

Estimation of Genetic (Co)variances of von Bertalanffy and Gompertz Growth Function Parameters in Pigs

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ABSTRACT: The objective of this study was to estimate genetic (co)variances for biological parameters associated with growth functions in pig. A total of 51,594 live-weight observations from 10,133 growing pigs were available. Genetic (co)variances were calculated for growth curve parameters for the von Bertalanffy and Gompertz growth functions estimated in either a fixed effects or mixed model framework. Low to moderate heritability estimates existed for parameters of the two growth functions for both the fixed effects (0.14 to 0.46) and mixed (0.33 to 0.38) models. Significant maternal heritabilities were evident for parameters of the Gompertz growth function only.

Keywords: pigs; genetic parameters; growth functions

Introduction

The final live-weight of an animal and the rate at which an animal reaches this target is of huge economic importance, as revenue from the sale of animals generally depends on the animal's slaughter weight. Growth can be defined as the relationship between age and lifetime weight of an animal. This relationship can be mathematically modeled using growth functions that have parameters with biological meaning. Growth functions have been extensively used to describe the growth patterns and development of body weight across a range of species including pigs (Koivula et al. (2008)). A growth function must be flexible to fit any type of commercial animal production system. Other studies have shown that the Gompertz (Koivula et al. (2008)) and the von Bertalanffy growth functions (Berry et al. (2005)) adequately describe animal growth and both require the estimation of only three parameters. It has also been reported that growth curve parameters are heritable; therefore the growth curve parameters could be included in a breeding program (Koivula et al. (2008)). This could facilitate altering the shape of the growth curve through the selection of these heritable, biological growth function parameters.

The objective of this study was to estimate the genetic (co)variance of the von Bertalanffy and Gompertz growth function parameters in Finnish Yorkshire and Landrace boars, gilts, and barrows

Materials and Methods

Data. A total of 67,785 live-weight records from 14,129 growing pigs were obtained from the Finnish pig breeding company Figen Oy, between the years 2006 and

2013, inclusive. All animals originated from one station located at Längelmäki central test station in Finland. The pigs evaluated in the test station are included in the Finnish national breeding evaluation. Animals ranged between 61 and 114 days of age on entry into the test station and included entire males, females, and castrates. Animals were housed in groups according to their date of entry and gender. The number of live-weight records per animal ranged from three to eight, recorded over a 7 to 99 test day period. Animals with less than five weight recording during the test-period (n=1,510) were discarded as were animals that failed to remain on test from 86 to 92 days (n=1,639). Only animals that were recorded as finishing the trial alive and without any record of sickness throughout the test period were retained. Contemporary group was defined as entry date to the test station by gender and only contemporary groups with a minimum of five records were retained for analysis. The final dataset consisted of 51,594 live-weight observations from 10,133 animals.

Models. The von Bertalanffy (Von Bertalanffy, (1947)) and Gompertz (Winsor, (1932)) were both fitted to the live-weight data for each animal separately. The growth functions are described as follows:

$$\text{Von Bertalanffy: } Y_t = A (1 - B \exp^{-kt})^3$$

$$\text{Gompertz: } Y_t = A \exp(-B \exp^{-kt})$$

Each growth function included a dependent variable (Y_t) representing the observed weight of the animal at t days of age, and three unknown biological parameters A , B and k . Parameter A represented the asymptotic mature weight of the animal as its age approaches infinity, however it does not approximate the heaviest weight attained by the animal; B represented the integration constant; k represented the maturing rate defining the ratio of maximum growth rate to mature weight. The growth functions were fitted initially to each animal separately as fixed effects models in PROC NLIN (SAS, 2011) and progressively built up to a mixed model. The predicted parameter estimates A , B and k were obtained for each animal and limits were imposed in order to maintain biological sense.

The predictive ability of the fixed effects and mixed model was determined by masking one quarter of the weight records after 160 d and predicting these weights from the fitted functions. The models were compared on the R^2 and root mean square error (RMSE); variance

components for parameters A , B and k were then estimated using the selected model.

Statistical analysis. A linear mixed model in ASReml (Gilmour et al., (2009)) was used to estimate variance components for the biological parameters A , B and k for both models under a fixed effect or mixed model framework. Contemporary group was included as a fixed effect in all models. A direct additive genetic effect of the pig, maternal genetic effect of the dam as well as a within litter and across litter dam permanent environmental effect was included as random effects. The log likelihood ratio test between the nested models was used to determine whether the addition of extra random components (i.e. dam, dam litter effect and dam permanent environmental effect) improved the fit of the data.

Results and Discussion

The R^2 and RMSE for the Gompertz fixed effects model was 0.997 and 1.63 kg, respectively; the corresponding R^2 and RMSE for the von Bertalanffy fixed effects model was 0.996 and 1.82 kg, respectively. The best fit mixed models for both functions had parameter A and B fitted as random effects and k fitted as a fixed effect; both functions had an $R^2 = 0.994$, but Gompertz had a lower RMSE (2.28 kg) than von Bertalanffy (2.36 kg).

The mean values of the growth parameters were consistent across the two growth functions for both the fixed effects models and mixed models (Table 1). The coefficient of variation for the A , B and k parameters for the Gompertz fixed effects model were 0.36, 0.25 and 0.34, respectively; whereas the co-efficient of variation for the von Bertalanffy fixed effects model growth function for A , B and k were 0.31, 0.27 and 0.38, respectively.

Table 1. Mean values of the Gompertz and von Bertalanffy growth function parameters for the fixed effects and mixed models.

Parameter	Von Bertalanffy		Gompertz	
	Fixed Effects	Mixed Model	Fixed Effects	Mixed Model
A , kg	344.20	366.01	281.60	254.56
B	1.05	0.94	5.72	5.15
k , kg per day	0.01	0.03	0.01	0.01

The co-efficient of variation for the parameters A and B in the Gompertz mixed models was 0.11 and 0.09, respectively; the co-efficient of variation for the parameters A and B parameters in the von Bertalanffy mixed models were 0.03 and 0.05. The co-efficient of variation was not calculated for parameter k as this was fitted as a fixed effect in the mixed models for both growth functions.

Dam litter effect was not included in the final models as it did not improve the fit of the model to the data. Therefore the direct additive genetic effect of the pig, maternal genetic effect and the across litter dam permanent environmental effects were retained, as random effects, for all models.

Genetic parameters. Heritability estimates for the fixed effects growth functions are summarized in Tables 2 and 3. The direct heritability for parameters A and k for both functions were relatively similar. Direct heritability for parameter B for both growth functions was moderate (Gompertz = 0.46; von Bertalanffy = 0.44).

Table 2. Direct heritability (h^2_d), maternal heritability (h^2_m), and maternal repeatability (R_m) for the parameters A , B and k in the fixed effects Gompertz model (SE in parentheses).

Parameter	h^2_d	h^2_m	R_m
A	0.14 (0.03)	0.03 (0.01)*	0.09 (0.01)*
B	0.46 (0.05)	0.15 (0.03)*	0.18 (0.02)*
K	0.20 (0.03)	0.03 (0.01)*	0.09 (0.01)*

*Maternal heritability and maternal repeatability significantly ($P < 0.05$) different from zero.

Across all three parameters a significant maternal heritability ($P < 0.05$) was observed for the Gompertz model; however the maternal heritability was non-significant for the von Bertalanffy. Maternal repeatability was significant for all parameters for both growth functions, however it was considerably higher for the B parameter in the Gompertz function (0.18 ± 0.02) compared to the von Bertalanffy (0.06 ± 0.02).

Table 3. Direct heritability (h^2_d), maternal heritability (h^2_m), and maternal repeatability (R_m) for the parameters A , B and k in the fixed effects von Bertalanffy model (SE in parentheses).

Parameter	h^2_d	h^2_m	R_m
A	0.14 (0.03)	0.02 (0.01)	0.08 (0.01)*
B	0.44 (0.05)	0.03 (0.02)	0.06 (0.02)*
K	0.19 (0.03)	0.01 (0.01)	0.07 (0.01)*

*Maternal heritability and maternal repeatability significantly ($P < 0.05$) different from zero.

Identical direct heritability estimates existed for parameters A and B in the Gompertz and von Bertalanffy mixed models ($h^2 = 0.33$ and $h^2 = 0.38$, respectively) and were slightly lower than previous published estimates reported for sheep and pigs (Lambe et al., (2006); Koivula et al., (2008)).

Table 4. Direct heritability (h^2_d), maternal heritability (h^2_m), and maternal repeatability (R_m) for the parameters A , B and k in the Gompertz mixed model (SE in parentheses).

Parameter	h^2_d (SE)	h^2_m (SE)	R_m
A	0.33 (0.04)	0.06 (0.02)*	0.17 (0.02)*
B	0.38 (0.05)	0.37 (0.03)*	0.42 (0.02)*

*Maternal heritability and maternal repeatability significantly ($P < 0.05$) different from zero.

Maternal heritability was not calculated for the growth functions parameters in previous studies and this may account for some of the difference in the direct heritability estimates. A significant maternal heritability was also estimated for parameters A and B in both growth functions. Maternal heritability for parameter B was higher (0.38) for both growth functions than parameter A (0.06). A significant maternal repeatability was calculated for A and B for both growth functions, however it was considerably lower for the B parameter in the Gompertz function (0.17) compared to the von Bertalanffy (0.43).

The heritability of the constant of integration (B) is of little importance to this study as it does not hold any biological meaning, unlike the asymptotic live-weight (A) and rate of maturation (k), which could be selected for in a breeding program.

Table 5. Direct heritability (h^2_d), maternal heritability (h^2_m), and maternal repeatability (R_m) for the parameters A , B and k in the von Bertalanffy mixed model (SE in parentheses).

Parameter	h^2_d (SE)	h^2_m (SE)	R_m
A	0.33 (0.04)	0.06 (0.02)*	0.17 (0.02)*
B	0.38 (0.05)	0.38 (0.03)*	0.43 (0.02)*

*Maternal heritability and maternal repeatability significantly ($P < 0.05$) different from zero.

Moderate to strong negative phenotypic and genetic correlations existed between parameters A and B for the Gompertz fixed effects models (Table 6). The strong negative genetic correlation between parameters A and k for the Gompertz fixed effects model is in agreement with previous studies (Koivula et al. (2008)) indicating that selection for asymptotic mature weight will result in a slower rate of maturation across the animal's lifetime.

Table 6. Phenotypic (above the diagonal) and genetic (below the diagonal) correlations (SE in parentheses) between the parameters A , B and k for the fixed effect model in the Gompertz growth function.

Parameter	A	B	k
A			
B	-0.72 (0.04)		
k	-0.92 (0.01)	0.82 (0.02)	

Strong negative genetic correlations existed between parameters A and k (-0.95) of the von Bertalanffy fixed effects model as well as a strong positive genetic correlation between parameters B and k (0.80).

The phenotypic correlation between parameters A and B in the Gompertz and von Bertalanffy mixed models was 0.36 (\pm 0.05) and 0.34 (\pm 0.01), respectively. The genetic correlation between parameters A and B in the Gompertz and von Bertalanffy mixed models was 0.28 (\pm 0.05) and 0.26 (\pm 0.05), respectively. The genetic correlation between parameters A and B in both the Gompertz and von Bertalanffy mixed models differed greatly from the equivalent genetic correlations in the fixed effects models. However the genetic and phenotypic correlations reported in the present study for both the Gompertz and von Bertalanffy in the mixed models were similar, albeit slightly lower, than those previously reported (Mignon-Grasteau et al. (2000); Koivula et al. (2008)).

Table 7. Phenotypic (above the diagonal) and genetic (below the diagonal) correlations (SE in parentheses) between the parameters A , B and k for the fixed effect model in the von Bertalanffy growth function.

Parameter	A	B	k
A		-0.51 (0.01)	-0.86 (0.003)
B	-0.76 (0.04)		0.77 (0.01)
k	-0.95 (0.01)	0.80 (0.02)	

Conclusion

Results for this study show that ample genetic variation exists in parameters A , B and k across the Gompertz and von Bertalanffy mixed models. Knowledge of the genetic component of these parameters will allow for the growth functions to be incorporated into pig breeding programs.

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