Genetic (co)variances and breeding value estimation of Gompertz growth curve parameters in Finnish Yorkshire boars, gilts and barrows

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Introduction

Income from the sale of an animal in livestock production usually depends on animal’s weight (Emmans & Kyriazakis 2000). Because, a livestock producer’s income is based on the weight of the animals themselves, it is important to add on weight in fast and efficient manner. Growth curves have long been used to describe the growth process of animals and several mathematical models have been developed to predict the growth rate of animals through various life cycle stages. Modelling growth with mathematical functions summarizes growth data for an individual, and many weight observations or measures recorded over time are reduced to a few parameters. Potential growth of an individual can be defined as the maximum rate at which the animal can grow under non-limiting conditions (i.e. ideal environmental conditions and unlimited nutritional resources). Actual growth may not always equate potential growth because of different environmental effects. Therefore, it is important that a growth function predicts potential growth rather than describes growth from a particular study or data set that occurred under some specific environmental conditions.

Keywords

Gompertz; growth curve; pigs.

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Summary

This paper’s objectives were to estimate the genetic (co)variance components of the Gompertz growth curve parameters and to evaluate the relationship of estimated breeding values (EBV) based on average daily gain (ADG) and Gompertz growth curves. Finnish Yorkshire central test station performance data was obtained from the Faba Breeding (Vantaa, Finland). The final data set included 121 488 weight records from 10 111 pigs. Heritability estimates for the Gompertz growth parameters mature weight (a), logarithm of mature weight to birth weight ratio (b) and maturation rate (c) were 0.44, 0.55 and 0.31, respectively. Genotypic and phenotypic correlations between the growth curve parameters were high and mainly negative. The only positive relationship was found between a and b. Pearson and Spearman rank correlation coefficients between EBV for ADG and daily gain calculated from Gompertz growth curves were 0.79. The Spearman rank correlation between the sire EBV for ADG and Gompertz growth curve parameter-based ADG for all sires with at least 15 progeny was 0.86. Growth curves differ significantly between individuals and this information could be utilized for selection purposes when improving growth rate in pigs.
Many different growth functions have been used in modelling the pigs’ growth and have been summarized by Wellock et al. (2004) in his review. Most appealing way to model growth data is to use non-linear functions, where predictions outside the data range can be made more reliably when compared with linear models. Generalized form of logistic functions with open inflection point like the Richards (1959) or Janoschek (1957) functions are flexible, but models often have convergence problems (Gille 2004). The functions having a fixed inflection point (e.g. logistic, von Bertalanffy, Gompertz), in relation to mature weight are easier to apply in practice. The Gompertz function has been shown to accurately describe pigs’ potential growth over age (Whittemore et al. 1988; Knap 2000; Wellock et al. 2004). In a preliminary study of Finnish pigs, the Gompertz function appeared to fit the data well and was an accurate predictor of growth (Sevón-Aimonen 2001). Gompertz function is a non-linear, sigmoidal function that requires the determination of only three parameters (Gompertz 1825). All three of the parameters used in the Gompertz function have biological meaning. The most important parameters are the mature weight and maturation rate. The third parameter describes the relative initial weight. With these parameters it is possible to describe the weight of animal (or components of growth, like protein and fat) at any point of the animal’s life cycle.

Growth curve parameters are heritable (Mignon-Grasteau et al. 1999; Lewis et al. 2002), and thus could be modified by selection through the implementation of an effective breeding programme. When designing breeding programmes, it is important to know the genetic relationships between early growth and mature size as well as the rate of maturing. Genetic selection for an increased growth rate and meat percentage will also change the parameters of the Gompertz growth curve. Taylor (1980) has suggested that the value of growth rate will decrease as mature size increases. On the other hand, if selection occurs at a very low degree of maturity, growth rate parameter is increased with little effect on mature weight. The breeding objective, however, is to change both mature weight and degree of maturity in the same direction. In practice, better knowledge of shape of growth curve improves the breeding, feeding and harvesting decisions of pork operations (Niemi 2006). However, this precise knowledge does not exist for many breeding populations, including the Finnish Yorkshire population. Hence, a study was conducted that had the following objectives: (i) to estimate the genetic (co)variance components of the Gompertz growth curve parameters and (ii) to evaluate the relationship of evaluated breeding values (EBV) between average daily gain (ADG) and Gompertz growth curves.

Materials and methods

Data

Performance data collected from 2000 through 2006 in the test stations were obtained from Faba Breeding (Vantaa, Finland). The pigs evaluated at the test stations are a part of the Finnish National Breeding Evaluation System (Serenius et al. 2004). The traits included in the station test index along with their relative weighting in parenthesis are growth trait (13%), feed efficiency (18%), carcass quality (39%) and loin and ham meat quality (combination of pH and colour 30%) (Faba Breeding 2006). Individuals that had been removed from the test before the end of the test period or had weight loss between consecutive weight measurements [indicative of some health problem(s)] were excluded from the data. The final data set included 121 488 weight records from 10 111 Finnish Yorkshire pigs. The weight measurements were from pigs placed on test in six individual-/sib-testing stations located at Piekäsmäki, Paimio, Ilmajoki, Panelia, Haapajärvi and Hyvinkää. Additionally, information was obtained from a single boar performance testing station located at Ilmajoki. The records from individual-/sib-testing stations included three full sibs. The pig weights were recorded weekly. The test period started at approximately 30 kg and ended at approximately 100 kg live body weight. The records from the boar performance testing station included one to three full sibs, and performance was evaluated from 25 to 100 kg. The overall test arrival weight and age averaged 25.0 kg (SD 2.85) and 78.3 days (SD 6.89), respectively. The average age at the end of the test period was 156 days (SD 8.9). From the recorded animals in the data, 4544 were gilts, 2967 barrows and 2600 boars. Animals were the offspring from 757 sires. The pen of pigs was fed based on the mean weight of the test group just under the expected consumption that would have been attained under an ad libitum access situation.

Gompertz growth curve parameters

Under the Gompertz function, the animal’s relative growth rate is considered as a simple function of its current size (Whittemore et al. 1988). The weights of
each pig were assumed to follow the Gompertz model:

\[ y_{ij} = a_i \exp(-\beta_i \exp(-\kappa_i t_{ij})) e_{ij}, \]

where \( y_{ij} \) is the observed weight of individual \( i \) \((i = 1, \ldots, n)\) at measurement time \( j \) \((j = 1, \ldots, n_i)\) for animal \( i \), \( t_{ij} \) is age of animal \( i \) in days at time \( j \) (in present study test age was used) and \( e_{ij} \) is the random residual term. The parameters of the Gompertz function for the \( i \)th animal are \( a_i, \beta_i, \kappa_i \), which are the mature weight, the logarithm of the ratio of mature weight to birth weight and the maturation rate, respectively. In this study, a multiplicative model was utilized and log-transformed data was analysed. This model is more realistic when compared with the additive model because the residuals are better accounted for when the real growth data are analysed. The Gompertz growth function using the logarithmic transformation is expressed in the following form:

\[ \ln(y_{ij}) = \ln(a_i) - \beta_i \exp(-\kappa_i t_{ij}) + \ln(e_{ij}). \]

The model used in variance component analysis was:

\[
\ln(y_{ijkno}) = \ln(\text{ssy}_{kno} + \text{sex}_{mx} + \text{ln}_{x} + \text{pe}_{o}) - (\text{ssy}_{kno} + \text{sex}_{mx} + \text{ln}_{x} + \text{pe}_{o}) \exp(-\text{ssy}_{kno} + \text{sex}_{mx} + \text{ln}_{x} + \text{pe}_{o})*t_{ij} + \ln(e_{ij}),
\]

where \( y_{ijkno} \) is the weight of individual \( i \) at time \( j \), and each of the three growth curve parameters (\( \alpha, \beta \) or \( \kappa \)) are affected by the fixed effect of station, season and year interaction \( \text{ssy}_{kno} \), the fixed sex effect \( \text{sex}_{mx} \), the random litter effect \( \text{ln}_{x} \) (contains the variance of common environment of litter and one-fourths additive genetic variance), random animal effect \( \text{pe}_{o} \) (includes permanent environmental variance of animal and three-fourths additive genetic variance) and the sire genetic effect \( \text{pe}_{s} \). These effects are accounted for in each of the three Gompertz function parameters, \( \alpha, \beta \) and \( \kappa \). After estimating variance components for the growth curve parameters using a sire model, variance components were converted for their use in the animal model by the following formulae:

\[
\sigma_a^2 = 4 \sigma_{sire}^2,
\]

\[
\sigma_c^2 = \sigma_{litter}^2 - \sigma_{sire}^2,
\]

\[
\sigma_{pe}^2 = \sigma_{animal}^2 - 2 \sigma_{sire}^2,
\]

where \( \sigma_a^2 \) is the additive genetic variance, \( \sigma_c^2 \) is the variance of common environment of litter, \( \sigma_{pe}^2 \) is the permanent animal variance and, \( \sigma_{sire}^2 \) is the genetic sire variance, \( \sigma_{litter}^2 \) is the litter component from the sire model and \( \sigma_{animal}^2 \) is the permanent animal component from the sire model. Heritability was calculated by dividing the additive genetic variance \( \sigma_a^2 \) by the total phenotypic variance \( \sigma^2 = \sigma_a^2 + \sigma_c^2 + \sigma_{pe}^2 \). Correspondingly, phenotypic correlations were calculated using additive genetic, common environment of litter and permanent animal variances and covariances.

The restricted maximum likelihood (REML)-based empirical best linear unbiased predictor (EBLUP) method presented by Wolflinger & Lin (1997) was utilized to implement the models similarly as described by Vuori et al. (2006). This method is based on linearization of Gompertz growth function with the second-order Taylor series expansion. The approach approximates maximum likelihood solutions by iteratively solving the parameter estimates and variance components from the linearized mixed effects model \( Y = X* + Z* + u + e \). Here, design matrices \( X* \) and \( Z* \) consist of current derivatives of non-linear Gompertz function with respect to fixed and random effects, respectively, and \( Y \) is a working variable created from non-linear model residuals and expectations of linearized model. First MiX99 (Strandén & Lindauer 1999) was used for solving the linearized model in order to obtain the growth curve parameter estimates, and then the design matrices \( X* \) and \( Z* \) with derivatives of Gompertz function were incorporated into the equations used in the DMU software (Jensen & Madsen 1994) to obtain REML estimates of covariance components for each growth parameter. Iteration between these two steps was continued until the relative change in the estimates of variance components and fixed effects between two consecutive iterations was less than 0.001.

### Production traits

Other production traits used in the breeding value estimation were considered from the same performance tested animals from each test station. The traits were ADG (g/day) and feed conversion ratio (FCR; FU:kg gain) during the station test period. FCR was an average of the full sib group that were penned together (i.e. feed efficiency was based on pen feed consumption).

The statistical model for the production traits was the model used for predicting breeding values of pigs in Finland (Serenius et al. 2001) except that the breeding values were calculated using two-trait
analysis in the present study whereas in practice, a multi-trait analysis is utilized. Briefly the model used in the present study is:

$$Z_{ijklm} = \beta_0 x + \beta_1 y + \beta_2 a + \varepsilon_{ijklm}$$

where $Z_{ijklm}$ is the observation of the trait, $x$ is the fixed effect of sex, $y$ is the fixed effect of station, $a$ is the fixed effect of age group of each animal at the beginning of the test period (1: under 66 days; 2: 66–72 days; 3: 73–78 days; 4: 79–84 days; 5: over 84 days), $\beta_0$ is the animal genetic effect and $\varepsilon_{ijklm}$ is the residual effect. The heritabilities were 0.35 and 0.40 for ADG and FCR, respectively, and the genetic and phenotypic correlations between traits were –0.90 and –0.63, respectively.

The goal was to compare the EBV obtained from the growth curve model and see how well they corresponded to the EBV from the Finnish pig breeding evaluation. Because variance component estimation did not converge using animal model, new breeding values were estimated using MiX99 for the animal model with the variance components assumed to be known. In the breeding value estimation, the statistical model was exactly the same as the model used when estimating variance components, except the animal model was used instead of a sire model. Pearson correlation ($r_{pearson}$) coefficients and Spearman rank correlation ($r_{spearman}$) coefficients (SAS 2003) were computed between the EBV for ADG, and ADG was estimated based on the Gompertz growth curve parameter estimates.

**Results and discussion**

**Growth curves**

Relatively low residuals indicated that the Gompertz growth function fits the current data well (Figure 1). Moreover, there is no difference in the trend over weights, which indicates that the model fit the data across the weight ranges. Variance–covariance matrices of the sire model were converted to corresponding variance–covariance matrices for the animal model and variances and heritabilities for the growth curve parameters were obtained (Tables 1 and 2). In general, $h^2$ estimates were quite high for the growth curve parameters. Hence, traditional selection methods should be able to improve the traits in an effective animal breeding scheme. Similar findings have been reported when data from other species were evaluated (Mignon-Grasteau et al. 1999; Akbas & Oguz 2000; Lewis & Brotherstone 2002; Lambe et al. 2006). Estimates of growth curve parameters ($\alpha$, $\beta$, $\kappa$) were on average 201.30, 2.06 and 0.016, respectively, and the inflection point was at 73.9 kg. In an earlier study of Finnish station test pigs where third-degree polynomial function was used (Sevón-Aimonen et al. 1997), the inflection point of growth curve was 71.9 kg, which is close to the estimate in this study. Birth weight was unknown in the present study and was estimated using arrival or on-test weight. The extrapolated birth weight was 1.61 kg. This is relatively close to the birth weight of piglets born in the previous study (Rautiainen et al. 1997). Whittemore et al. (1988) have suggested that the Gompertz growth function parameter $\alpha$ ranges from 220 to 330, and $\kappa$ from

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**Table 1** Additive genetic variance ($\sigma_a^2$), common environmental litter variance ($\sigma_c^2$) and permanent animal ($\sigma_p^2$) variance for Gompertz growth curve parameters obtained from an evaluation of Finnish Yorkshire centrally tested boars, gilts and barrows

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\sigma_a^2$</th>
<th>$\sigma_c^2$</th>
<th>$\sigma_p^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>657.09</td>
<td>323.15</td>
<td>499.55</td>
</tr>
<tr>
<td>$\beta$</td>
<td>0.0376</td>
<td>0.0121</td>
<td>0.01809</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>0.00000253</td>
<td>0.00000169</td>
<td>0.00000384</td>
</tr>
</tbody>
</table>

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**Table 2** Genetic (below the diagonal) and phenotypic (above the diagonal) correlations and heritability estimates on the diagonal obtained from an evaluation of Finnish Yorkshire centrally tested boars, gilts and barrows

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\alpha$</th>
<th>$\beta$</th>
<th>$\kappa$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha$</td>
<td>0.44</td>
<td>0.90</td>
<td>–0.86</td>
</tr>
<tr>
<td>$\beta$</td>
<td>0.88</td>
<td>0.55</td>
<td>–0.82</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>–0.80</td>
<td>–0.80</td>
<td>0.31</td>
</tr>
</tbody>
</table>

$^1\alpha$, $\beta$, $\kappa$ represent the mature weight, the logarithm of the ratio of mature weight to birth weight and the maturation rate parameters used in the Gompertz growth curve equations, respectively.
0.010 to 0.014 dependent on the sex and the genotype of the animal evaluated.

Genotypic and phenotypic correlations between the growth curve parameters were relatively high and negative with one exception (Table 2). The only positive correlation was between mature weight and ratio of mature weight to birth weight. Negative correlation between mature weight and maturation rate has been commonly reported from analyses of data from other livestock species (Meyer 1995; Lewis & Brotherstone 2002). The negative correlations between mature weight and maturation rate observed in the present study indicates that if selection is used to increase mature weight, then there will be negative indirect selection on maturation rate and maturation rate is slowing down. The components of growth are likely innately in balance and it is biologically impossible that maturation rate would increase infinitely in relation to mature weight.

Breeding values

Each individual received EBV for all growth curve parameters. Thus, it was possible to compare growth curves and observe genetic differences in growth between individuals. Connections between standardized EBV (mean 100 and SD 10, feed efficiency was inverted so that greater values are indicative of superior feed efficiency) showed that current selection for ADG has in reality, at least to some extent, been selection for mature weight (a) (Figure 2a). The correlation between EBV of mature weight and ADG was 0.44. On the other hand, there was no connection ($r_{\text{pearson}} = -0.01$) between EBV for maturation rate (k) and ADG (Figure 2b). EBV for feed efficiency are highly correlated with ADG ($r_{\text{pearson}} = 0.95$). The correlation between feed efficiency and growth curve parameters were of similar magnitude to those between ADG, and mature weight and ADG and maturation rate, which were 0.38 and $-0.01$, respectively.

Means of EBV by year for mature weight, maturation rate, ADG and FCR by birth year of the pig are shown in Figure 3. The EBV for ADG and mature weight have increased during the past 10 years. This is in agreement with the positive correlation of breeding values for ADG and mature weight. Similarly, there was no genetic change for maturation rate over time which is in agreement with the zero correlation for EBV found in the present study. However, little improvement, if any, has occurred in FCR and maturation rate. The current breeding goal in the Finnish National Pig Breeding Scheme is to improve both growth and feed efficiency of pigs and changes of EBV means by year of birth show that improvement in fact has occurred. The mature weight and maturation rate changes indicated that if growth curves instead of ADG and feed efficiency were used in an effective animal breeding scheme, both growth rate and feed efficiency would still improve.
To capture the entire advantage from the growth curve model, we need to turn the Gompertz growth curve parameter EBV obtained for each individual back to growth curves. Therefore, breeding values of daily gain for all pigs were calculated using growth curve parameters. For all sires, in daily gain the $r_{\text{pearson}}$ between the EBV from the ADG model and the EBV calculated from growth curves was 0.79. Additionally, sires with at least 15 offspring in the data were ranked based on their ADG. The Spearman rank correlation for sires’ having 15 or more progeny ranking based on the two traits was 0.86. Moreover, it was found that with both the growth curve and ADG models, 16 sires out of 20 were the same in the top 20, although the order of the sires differed to some extent. Figure 4a shows the growth curves for the sires ranked to be the best and the poorest for ADG. The best sire reached slaughter weight (at approximately 103 kg) 19 days earlier and its mature weight was greater when compared with the same data from the poorest sire. The difference is emphasized more when the daily gains for the station test period (30–100 kg) of the sires is plotted (Figure 4b). Results indicate that growth curves differ significantly between individuals and this information could be utilized in a pig breeding system where selection is based on improving the Gompertz growth curve parameters.

Growth curve parameters are not currently used directly in the Finnish National Pig Evaluation Programme. However, growth curve models do result in more accurate breeding value estimates because differences in the initial and final weight from the test period impact breeding values to a lesser degree when compared with the model currently used to evaluate ADG.

Gompertz growth curve EBV programme are available in the MiX99 version IX/2006 (Lidauer et al. 2006). It is relatively easy to use for serial age and weight record data, if the variance components for the traits are known. Before these methods are used in practice to evaluate test station data from the Finnish National Breeding Evaluation System, more research is needed to determine how the number of records per animal, test period length or missing observations affect breeding value accuracy. In designing a breeding scheme it is important to know the genetic relationships between growth that occurs relatively early and later in the life cycle and mature size as well as maturation rate. Growth curve models allow more accurate modelling of environmental factors, and aid in developing nutritional programmes and in establishing the appropriate harvest weights and can be modified to meet differing economic conditions across time.

The present study demonstrates that selection for improved growth curve parameters could be used to improve growth rate in an effective pig breeding system. The growth curve parameters should be combined with other economically important traits to improve the overall net merit of the breeding population. Use of multi-trait selection, in this manner, can help breeders in avoiding adverse issues that could arise when selection is based solely on growth rate (Emmans & Kyriazakis 2000).

**Conclusion**

The heritabilities for Gompertz growth curve parameters were of sufficient magnitude to enable effective EBV evaluation. Thus, because of the relatively large genetic correlation between the Gompertz growth curve parameters, it is difficult to increase mature weight without decreasing maturation rate. However, based on the shape of the growth curve it is still possible to change maturation rate if needed. Because of convergence difficulty when the animal model was used, the genetic growth curve parameters were estimated using a sire model. When EBV
were calculated assuming the genetic parameters as known, there was no problem in fitting an animal model to the present data. The correlation between EBV of ADG obtained by Gompertz growth curve model or linear model was high, however individual animals’ rank differed which could impact selection decisions in an animal breeding system designed to improve growth in a pig population. The benefit of utilizing growth curves rather than ADG is that it is possible to identify pigs that grow fast when the growth rate of the pigs is evaluated in a relatively short test period. Additionally, utilization of growth curves allows recognition of pigs that can grow to relatively greater slaughter weights and produce carcases that remain lean.

References


