herd (Schaeffer et al., 2000), many countries followed. Random regression models are preferred to lactation models, because random regression models describe both the level and the shape of the lactation curve (Pool, 2000). Single test-day yields are used instead of cumulative yields resulting in a better and a more precise correction for fixed effects. If the lactation curve is modeled by a random regression model information from the number, intervals and ordering of test-day records is included. The implementation of random regression models is expected to yield a more accurate genetic evaluation of cows. De Haas et al. (2002) used random regression models to describe the course of somatic cell count during lactation. Typical characteristics of mastitis causing pathogens were described using random regression models. Results in this study showed that somatic cell count curves differ for different pathogens. Live weight, condition score and dry matter intake of lactating heifers were described by Koenen and Veerkamp (1998) using random regression methodology. They showed that genetic variance for live weight, condition score and dry matter intake varied within lactation.

Current management and breeding strategies, implemented to improve growth rate in broilers, have an impact on carcass characteristics and incidence of ascites. Several management measures to reduce growth rate and consequently promote the health of broilers were proposed by Boersma (2001). Albers et al. (1990) suggested to feed broilers restricted early in life to prevent the occurrence of ascites. Random regression models could identify and select those broilers that have a desired growth pattern and facilitate the breeding of more healthy broilers. In laying hens, increased egg production was associated with decreased mature weight and decreased egg weight, while selection for body weight increased mature weight and egg weight (Nestor and Noble, 1995). Random regression models could be helpful in selecting those hens that produce a lot of eggs with a high weight, in other words to tune egg weight to egg production.

General Conclusions

Random regression models provide a method to analyze longitudinal records in animal breeding that reveal specific patterns of change over a trajectory. Advantages of the application of random regression models are a higher accuracy of selection, the use of information of the course of traits, and the possibility to change the course of a trait through selection. Random regression models were applied to estimate genetic parameters for various traits. It was demonstrated that genetic correlation between live weight, daily gain and daily feed intake at different ages is not equal to one, and that variances were not constant in this particular age trajectory. As a consequence, measurements of live weight, daily gain, and daily feed intake taken at different points along this trajectory cannot be regarded as measurements of the same trait. It is possible to change patterns of weight, daily feed intake, and daily gain over an age trajectory through genetic selection. The desired pig should meet the requirements for the market for which it is destined in reasonable time. The entire animal has to be in balance, its feed intake capacity has to be in tune with the ability of the animal to retain protein during each day of the growth period. Random regression models are capable of identifying differences in growth and feed intake patterns. To change performance patterns, it is necessary to have measurements in the period of interest. The interval between subsequent measurements can be increased, depending on genetic correlation. For the estimation of breeding values over a certain trajectory random regression models are preferred to growth functions. A set of multivariate random regression models can be set up, yielding estimated breeding values for traits of interest along a trajectory, e.g. a weight - or age trajectory. These estimated breeding values for different points along a trajectory can be considered as estimated breeding values of separate traits. A breeding goal that incorporates all these traits can be set up, putting more emphasis on that part of the trajectory that we want to change. Ad libitum access to feed is preferred to a restricted access to feed of tested animals. Ad libitum fed animals are able to show their full genetic potential for lean growth and feed intake. If animals have ad libitum access to feed, a multivariate random regression could tune ad libitum feed intake to an optimum to realize maximum lean growth at all points along the trajectory of interest. Resulting in pigs that show a good lean growth in any feed environment. When we want to change performance patterns through genetic selection, we have to keep in mind that genetic selection has consequences on the physiological state of the pig, and even could have a negative influence

on production or welfare of the animal. Random regression models could be a helpful tool in identifying and selecting animals that show desired patterns for a combination of traits, and in this way prevent the unwanted side-effects of selection to happen.

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Summary

Objective of this thesis was to quantify genetic differences in performance patterns of pigs by means of random regression models. Emphasis was on growth and feed intake patterns in pigs. Genetic parameters for weight, daily gain and daily feed intake were estimated using random regression models, where traits were modeled on a continuous scale, i.e. age, days on test or weight. Interactions between weight, daily gain, and daily feed intake during a trajectory were studied. The possibilities to change (part of) performance pattern of pigs through selection were investigated using simulation.

Objective of *Chapter 2* was to investigate which kind of random regression model fits best to weight data of pigs. Different random regression models have been advocated for the fitting of covariance structures of traits along a trajectory. It was suggested that a spline model would fit better to weight data than a random regression model that utilizes orthogonal polynomials. Two different random regression models were compared on their ability to describe weight of individual pigs. The first random regression model utilized orthogonal polynomial functions, while the other random regression model utilized spline functions. Data used in this analysis were weights, all animals had three weights, one at roughly 73 days of age, one at roughly 135 days of age, and one at roughly 190 days of age. Data was analyzed with a sire model; each sire had on average 100 weight measurements spread out over the age trajectory. Genetic, permanent environmental and total variances increased with age. Heritabilities for the multivariate model ranged from 0.14-0.19, heritabilities were fluctuating around 0.17 for both random regression models. Both genetic and phenotypic correlations decreased when the interval between measurements increased. The spline model needed fewer parameters than the multivariate and polynomial models. Akaike's Information Criterion had the smallest value for the spline model and the biggest value for the multivariate model. Bayesian-Schwarz Information Criterion had the smallest value for the polynomial model and the biggest value for the multivariate model. Smaller values for both information criteria indicate a better description of the data. Residuals of all models were normally distributed. Based on these results, it was concluded that both random regression models provide a better fit to pig weight data than a multivariate model. For this data the random regression model, which utilized orthogonal polynomial functions provided the best fit.

In *Chapter 3* daily feed intake was described as a function of days on test using a spline random regression model. Order of fit for the spline random regression model was varied; models were compared using Schwarz's Bayesian Information Criterion. The

objective was to investigate whether there are genetic differences in DFI patterns. Data were DFI records of growing gilts, which had ad libitum access to food. Gilts were 94 days old at start of test. All gilts were from a Dutch Landrace line. Number of random regression coefficients were varied from zero to nine, the model with four random regression coefficients per test day resulted in the most optimal fit. Six traits were derived to capture differences in DFI patterns: average DFI over 100 testdays, variance in DFI over 100 testdays, DFI at testday five, DFI at testday 50, DFI at testday 95, and DFI at testday 95 minus DFI at testday five. Heritability for DFI decreased from 0.53 at five days on test to 0.24 at 95 days on test. Genetic correlations between DFI at five days on test and 95 days on test and between DFI at 50 days on test and 95 days on test were low (around 0.3). The results clearly demonstrate that DFI at different days on test cannot be regarded as repeated measurements of a single trait with constant variance and heritability. Based on the results in this chapter it can be concluded that there is scope to change feed intake patterns through selection.

In *Chapter 4* the aim was to estimate genetic parameters for live weight, daily feed intake, and daily gain - including correlations among traits and ages - over an age trajectory using a multivariate random regression model. Data were weight and feed intake of boars with restricted access to feed. Boars were tested for a 7-week period, with an additional week prior to test being an adjustment period to their new environment. Pigs entered the test at an average age of 128 d ± 4 d. Each boar had approximately 34 valid daily weight records and 50 daily feed intake records. Heritability estimates for live weight, daily feed intake, and daily gain at different ages, and genetic and phenotypic correlations between different ages for live weight, daily feed intake, and daily gain were presented, as well as genetic and phenotypic correlations for all age and trait combinations. Correlations between live weight and daily feed intake at various age combinations were fairly constant, genetic (0.8) and phenotypic (0.15). Genetic correlation between live weight at different ages and daily gain at a given age increased with age. Genetic correlations between live weight at a given age and daily gain at different ages were fairly constant. The phenotypic correlation between live weight at a given age and daily gain was higher when the daily gain measurement was before the live weight measurement, and lower when the daily gain measurement was after the live weight measurement. Estimates for the genetic correlation between daily feed intake and daily gain at different ages showed similar values for all age combinations. Phenotypic correlations between daily feed intake and daily gain showed an increase over age. Live

weight, daily feed intake, and daily gain were not the same trait at different ages with constant heritability and variance. An increased interval between subsequent measurements is likely to yield lower genetic correlations between ages for one of these traits, which is indicating that altering curves through selection is a viable option. The estimated genetic correlation of approximately 0.35 between daily gain and daily feed intake indicates that it is possible to increase daily gain through selection without increasing daily feed intake.

The objective in *Chapter 5* was to investigate the possibilities to alter the growth curve of pigs through selection. The impact of genetic correlation structure, measurement design, and missing records on achieved changes in growth curve and the accuracy of breeding value estimation have been investigated using stochastic simulation. Phenotypes of animals were simulated and subsequently breeding values were estimated using a random regression model. The best animals were selected and used to produce the next generation. This selection process was repeated for three generations. Animals were mated at random with no restrictions on inbreeding. The presented results were the average of 100 replicates. Traits of interest were early growth, intermediate growth, late growth and total growth to put different emphasis on parts of the growth curve. Phenotypes of animals over an age period of 100 days were simulated for two genetic correlation structures. Parameter structure one - resembling weight - had high genetic correlations between days of age, for parameter structure two - resembling feed intake - the genetic correlation between days of age decreased more rapidly. A number of recording strategies that differed in interval between subsequent measurements were applied. For correlation structure one the interval between subsequent measurements could be increased to 25 days without substantial loss in achieved genetic gain, while for correlation structure two achieved genetic gain already dropped when the interval was increased to 10 days. A number of sampling strategies were investigated, these sampling strategies differed in number of measurements per animal and length of test period. In general it can be stated that fewer measurements results in lower genetic gain. It is possible to change patterns through selection; the magnitude of change depends on the underlying genetic structure. It was shown that it is possible to improve the four traits by 1.4 to 1.6 genetic standard deviations for correlation structure one, while for correlation structure two the improvements for the four traits were about 1.4 genetic standard deviations. Increasing the number of recordings will result in higher genetic gain; increments up to about 10% are possible.

Objectives of *Chapter 6* were to describe daily gain and feed intake as a function of weight using random regression models, and to derive variance components for feed efficiency at different weights from the estimated variance components of daily gain and daily feed intake. Data were from boars tested for a 7-week period, with an adjustment period of one week prior to test. Pigs entered the test at an average live weight of 71.3 kg ± 9 kg. Pigs were fed restricted by scale-equipped electronic feeders. Individual feeder visits of each pig were used to derive daily records. Only pigs that had at least 10 weight records were kept to fit a quadratic curve of weight over age, daily gain on each test day was derived from this curve. In the random regression analysis daily gain and daily feed intake were modeled as a function of live weight using spline functions. When variances and covariances of daily gain and daily feed intake are known as a function of live weight, it is possible to approximate variances for feed efficiency, which is defined as gain divided by feed intake. Genetic correlations between daily gain at different weights were not different from one, in contrast to the results obtained in Chapter 4 where the genetic correlations between daily gain at different ages decreased with an increasing interval between subsequent ages. However, genetic variance and heritability differed between weights. Phenotypic correlations between daily gain at different weights decreased with an increase in weight interval. Heritability of daily gain was highest (0.18) between 105 and 110 kg. Genetic correlations between daily feed intake at different weights decreased with increase in weight interval, phenotypic correlations between daily feed intake at different weights were low. Highest heritability (0.18) of daily feed intake was found between 80 and 90 kg. Variance components for feed efficiency were derived from the estimated variance components for daily gain and daily feed intake at different weights. Highest heritability (0.18) for feed efficiency was found between 100 and 115 kg. Genetic correlation between daily gain and feed efficiency increased with weight, phenotypic correlations decreased slightly. Genetic and phenotypic correlations between daily feed intake and feed efficiency were fairly constant for this weight trajectory, phenotypic correlation decreased slightly at end of weight trajectory. In general, variance components for all three traits decreased with increased weights. This suggested that feed intake of animals was more restricted by the applied feeding regime towards higher weights. In this evaluation system, where pigs have restricted access to feed, selection on daily gain will lead to a decrease in daily feed intake.

In *Chapter* 7 the application of random regression models in pig breeding was discussed. Random regression models provide a method to analyze longitudinal records in animal breeding that reveal specific patterns of change over a trajectory. Advantages of the

application of random regression models were a higher accuracy of selection, the use of information of the course of traits, and the possibility to change the course of a trait through selection. Random regression models were applied in this thesis and in literature to estimate genetic parameters for various traits. Analysis in this thesis and in literature demonstrated that genetic correlation between live weight, daily gain and daily feed intake at different ages is not equal to one, and that variances were not constant in the trajectories analyzed in this thesis. As a consequence, measurements of live weight, daily gain, and daily feed intake taken at different points along this trajectory cannot be regarded as repeated measurements of the same trait. It is possible to change patterns of weight, daily feed intake, and daily gain over an age trajectory through genetic selection; the extent of change depends on the genetic correlation structure. The desired pig should meet the requirements for the market for which it is destined in reasonable time. The animal has to be in balance, its feed intake capacity has to be in tune with the ability of the animal to retain protein during each day of the growth period. Random regression models are capable of identifying differences in growth and feed intake patterns. To change performance patterns, it is necessary to have measurements in the period of interest. The interval between subsequent measurements can be increased, depending on genetic correlation. For the estimation of breeding values over a certain trajectory random regression models are preferred to growth functions. A set of multivariate random regression models can be set up, yielding estimated breeding values for traits of interest along a trajectory, e.g. a weight - or age trajectory. These estimated breeding values for different points along a trajectory can be considered as estimated breeding values of separate traits. A breeding goal that incorporates all these traits can be set up, putting more emphasis on that part of the trajectory that we want to change. For feed intake and/or efficiency ad libitum access to feed is preferred to a restricted access to feed of tested animals. Ad libitum fed animals are able to show their full genetic potential for growth and feed intake. If animals have ad libitum access to feed, a multivariate random regression could help tune ad libitum feed intake to an optimum to realize maximum lean growth at all points along the trajectory of interest, resulting in pigs that show optimum lean growth in any feed environment. In altering performance patterns through genetic selection, we have to keep in mind that genetic selection has consequences on the physiological state of the pig, and even could have a negative influence on production or welfare of the animal. Random regression models are a helpful tool in identifying and selecting animals that show desired patterns for a combination of traits.

Samenvatting

genetische analyse van groei- en voeropnamepatronen van varkens

Inleiding

De afgelopen decennia zijn varkens-fokprogramma's erg succesvol geweest in het boeken van genetische vooruitgang voor economisch belangrijke kenmerken. Met name voor de kenmerken (gemiddelde) dagelijkse groei, rugspekdikte en voer-efficiëntie zijn enorme verbeteringen gerealiseerd. Selectie in de varkensfokkerij was (en is) voornamelijk gericht op het efficiënter produceren van varkensvlees. Dit werd (en wordt) gedaan door te selecteren op een hoger mager vlees gehalte en een efficiëntere benutting van voer[1] in groeiende varkens. Deze twee kenmerken zullen in de toekomst waarschijnlijk belangrijk blijven.

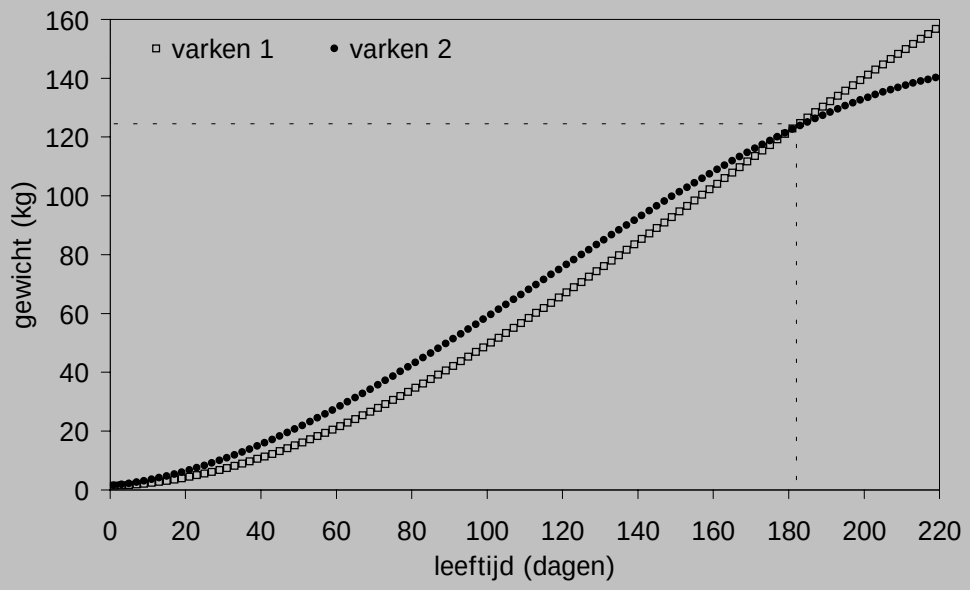
Door de introductie van elektronische voerstations, met weegschaal, is het mogelijk om gedetailleerde gegevens over voeropname, voeropname-gedrag en veranderingen in gewicht van individuele dieren te verzamelen. Tot nu toe was selectie gebaseerd op gerealiseerde gemiddeldes en/of totalen, bijvoorbeeld gemiddelde groei, en/of totale voeropname, in een bepaalde testperiode. De testperiode is meestal een vast leeftijds- of gewichtstraject. Op de huidige manier van testen (op gemiddelden en/of totalen) worden mogelijke verschillen in groei- of voeropname-patronen genegeerd (zie kader 1).

Model

Om verschillen in prestatiecurven te kunnen analyseren voldoen de op dit moment gebruikte modellen voor fokwaardeschatting van dieren niet. Elektronische voerstations registreren elke dag van de testperiode voeropname en gewicht van elk dier, en genereren een heleboel extra gegevens. Meer geavanceerde modellen - die kunnen omgaan met de extra gegevens - zullen moeten worden ontwikkeld en toegepast. Zogenaamde '*stochastische regressie modellen*', maken het mogelijk kenmerken te modelleren op een continue schaal. Voorbeelden van een continue schaal zijn leeftijd of gewicht. Met deze modellen is het mogelijk om gemiddelden en totalen te schatten, maar ook kan worden beschreven hoe de kenmerken verlopen met de tijd of met gewicht. De regressie coëfficiënten variëren met leeftijd, testdag of gewicht en beschrijven het verloop van het kenmerk. De term *stochastisch* geeft aan dat de geschatte oplossingen kunnen verschillen van dier tot dier,

[1] Met een efficiëntere benutting van voer wordt bedoeld: dezelfde hoeveelheid groei met minder voer of meer groei met dezelfde hoeveelheid voer. Een andere term hiervoor is voeder efficiëntie, wat gelijk is aan groei per kilogram opgenomen voer.

Kader 1.



In deze figuur zijn de groeicurven van twee varkens te zien, varken 1 en varken 2. Beide varkens hebben bij geboorte hetzelfde gewicht, vervolgens groeit varken 2 sneller, om op ongeveer 180 dagen op hetzelfde gewicht uit te komen als varken 1. Hoewel varken 1 en 2 gemiddeld even snel gegroeid zijn is het duidelijk dat varken 1 en 2 niet op dezelfde manier dat gewicht op 180 dagen bereikt hebben. Varken 2 groeit op jongere leeftijd sneller dan varken 1, terwijl varken 1 op latere leeftijd sneller groeit dan varken 2.

voor elk dier wordt een individueel prestatie-patroon geschat. Dit individuele prestatie-patroon geeft dan aan hoe individuen afwijken van het gemiddelde prestatie-patroon. Deze afwijking is deels erfelijk en deels wordt deze afwijking veroorzaakt door omgevingsfactoren. Omgevingsfactoren zijn bijvoorbeeld in welk hok, en met hoeveel andere dieren het dier in dit hok gezeten heeft. Het individuele prestatie-patroon beschrijft de genetische aanleg voor het verloop van een kenmerk gedurende een traject. Voor elk dier is hierdoor op elke leeftijd, testdag of gewicht in het traject een fokwaarde voor bijvoorbeeld groei of voeropname beschikbaar. Op deze manier kunnen verschillen in patronen zichtbaar gemaakt worden.

Doel van dit proefschrift was om genetische verschillen in prestatiepatronen zo goed mogelijk te beschrijven met een model en deze vervolgens te kwantificeren. Daarnaast

is gekeken naar de mogelijkheden om prestatiepatronen door selectie te veranderen. Er is met name gekeken naar groei- en voeropname-patronen in groeiende varkens.

Resultaten

In *Hoofdstuk 2* is gewicht van groeiende varkens gemodelleerd als functie van hun leeftijd. Verschillende vormen van een stochastisch regressie model zijn vergeleken. Om het beste model te kiezen, zijn de met de stochastische regressie modellen geschatte parameters vergeleken met op de klassieke manier geschatte parameters. Daarnaast werden de modellen vergeleken aan de hand van twee informatie-criteria, deze informatie-criteria geven aan in hoeverre de werkelijke gegevens en de modeluitkomsten van elkaar afstaan. De variatie in gewicht nam toe met leeftijd. Erfelijkheidsgraden[2] voor gewicht op verschillende leeftijden schommelden rond de 0.17. De genetische correlaties[3] tussen gewicht op verschillende leeftijden waren hoog wanneer deze leeftijden vlakbij elkaar lagen, en lager wanneer de leeftijden verder uit elkaar lagen. Beide stochastische regressie modellen beschreven gewicht een stuk beter dan het klassieke model en hadden minder parameters nodig om dezelfde gegevens te beschrijven. Gebaseerd op de gebruikte informatie criteria was er geen duidelijk voorkeur voor één van beide stochastische regressie modellen.

In *Hoofdstuk 3* is onbeperkte voeropname van groeiende varkens gemodelleerd als functie van de lengte van de testperiode in dagen. Het aantal gebruikte coëfficiënten in het stochastisch regressie model werd gevarieerd, om uit te zoeken met hoeveel coëfficiënten voeropname afdoende kan worden beschreven. De verschillende modellen werden vergeleken met behulp van een Informatie Criterium. Dit criterium geeft aan in hoeverre de schattingen van het gebruikte model afwijken van de oorspronkelijke gegevens. Het aantal coëfficiënten werd gevarieerd van nul tot negen, voor zowel het genetische als het permanente milieu-effect. Alle varkens die gebruikt zijn in deze analyse waren van het vrouwelijk geslacht (gelten). De gelten waren ongeveer 94 dagen oud bij aanvang van de

[2] Erfelijkheidsgraad is dat gedeelte van de totale variatie in een kenmerk dat het gevolg is van genetische verschillen tussen dieren. Als de erfelijkheidsgraad voor een kenmerk 1 is, betekend dit dat alle variatie in een kenmerk verklaard kan worden door genetische verschillen tussen dieren.

[3] De genetische correlatie beschrijft de mate van genetische samenhang tussen verschillende kenmerken. Als de genetische correlatie een waarde 1 heeft, betekend dat beide kenmerken waarschijnlijk door dezelfde genen aangestuurd worden. Omgekeerd als de genetische correlatie 0 is, betekend dat beide kenmerken door verschillende genen worden aangestuurd.

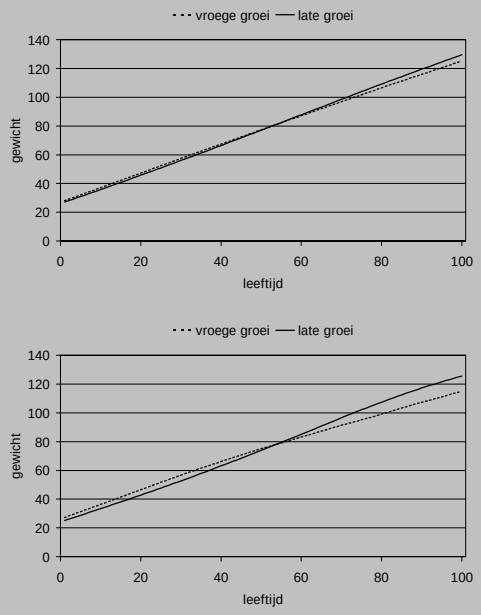
test. Het stochastische regressie model met vier coëfficiënten voor het genetische en het permanente milieu-effect resulteerde in de meest optimale beschrijving van voeropname. De erfelijkheidsgraad van voeropname daalde van 0.53 op testdag vijf naar 0.24 op testdag 95. Genetische correlaties tussen voeropname op de vijfde testdag en de 95ste testdag en tussen voeropname op de 50ste testdag en de 95ste testdag waren laag (±0.3).

In *Hoofdstuk 4* is een stochastisch regressie model gebruikt om tegelijkertijd gewicht, voeropname en dagelijkse groei te modeleren als functie van leeftijd voor groeiende varkens. Alle varkens die gebruikt zijn in deze analyse waren van het mannelijk geslacht (beren). De beren werden getest gedurende een periode van zeven weken, de week voorafgaand aan die zeven weken was bedoeld als gewenningsperiode. De test periode startte op een gemiddelde leeftijd van 128 dagen. Van iedere beer is het gewicht ongeveer 34 maal gemeten, en de totale dagelijkse voeropname ongeveer 50 maal. Schattingen van de erfelijkheidsgraden voor gewicht, dagelijkse voeropname en dagelijkse groei zijn terug te vinden in Hoofdstuk 4. De geschatte correlaties tussen gewicht en dagelijkse voeropname op verschillende leeftijden waren tamelijk constant, ongeveer 0.8 voor de genetische correlatie en ongeveer 0.15 voor de fenotypische correlaties[4]. De genetische correlatie tussen gewicht en dagelijkse groei op dezelfde leeftijd nam toe naarmate de beren ouder werden. Genetische correlaties tussen gewicht op een bepaalde leeftijd en dagelijkse groei op alle leeftijden waren tamelijk constant. Fenotypische correlaties tussen gewicht op een bepaalde leeftijd en dagelijkse groei waren hoger wanneer dagelijkse groei op een jongere leeftijd dan gewicht gemeten was, en lager wanneer dagelijkse groei op een latere leeftijd dan gewicht gemeten was.

In *Hoofdstuk 5* is door middel van een simulatie studie onderzocht of het mogelijk is om groeicurven door selectie te veranderen. Verschillende scenario's werden gesimuleerd om te onderzoeken wat het effect was op nauwkeurigheid van geschatte fokwaardes en op de geboekte genetische vooruitgang na drie generaties. De scenario's verschilden in het aantal metingen, het interval tussen opeenvolgende metingen en de genetische correlatie structuur. Twee verschillende genetische correlatie-structuren werden bestudeerd. De eerste

[4] De fenotypische correlatie beschrijft de mate van samenhang tussen verschillende kenmerken. In tegenstelling tot de genetische correlatie beschrijft de fenotypische correlatie de samenhang tussen fenotypes, een fenotype is wat we zien aan een individu. Fenotypes komen tot stand door de genen van het individu en door het milieu waarin het individu verkeert.

Kader 2.



In de twee figuren links is de verandering in groeicurve na drie generaties van selectie op vroege en op late groei te zien.

De bovenste figuur laat de verandering in groeicurve zien wanneer uitgegaan wordt van een langzaam afnemende genetisch correlatie tussen gewicht op verschillende leeftijden.

De onderste figuur laat de verandering in groeicurve zien wanneer uitgegaan wordt van een sneller afnemende genetische correlatie tussen gewicht op verschillende leeftijden.

correlatie-structuur was er één met hoge genetische correlaties tussen gewicht op verschillende leeftijden, en leek op de werkelijke situatie. De tweede correlatie-structuur was er één met een sneller afnemende genetische correlatie tussen verschillende leeftijden, en leek op de werkelijke situatie voor voeropname. Fenotypes van dieren werden gesimuleerd en van deze dieren werden de fokwaardes geschat met een stochastisch regressie model. De dieren met de hoogste fokwaarde werden geselecteerd om de volgende generatie dieren mee te fokken. Het paren van dieren gebeurde volkomen willekeurig. Er werd op vier kenmerken geselecteerd: vroege groei, groei in het midden van de groeiperiode, late groei en totale groei. Het interval tussen opeenvolgende metingen werd gevarieerd van één tot 45 dagen. Naarmate de genetische correlaties tussen kenmerk op verschillende leeftijden hoger waren wordt het moeilijker om patronen door middel van selectie te veranderen (kader 2).

In *Hoofdstuk 6* is een stochastisch regressie model gebruikt om tegelijkertijd dagelijkse groei en dagelijkse voeropname te modeleren als functie van gewicht voor groeiende varkens. De gegevens die in deze analyse gebruikt zijn, zijn dezelfde als in Hoofdstuk 4. De beren hadden een gemiddeld gewicht van ongeveer 71 kilogram bij

aanvang van de test. Alleen de varkens met tenminste 10 gewichtsmetingen werden gebruikt in de analyse. Voor elk varken werd een gewichts-curve geschat, aan de hand van deze curve werd dagelijkse groei voor de aanwezige gewichten afgeleid. Als de varianties en covariantie tussen groei en voeropname bekend zijn is het mogelijk om voeder efficiëntie af te leiden. Dagelijkse groei had de hoogste erfelijkheidsgraad tussen 105 en 110 kilogram lichaamsgewicht. Genetische correlaties tussen dagelijkse groei op verschillende gewichten waren allemaal ongeveer één. De fenotypische correlaties tussen dagelijkse groei namen af met een toename in het verschil tussen gewichten. De genetische correlaties tussen dagelijkse voeropname op verschillende gewichten namen af met een toename in het verschil tussen gewichten, fenotypische correlaties tussen dagelijkse voeropname op verschillende gewichten waren laag. Dagelijkse voeropname had de hoogste erfelijkheidsgraad (0.18) tussen 80 en 90 kilogram lichaamsgewicht. Voeder efficiëntie had de hoogste erfelijkheidsgraad (0.18) tussen 105 en 110 kilogram lichaamsgewicht. De genetische correlatie tussen dagelijkse groei en voeder efficiëntie nam toe met gewicht, terwijl de fenotypische correlaties licht daalden naarmate gewichten hoger werden. Over het algemeen nam de variantie voor alle drie kenmerken af met een toenemend gewicht.

Conclusies

In *Hoofdstuk 7* is de toepassing van stochastische regressie modellen in de varkensfokkerij bediscussieerd. Stochastische regressie modellen verschaffen fokkerorganisaties een methode om specifieke patronen in herhaalde waarnemingen aan hetzelfde dier op een leeftijds- of gewichtstraject te analyseren. De voordelen van het gebruik van een stochastisch regressie model zijn: de mogelijkheid om nauwkeuriger te selecteren, informatie over het verloop van een bepaald kenmerk en de mogelijkheid om prestatiepatronen te kunnen wijzigen door middel van selectie. In dit proefschrift zijn stochastische regressie modellen gebruikt om het verloop van gewicht, dagelijkse voeropname en dagelijkse groei van varkens te beschrijven. Een belangrijke conclusie is dat de deze drie kenmerken niet gezien kunnen worden als genetisch constante kenmerken, maar dat er sprake is van variatie in patronen van deze kenmerken. Gewicht op een leeftijd van 70 dagen is een ander kenmerk dan gewicht op 190 dagen, elk met hun eigen erfelijkheidsgraad en variantie. Het is mogelijk om het verloop van deze kenmerken te beïnvloeden door genetische selectie.

De gewenste eigenschappen van een varken worden bepaald door de markt waarvoor het bestemd is. De markt is van invloed op eindgewicht en mate van vetheid. Selectie is erop gericht om dit te bereiken in een zo kort mogelijke periode, om zo de kostprijs laag te houden. Om dit doel te bereiken moeten verschillende eigenschappen van het dier gedurende de groeiperiode met elkaar in balans zijn, de voeropname-capaciteit moet afgestemd zijn op het vermogen om eiwit (mager vlees) aan te zetten op elk moment van de groeiperiode, hetgeen op dit moment niet het geval is. Stochastische regressie modellen zijn in staat om verschillen in groei en voeropname patronen te identificeren. Als we groei en/of voeropname patronen willen veranderen zodat ze beter op elkaar afgestemd zijn is het noodzakelijk om metingen te doen in de periode waarin we geïnteresseerd zijn. Het interval tussen opeenvolgende metingen kan vergroot worden als de genetische correlatie tussen waarnemingen hoog is.

Om op prestatiepatronen te kunnen selecteren zou het wenselijk zijn om een stochastisch regressie model op te zetten dat op meerdere kenmerken tegelijk gericht is. Dit stochastische regressie model wordt dan gebruikt om fokwaardes te genereren voor elk kenmerk - gemeten over een bepaald traject - waarin we geïnteresseerd zijn. De geschatte fokwaardes voor verschillende punten op dat traject kunnen dan beschouwd worden als fokwaardes voor verschillende kenmerken. Om de juiste balans in kenmerken te bewaren kan een fokdoel met al deze kenmerken dan gedefinieerd worden, waarbij de nadruk wordt gelegd op dat gedeelte van het traject dat we willen veranderen.

Stochastische regressie modellen zijn een waardevol gereedschap om dieren die een gewenst prestatie-patroon, of een combinatie van gewenste prestatie-patronen, te identificeren en te selecteren.

Curriculum Vitae

Abe Eduard Huisman werd op 11 september 1975 geboren te Arnhem. Hij is getogen - in chronologische volgorde - in Arnhem, Doesburg, Best en Almelo. In 1993 behaalde hij het VWO-diploma aan het Greijdanus College te Zwolle. Datzelfde jaar begon hij met de studie Bioprocestechnologie aan de toenmalige Landbouwuniversiteit te Wageningen, drie maanden later stapte hij over op de studie Zoötechniek aan dezelfde Landbouwuniversiteit. De stage Fokkerij en Genetica werd gedaan aan Massey University te Palmerston North, New Zealand, met als onderwerp QTL-detectie voor de nonproductiekenmerken in melkvee. Na de stage werd een afstudeervak Fokkerij en Genetica gedaan bij de Leerstoelgroep Fokkerij en Genetica, hier werden de effecten van inteelt op de vruchtbaarheid van melkstieren onderzocht. Tenslotte werd een afstudeervak Wiskundige Statistiek bij het Centraal Bureau voor de Statistiek, te Heerlen gedaan, waar de verdeling van een toetsingsgrootheid onder verschillende steekproefontwerpen onderzocht werd. In september 1998 werd het diploma behaald. Vanaf 16 november 1998 was hij als onderzoeker in opleiding aangesteld bij de leerstoelgroep Fokkerij en Genetica op het in dit proefschrift beschreven onderzoek. Een gedeelte van dit onderzoek werd uitgevoerd bij de Animal Genetics and Breeding Unit te Armidale, Australië.