Additive genetic and phenotypic aspects of feed intake and feed efficiency using random regression

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Summary

Linear models with fixed and random regression coefficients were used to describe the cumulative feed intake as a function of live weight in the period from 30 kg to 100 kg for performance tested boars (DanBred) from the Danish test station. For each animal, data consist of periods with daily feed intake measurements and weekly live weight measurements. Random regression coefficients of both additive genetic and permanent animal effects were estimated. Based on the models applied, the changes in additive genetic, permanent, and phenotypic variability over the growth period are presented. Correlations between feed efficiency in sub periods and mean feed intake during the total test period are presented.

The estimated fixed regression coefficients in the model allow calculating the mean daily efficiency from the derivative of the cumulative feed intake curves. The result shows how the feed efficiency of growing pigs increases during the growth period. Implications of random regression models for selection for feed efficiency are discussed.

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1 Introduction

Feed is a major component in the total costs of production, and feed efficiency, the ratio between feed intake and weight gain, is an important trait in the breeding goal for commercial pig breeding. In breeding programs, (live) weight gain and feed intake are recorded on growing pigs, usually from 30 kg to approximately 100 kg (Andersen et al., 1996).

The introduction of electronic feeding stations provides accurate measurements of the feed intake and the feeding patterns of individual pigs housed in groups. The output from feeding stations is an on-line recording of the feed intake of each animal, and data is an example of longitudinal data, where feed intake is considered to vary over time.

The objective of this study was to estimate genetic and environmental sources of variation for feed intake of boars tested from 30 kg to 100 kg, by modelling feed intake as a function of live weight. The regression model with random coefficients is validated and implications of the model studied, particularly with respect to predicting feed efficiency.

2 Material and methods

At the age of 4 weeks, purebred boars of Duroc and Hampshire were transported from the breeding farms to the early weaning unit at test station Bøgildgaard, used by DanBreed in Denmark. At the weight of about 25 kg, the boars were transferred to the test unit and penned in groups of fourteen pigs in a mix of the two breeds. The boars were individually put on test at 30 kg live weight and the tests were individually ended when the boars achieved a weight in the interval from 70 kg to 115 kg live weight. Most boars achieved 94 kg live weight. During the test period, body weight measurements were recorded.

In the test unit, boars were given dry pelleted feed *ad libitum*. The feed consisted of 1.05 FUgp (Feed Units for growing pigs)[1], 16.1% crude protein, 0.9% lysine per kilogram feed.

Feed intake was individually recorded for each animal with the "ACEMA-48" electronic feeding stations. Records consisted of date, animal identification number, time at the beginning of the feed intake (s), time at the end of feed intake (s), and the amount of feed consumed (g). All records were aggregated in individual daily feed intake of the boars using midnight as separation in-between days.

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[1] 1 FUgp approximate 12.5 MJ to 12.8 MJ metabolizable energy

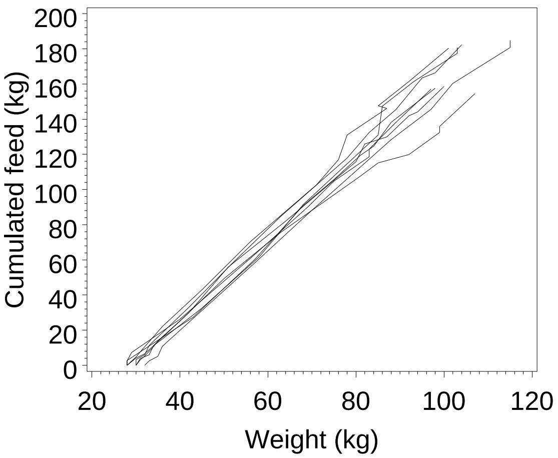

Figure 1: Cumulated feed intake and weight gain of twelve animals in data

Aggregated daily feed intake was summarised individually for each animal. Due to missing values of feed intake the aggregated daily feed intake may be missing or ended before the end of the test period. However, to retain longer periods of feed intake and to obtain usable data of the greatest possible number of animals, few observations of missing values of daily feed intake within the test period were interpolated and replaced by fitted values using a method of joining non-missing values of daily feed intake. In that way, connecting successive non-missing values of daily feed intake with straight lines fits missing values of daily feed intake. Replacements of missing values were only applied in 0.31% of data of daily feed intake and only for few animals with short periods of one or few days.

Live weights of each animal were frequently measured manually. Higher frequencies were observed at the beginning and at the end of the test period. During the total test period, approximately 10 live weight measurements were obtained.

The data set contained measurements of 2431 Hampshire boars and 5578 Duroc boars. The number of live weight measurements is 24894 and 51272 in data of Hampshire and Duroc. The number of animals in pedigree is 5226 and 13561 in Hampshire and Duroc.

2.1 Models with random regression coefficients

The cumulated feed intake is almost linear as a function of live weight (Fig. 1).

Linear regression models with random regression coefficients were used to describe the data.

Let w_{ij} describe the live weight of animal i at observation j during the test period from about 30 kg to about 105 kg, let Y_{ij} denote the cumulated feed intake from start of the test to the day where w_{ij} is recorded, and let y_{ij} be the observed value of Y_{ij}. Thus we may obtain the regression model with random coefficients as

$$y_{ij} = \boldsymbol{x}_i^T \boldsymbol{\alpha} + \sum_{m=0}^{p} \beta_m w_{ij}^m + \sum_{m=1}^{q} \gamma_{mg(i)} w_{ij}^m + \sum_{m=0}^{r} p_{im} w_{ij}^m + \sum_{m=0}^{s} a_{im} w_{ij}^m + \varepsilon_{ij} \quad (1)$$

where $\boldsymbol{x}_i$ is a design vector relating fixed year-month-herd effects in vector $\boldsymbol{\alpha}$ to animal i, β_m are regression coefficients of live weight gain w_{ij} in power of m, $\gamma_{mg(i)}$ are random regression coefficients of group effects, $g(i)$ is a function that relate animal i to groups, p_{im} are random regression coefficients of the permanent environmental effects, a_{im} are random regression coefficient of the additive genetic effects, and ε_{ij} is the random error, which is independent and $N(0, \sigma_\varepsilon^2)$.

Vectors of the random regression coefficients $\boldsymbol{\gamma}_k = (\gamma_{k0}, \gamma_{k1}, ..., \gamma_{kq})^T$, $\boldsymbol{p}_i = (p_{i0}, p_{i1}, ..., p_{ir})^T$, and $\boldsymbol{a}_i = (a_{i0}, a_{i1}, ..., a_{is})^T$ are assumed independent and multivariate normally distributed, i.e.,

$$\begin{aligned} \boldsymbol{\gamma}_k &\sim N_q(\boldsymbol{0}, \boldsymbol{\Gamma}), \\ \boldsymbol{p}_i &\sim N_r(\boldsymbol{0}, \boldsymbol{P}), \\ \boldsymbol{a}_i &\sim N_s(\boldsymbol{0}, \boldsymbol{G}), \end{aligned}$$

where q, r and s are the dimensions of $\boldsymbol{\gamma}_k$, $\boldsymbol{p}_i$, and $\boldsymbol{a}_i$.

Heritability of the cumulated feed intake as a function of live weight was obtained by

$$h^2(w) = \frac{\boldsymbol{w}_s^T \boldsymbol{G} \boldsymbol{w}_s}{\boldsymbol{w}_q^T \boldsymbol{\Gamma} \boldsymbol{w}_q + \boldsymbol{w}_r^T \boldsymbol{P} \boldsymbol{w}_r + \boldsymbol{w}_s^T \boldsymbol{G} \boldsymbol{w}_s + \sigma_\varepsilon^2} \quad (2)$$

where $\boldsymbol{w}_q = (1, w^1, ..., w^q)^T$, $\boldsymbol{w}_r = (1, w^1, ..., w^r)^T$, and $\boldsymbol{w}_s = (1, w^1, ..., w^s)^T$.

2.1.1 Feed efficiency in sub periods

Feed efficiency is calculated as the ratio between feed intake and weight gain. The feed efficiency of animal i in a given period from the live weight w_{i1} to live weight w_{i2} is obtained from (1) by

$$\begin{aligned} &\tfrac{y_{i2}-y_{i1}}{w_{i2}-w_{i1}} = \\ &\tfrac{\sum_{m=0}^{p} \beta_m (w_{i2}^m - w_{i1}^m) + \sum_{m=1}^{q} \gamma_m (w_2^m - w_1^m) + \sum_{m=0}^{r} p_{mi} (w_{i2}^m - w_{i1}^m) + \sum_{m=0}^{s} a_{im} (w_{i2}^m - w_{i1}^m) + \varepsilon_{i2} - \varepsilon_{i1}}{w_{i2}-w_{i1}} \end{aligned} \quad (3)$$

The expected feed efficiency in a sub period from the live weight w_1 to live weight w_2 is given by

$$\frac{E\left[Y_2 - Y_1\right]}{w_2 - w_1} = \frac{\sum_{m=0}^{p} \beta_m (w_2^m - w_1^m)}{w_2 - w_1} \tag{4}$$

The variance of mean feed efficiency from the live weight w_1 to live weight w_2 is

$$\frac{\Delta \boldsymbol{w}_{q12}^T \boldsymbol{\Gamma} \Delta \boldsymbol{w}_{q12} + \Delta \boldsymbol{w}_{r12}^T \boldsymbol{P} \Delta \boldsymbol{w}_{r12} + \Delta \boldsymbol{w}_{s12}^T \boldsymbol{G} \Delta \boldsymbol{w}_{s12} + 2\sigma_\varepsilon^2}{(w_2 - w_1)^2} \tag{5}$$

where $\Delta \boldsymbol{w}_{q12} = \boldsymbol{w}_{q2} - \boldsymbol{w}_{q1}$, $\Delta \boldsymbol{w}_{r12} = \boldsymbol{w}_{r2} - \boldsymbol{w}_{r1}$, and $\Delta \boldsymbol{w}_{s12} = \boldsymbol{w}_{s2} - \boldsymbol{w}_{s1}$ describe the changes in weight in the sub period from start weight 1 to end weight 2.

I follows that heritability of feed efficiency in the sub period is given by

$$h^2(\Delta \boldsymbol{w}_{r12}) = \frac{\Delta \boldsymbol{w}_{s12}^T \boldsymbol{G} \Delta \boldsymbol{w}_{s12}}{\Delta \boldsymbol{w}_{q12}^T \boldsymbol{\Gamma} \Delta \boldsymbol{w}_{q12} + \Delta \boldsymbol{w}_{r12}^T \boldsymbol{P} \Delta \boldsymbol{w}_{r12} + \Delta \boldsymbol{w}_{s12}^T \boldsymbol{G} \Delta \boldsymbol{w}_{s12} + \sigma_\varepsilon^2} \tag{6}$$

Now consider two periods where the first one is obtained from w_1 to w_2 and the second one is obtained from w_3 to w_4 then the covariance between the two periods is given by

$$Cov\left(\frac{y_{i2} - y_{i1}}{w_{i2} - w_{i1}}, \frac{y_{i4} - y_{i3}}{w_{i4} - w_{i3}}\right) = \frac{+\Delta \boldsymbol{w}_{q12}^T \boldsymbol{\Gamma} \Delta \boldsymbol{w}_{q12} + \Delta \boldsymbol{w}_{r12}^T \boldsymbol{P} \Delta \boldsymbol{w}_{r34} + \Delta \boldsymbol{w}_{s12}^T \boldsymbol{G} \Delta \boldsymbol{w}_{r34}}{(w_2 - w_1)(w_4 - w_3)} \tag{7}$$

2.1.2 Continuous model of feed efficiency

Continuous calculation of the feed efficiency at live weight w of animal i may be obtained from the first derivation of (1), e.i.

$$\begin{gathered} f.e.(w) = \frac{dy_{ij}}{dw_{ij}} = \\ \sum_{m=1}^{q} m\gamma_{mg(i)} w_{ij}^{m-1} + \sum_{m=1}^{p} m\beta_m w_{ij}^{m-1} + \sum_{m=1}^{r} m p_{im} w_{ij}^{m-1} + \sum_{m=1}^{s} m a_{im} w_{ij}^{m-1} \end{gathered} \tag{8}$$

The variance of feed efficiency is

$$\boldsymbol{w}_q^T \boldsymbol{\Gamma} \boldsymbol{w}_q + \boldsymbol{w}_r^T \boldsymbol{P} \boldsymbol{w}_r + \boldsymbol{w}_s^T \boldsymbol{G} \boldsymbol{w}_s \tag{9}$$

where we now have $\boldsymbol{w}_q = (1, 2w^1, ..., qw^{q-1})^T$, $\boldsymbol{w}_r = (1, 2w^1, ..., rw^{r-1})^T$ and $\boldsymbol{w}_s = (1, 2w^1, ..., sw^{s-1})^T$.

2.2 Multivariate model of feed efficiency

For the three periods 30 kg to 45 kg, 40 kg to 75 kg and 70 kg to 100 kg and for the total test from 30 kg to 100 kg, feed efficiency was computed for all animals with at least two records in a period. These four traits were analysed with a multivariate linear mixed animal model considering fixed year-month-herd effects, a fixed regression on mean weight in the period, random group effects and random additive genetic effects.

Variance components of all models in the present paper were estimated by restricted maximum likelihood (REML) using an average information algorithm in DMU (Madsen et al., 2000). To avoid colinearity orthogonal Legendre polynomials (Krezig, 1988) of appropriate order were obtained from the weight gain and used in the estimation procedure of model (1). Also derivates of the Legendre polynomials were obtained to estimate the feed efficiency in (8) and (9).

3 Results and discussion

3.1 Multivariate model

The total numbers of animals were 2431 and 5578 in Hampshire and Duroc populations, respectively (Table 1). In sub periods, at least two measurements of live weight were needed to calculate the feed efficiency. In three sub periods of each breed, the number of animals with at least two live weight measurements were reduced compared to the number of animals in the total test period (Table 1). To obtain the same number of animals in sub periods as in total test period require designed experiments with systematic measurements of live weight during test period. The mean number of live weight measurement per animal were 10.5 and 9,7 in Hampshire and Duroc populations, respectively (Table 1).

In both breeds, the heritability in sub periods was highest in the first sub periods from 30 kg to 45 kg, and is decreased the following periods. The highest heritability was obtained for the total period of test, which was actually used as a trait in the breeding goal (Table 1).

The highest genetic correlations between sub periods and the total period on test were obtained for the last two periods (Table 1).

3.2 Models with random regression coefficients

For both breeds, a fourth-order polynomial of fixed effect and second-order polynomials of the random group effects, permanent effect, and genetics ef-

Table 1: Number of animals, mean number of observations per animal, heritabilities, genetic correlations of feed efficiency estimated in sub periods by a multivariate model of feed efficiency in Hampshire and Duroc.

Breed and period	No. of animals	Mean no. of obs. per animal	h^2	Correlations		
				2	3	4
Hampshire						
1: 30 kg-45 kg	1544	3.8	0.27	0.48	0.17	0.46
2: 40 kg-75 kg	2096	3.8	0.12		0.45	0.85
3: 70 kg-100 kg	1558	5.2	0.09			0.85
4: 30 kg-100 kg	2431	10.5	0.26			
Duroc						
1: 30 kg-45 kg	3575	3.7	0.16	0.54	0.51	0.71
2: 40 kg-75 kg	4373	3.0	0.11		0.63	0.90
3: 70 kg-100 kg	3352	4.2	0.09			0.86
4: 30 kg-100 kg	5578	9.7	0.22			

fect were chosen. Other alternative models with different order were also considered, but they were not candidates for a reasonable model. Lower order models were not significantly better than the shown model, and in higher order models the convergence was questionable.

The estimated gain curves of cumulated feed intake (Fig. 2) showed similar increases as was already indicated by the raw data of the animals shown in Fig. 1. The 95%-confidence limits in Fig. 2 shows that the variance increases during time.

Plot of residuals shows homogeneous variance (Fig. 3). Since feed intake increased with live weight (Fig. 1), homogeneous variance was also obtained with respect to live weight gain (Fig. 3).

Probability plot of residuals showed a slight s-shape indicating a tendency of heavy tails affected by too many extreme values (Fig. 3). However, the distribution of residuals was symmetric, and overall we may consider the distribution being approximately normal.

Considering neighbour observations within animals no significant correlations between residuals were obtained (not shown). Thus, independence of residuals within animals were indicated, which satisfies the assumptions in the estimations procedure of model (1).

Splitting up the variance in group, permanent, genetic variances showed that the main variances were described by the permanent effect, which covered the variance between measurements within the same animal (Fig. 4).

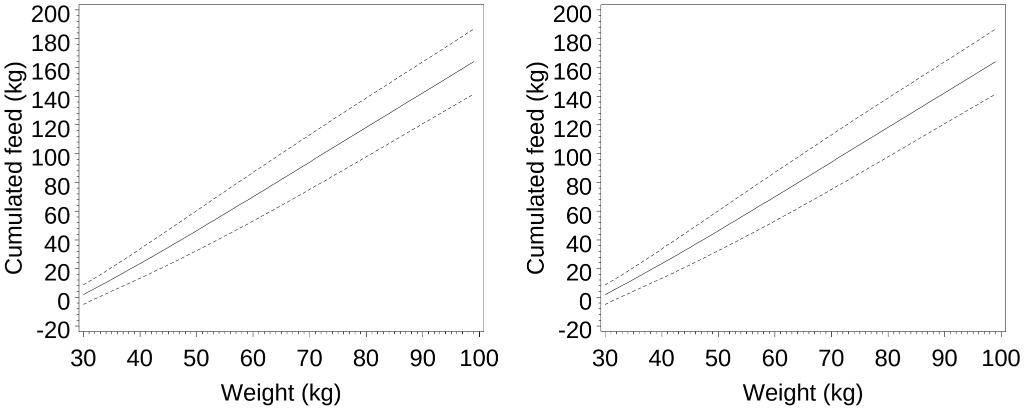

Figure 2: Main cumulated feed intake related to weight gain (solid line) with 95-confidens limit (dashed line) of Hampshire (left) and Duroc (right).

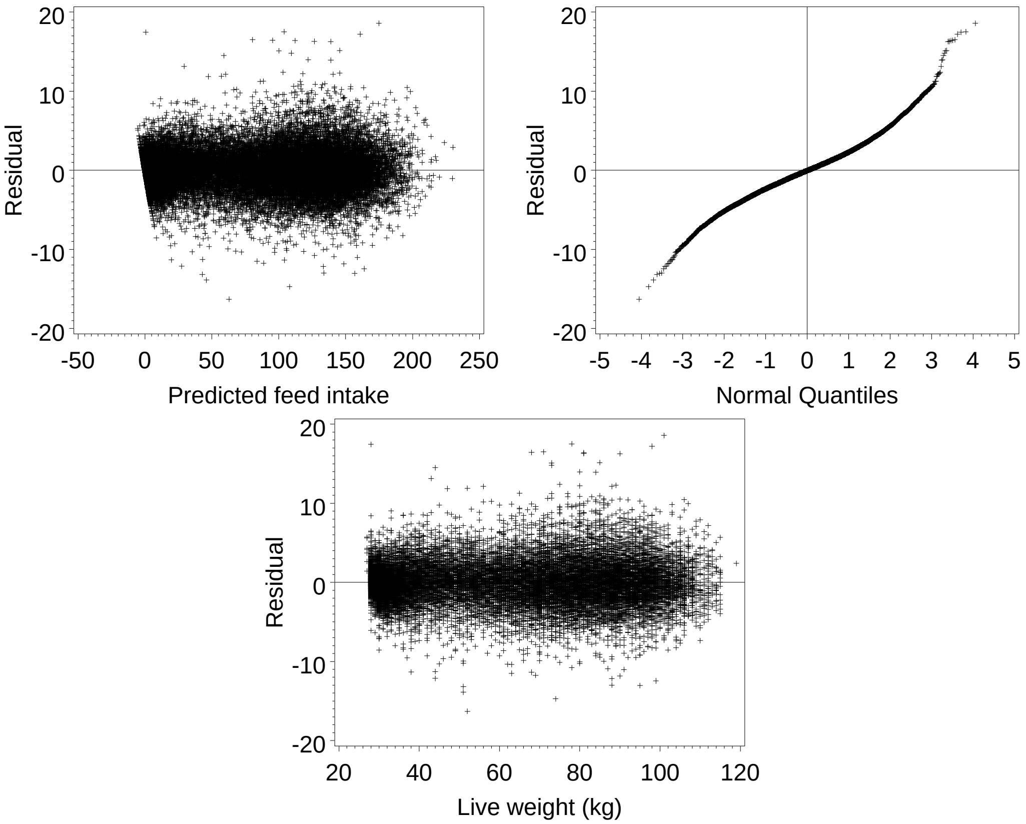

Figure 3: Residual plot and probability plot of residuals of the estimated model of Hampshire.

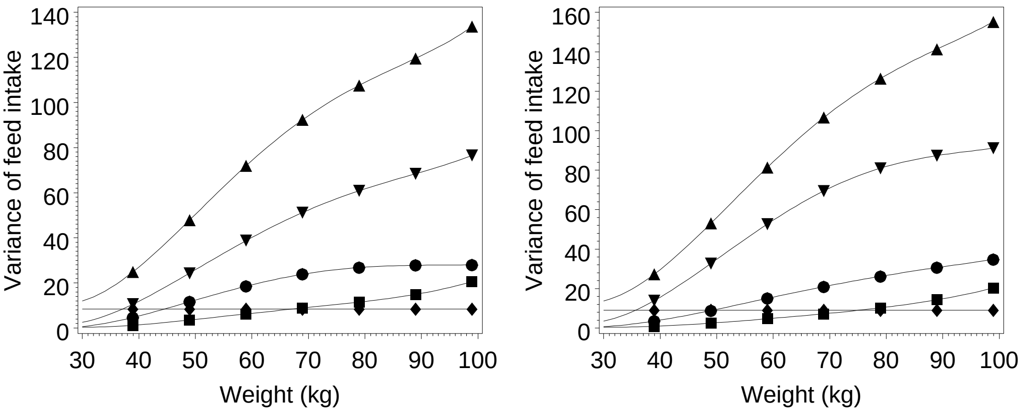

Figure 4: Variance: total (▲), permanent (▼), genetic (●), group (■), and random error (◆) of Hampshire (left) and Duroc (right).

Variance between groups was low, and error variance remains constant during the total growth period from 30 kg to 100 kg. Relatively to the total variance the error variance was high in the first part of the period whereas, it was of minor influence in the latter part (Fig. 4). This is also shown by the change in repeatability (Fig. 5).

The change of heritability of cumulated feed intake during the test period was calculated by (2). In Hampshire population, the heritability of feed intake increased to a maximum of 0.22 at about 65 kg live weight, but in the Duroc population the highest heritability was obtained at the end of the test at the live weight of 100 kg (Fig. 5). As expected the repeatability of accumulated feed intake increased with increasing weight gain on test (Fig. 5).

Continuous change in feed efficiency during the total test period of the two populations shows that feed efficiency in the Hampshire population increases more rapidly than in the Duroc population, and in the latter half of the test period the Hampshire population showed a constant level of feed efficiency. Feed efficiency in the Duroc population increased during the whole test period attaining maximum at the end of test (Fig. 6). Furthermore, Duroc had a lover initial level than Hampshire. Totally, the Duroc population had a lover feed efficiency than Hampshire.

The lowest variance of feed efficiency was obtained in the middle of the test period around 70 kg (Fig. 7). This would be expected, as the variance on feed efficiency is conditional on all records of accumulated feed intake and weight gain.

During the total test period, a number of sub periods may be obtained and the heritability of feed efficiency in the periods may be calculated by

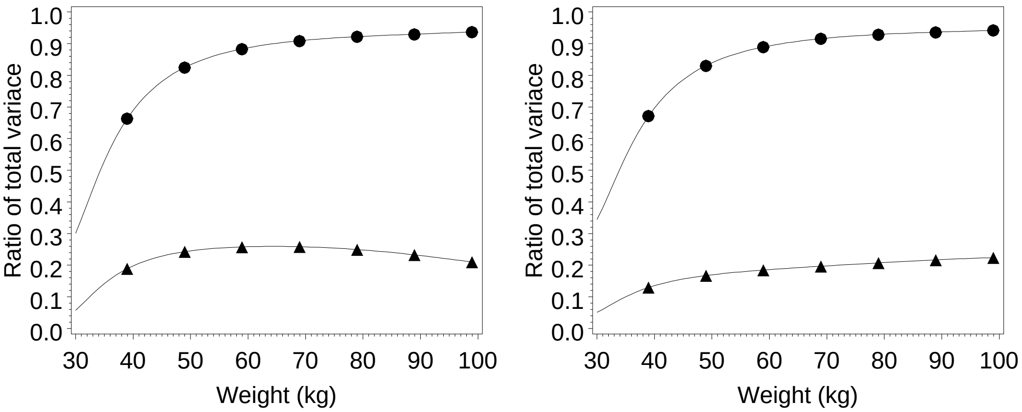

Figure 5: Heritability (▲) and repeatability (●) of cumulated feed intake related to live weight in Hampshire (left) and Duroc (right).

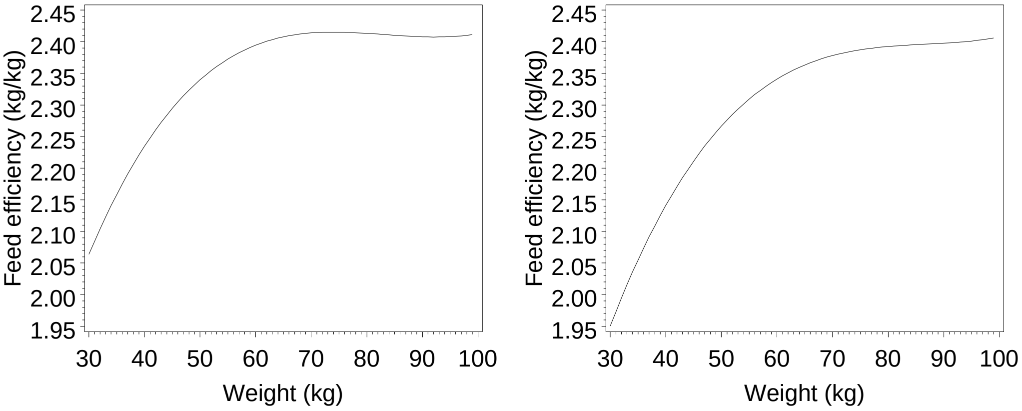

Figure 6: Mean feed efficiency in population of Hampshire (left) and Duroc (right) calculated as the amount of feed that gives 1 kg live weight.

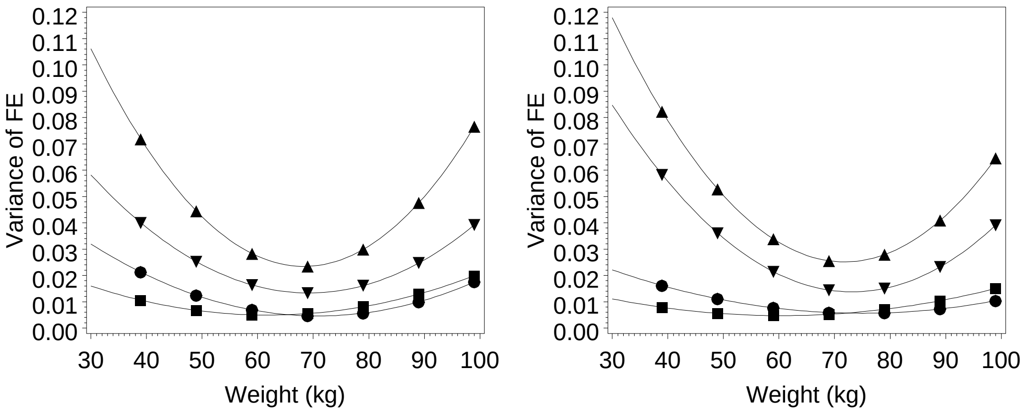

Figure 7: Variance of feed efficiency (FE): total (▲), permanent (▼), genitic (●), and group (■)of Hampshire (left) and Duroc (right).

Eqn. (6). The heritability in sub period with initial live weight of 30 kg, 40, ..., 90 kg is shown in Fig. 8. In the Duroc population the highest heritability is obtained for the total period test from 30 kg to 100 kg. This is in according to results of multivariate model (Table 1). If the test period is terminated at 80 kg the heritability decreases from 0.21 to 0.19. A similar reduction is obtained if we increase the start weight from 30 kg to 40 kg and use a test period from 40 kg to 100 kg (Fig. 8).

In the Hampshire population, the highest heritability was obtained in the sub period from 30 kg to 70 kg, whereas the heritability decreased if the total test period from 30 kg to 100 kg was used (Fig. 8). Also, in the sub period from 30 kg to 45 kg the lower level of heribility is obtained equally to the level of heritability in the total test period. Similarly results were obtained by the multivariate model (Table 1).

From (7) a number of genetic correlations between feed efficiency in sub periods may be obtained. In Fig. 9 genetic correlations between the total test period and sub periods with initial weights of 30 kg, 40, ... ,90 kg are shown. The genetic correlations between feed efficiency in the total test period and the feed efficiency in the sub period from 30 kg to 45 kg were 0.71 and 0.87 in Hampshire and Duroc, respectively. The comparable correlations obtained by the multivariate model (Table 1) were 0.46 and 0.71.

Mathematic calculations (not shown) of a second ordered model ($s = 2$ in Eqn. 1) shows that the genetic correlation between sub periods and the total test period from 30 kg to 100 kg is a function of the sum of the initial weight and the weight at the end of the test in the sub period. Hence, a ridge of maximum genetic correlation with values equal 1 is obtained when sums of initial and end weights are 130 kg (Fig. 9). This indicates that the

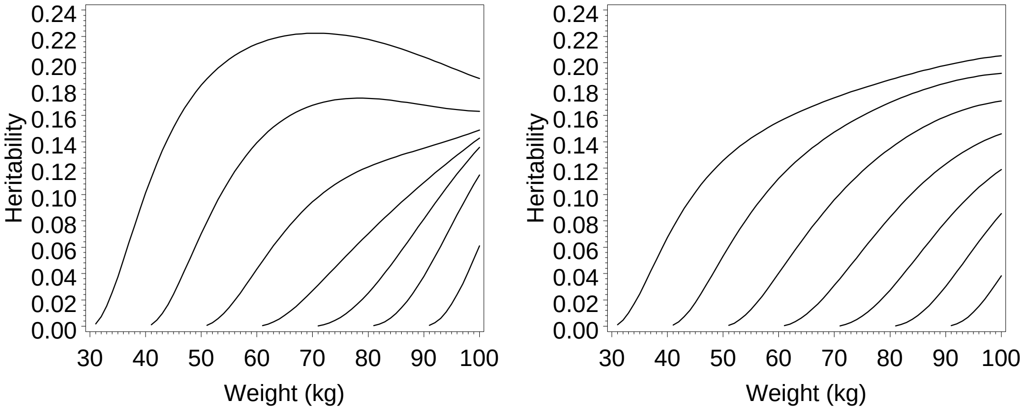

Figure 8: Heritability in sub periods with different combinations of live weight at end of test and initial weight of 30 kg, 40 kg, 50 kg, 60 kg, 70 kg, 80 kg and 90 kg in population of Hampshire (left) and Duroc (right).

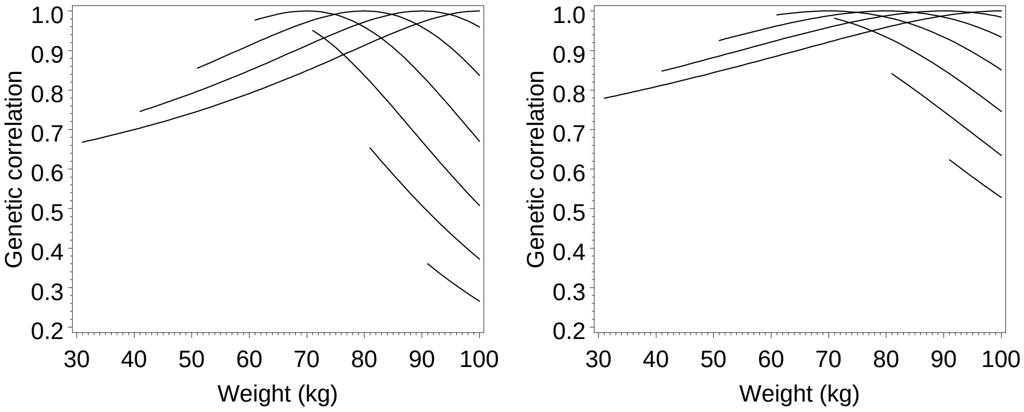

Figure 9: Genetic correlation between the total test period (30 kg to 100 kg) and different combinations of sub periods with initial weight of 30 kg, 40 kg, 50 kg, 60 kg, 70 kg, 80 kg and 90 kg in population of Hampshire (left) and Duroc (right).

order of the polynomials used in (1) has severe constraints for the ability to predict the covariance structures. In the present case the fit of second order model of the genetic effect predicts that, with respect to genetic correlation, it is equivalent to measure feed efficiency from e.g. 60 kg to 70 kg as from 30 kg to 100 kg. Biological, this is unlikely. However, the heritability in the sub period from 60 kg to 70 kg is low indicating that use of such short period in a breeding program is unsuitable (Fig. 8).

3.3 Conclusion

Additive genetic and phenotypic aspects of feed intake and feed efficiency have been analysed. Cumulated feed intake as a function live weight was fitted using regression with random coefficients. The random coefficients in the models manage to describe correlations between measurements of the longitudinal traits, and no correlations between residuals were observed. The model allows continuous estimation of feed efficiency related to live weight together with estimated variances. Heritability in sub periods and genetic covariances between sub periods can be obtained by the model. The results indicate some agreement with estimates of a multivariate model fit. However, the results also indicate that a regression model with random coefficients are sensitive to the order of the polynomials, e.g. calculating genetic correlations between sub period might result in biological absurd conclusions.

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