Genetic parameters for growth of young beef bulls

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Abstract

The average daily gains of young bulls on test stations (ADGT) were analysed for the most frequent breeds of beef cattle in the Czech Republic using a multiple-trait animal model. Body weights at birth (W0), at 120 days of age (W120) and at weaning at 210 days (WW) were considered in this model as pre-weaning growth. The tested models comprised some of the random effects: direct genetic effect, maternal genetic effect, permanent animal environment effect, permanent maternal environment effect, and some of the fixed effects: dam's age, sex, herd-year-season, linear and quadratic regression on age at the beginning of the test. For optimization of the models Akaike information criterion (AIC), residual variance and likelihood ratio test were used. Coefficients of direct and maternal heritability across breeds of about 0.25 for W0, about 0.17 for W120, about 0.17 for WW and about 0.29 for ADGT were estimated by all models. All criteria selected models including the permanent animal environment effect, which was the most important effect in the model.

Keywords: beef cattle, breed, growth, genetic parameters

Introduction

Growth is a cumulative characteristic where weight gain at a given moment is influenced by the preceding history of the animal. It was demonstrated in several studies that the herd of origin effect was closely related to the growth ability of bulls in a subsequent test (Schenkel *et al.* 2004, Nephawe *et al.* 2006). This is so because environmental conditions and herd management influence weight variability at the beginning of the test, and consequently, average daily weight gains during the test are influenced. Liu & Makarechian (1993), e.g., studied the influence of bull age and weight at the beginning of the test on the growth ability of bulls under test. Different herd conditions lead to growth compensation in animals which should be distinguished from the effect of genetic potential. This is the reason why in repeated performance records (longitudinal data) the animals' permanent environment should be usually taken into account (Přibyl *et al.* 2008). These authors stated that the evaluation of growth on the basis of weight gains in consecutive growth segments was more suitable than evaluation according to body weights because it is possible to determine more exactly the effects of fixed and random environment which influence the animal growth during particular periods. In recent years great progress has been made in beef cattle breeding in the Czech Republic and other countries (Přibyl *et al.* 2003, Vostrý *et al.* 2007, Vostrý *et al.* 2008, Vostrý *et al.* 2009, Bartoň *et al.* 2010, Bene *et al.* 2010, Zahrádková *et al.* 2010, Veselá *et al.* 2011).

The objective of the present paper is the estimation of genetic parameters and the influence of pre-weaning growth on the subsequent growth of young beef bulls on performance test stations.

Material and methods

Data from a field test and from performance test stations on both body weight and average daily gains were provided by the Czech Beef Breeders Association. The evaluation was performed by a multi-breed animal model (AM) with genetic groups according to breeds incorporated into the relationship matrix. Nine breeds of beef cattle were included in the analysis – Beef Simmental (20 %), Belgian Blue (3 %), Gascon (3 %), Hereford (7 %), Aberdeen Angus (23 %), Charolais (30 %), Limousine (8 %), Blonde d'Aquitane (3 %), Piemontese (3 %). Each breed was represented by animals with an 88-100 % gene share of the given breed born between 1990 and 2005. The input database was adjusted so that the components of variance among all the considered effects in all traits would be estimable (progeny of sires that had at least 5 offspring with performance testing records).

Data

Data from the field test comprised 20 277 records of birth weight (W0), 15 598 records of weight at 120 days of age (W120) and 14 452 records of weight at 210 days of age (WW) for bulls and heifers. Data from the performance test station comprised 2 819 data on the ADGT.

From performance test station were selected only animals with complete data sets. From field test were selected only animals with a minimum of two body weight. Proportion of animals with three measurements was 90 % from animals with body weight at 210 days of age.

The data were edited so that the components of variance between all the considered effects would be estimable (Vostrý *et al.* 2007). The data set included:

1. Sires which had at least 5 offspring with tested performance.
2. Sires which had offspring in at least two herd × year × season.
3. Herd × year × season which had progeny of at least two sires.
4. Herd × year × season had at least 5 individuals.
5. Mothers which had at least two offspring and at least one half-sister.

Statistical model

Variance components and genetic parameters were estimated using the multiple-trait animal model. Different models were tested that were based on animal models used for the standard estimation of breeding value in a field test (Přibyl *et al.* 2003) and bulls on performance test stations (Přibylová *et al.* 2004). In this study, contrary to standard evaluation, herd-year-season (HYS) was included as a fixed effect in the model of pre-weaning growth evaluation. This was done because the effect corresponding to a time trend was omitted for simplification from the tested models to avoid a biased estimation of direct and maternal effect.

Models:

Multiple-trait AM –BLUP (MTAM)

I $\boldsymbol{y_1} = AgeD + Breed + Sex + HYS + a + m + peM + e$ (1)

   $y_2 = AgeD + Breed + HYS + HLCO + bAB + b^2AB + a + e$ (2)

II $\boldsymbol{y_1} = AgeD + Breed + Sex + HYS + a + m + peM + peA + e$ (3)

   $y_2 = AgeD + Breed + HYS + HLCO + bAB + b^2AB + a + peA + e$ (4)

III $\boldsymbol{y_1} = AgeD + Breed + Sex + HYS + a + m + peM + peA + e$ (5)

   $y_2 = AgeD + Breed + HYS + bAB + b^2AB + a + peA + e$ (6)

Single – trait AM – BLUP (STAM)

   $y_2 = AgeD + Breed + HYS + HLCO + bAB + b^2AB + a + e$ (7)

where y_1 is the vector of pre-weaning weight (*W0, W120, WW*), y_2 is the average daily gain in performance test stations, *AgeD* is the fixed effect of dam's age, *SEX* is the fixed effect of sex, *Breed* is the fixed effect of breed, *HYS* is the fixed effect of herd×year×season (the preweaning growth) or test station×year×season (the growth in the test station), *HLCO* is the fixed effect of herd level of calf's origin according reaction norm, $bAB+b^2AB$ is the fixed linear and quadratic regression on age at the beginning of test, *a* is the random direct genetic effect of animals, *m* is the random maternal genetic effect, *peM* is the random maternal permanent environment effect, *peA* is the random permanent environmental effect of animal and *e* is the random residual error.

Bulls were the offspring of highly selected dams and sires from the total population. There was usually only one son tested for each dam. For the reason of estimability the maternal effect was not included in the model for average daily gains traits.

We assume that effects *a* and *m* are correlated with each other and that the remaining effects (*peM, peA* and *e*) are independent each other within the particular traits. We also assume that the effects show normal random distribution with zero average and variance (σ^2).

$$V \begin{bmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{am} & \sigma_m^2 \end{bmatrix}$$ (8)

$$\boldsymbol{V}(peM) = \boldsymbol{I}\sigma_{peM}^2$$ (9)

$$\boldsymbol{V}(peA) = \boldsymbol{I}\sigma_{peA}^2$$ (10)

$$\boldsymbol{V}(e) = \boldsymbol{I}\sigma_e^2$$ (11)

where σ_a^2 is the additive genetic variance of direct effect, σ_m^2 is the additive genetic variance of maternal effect, σ_{am} is the covariance of direct and maternal genetic effects [*Cov(a,m)*], σ_{peM}^2 is the variance of the effect of maternal permanent environment, σ_{peA}^2 is the variance of the effect of animal permanent environment, σ_e^2 is the residual error variance, *A* is the additive genetic relationship matrix and *I* is the identity matrix.

The REMLF90 computation programme was used for the estimation of variance and covariance components (Misztal *et al.* 2002). The following population parameters were derived from the estimated variance-covariance components:

   σ_y^2 – *phenotype variance* [$\sigma_y^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_{peM}^2 + \sigma_{peA}^2 + \sigma_e^2$] (Willham 1972)   (12)

h_a^2 – coefficients of direct heritability $[h_a^2 = \frac{\sigma_a^2}{\sigma_y^2}]$ (13)

h_m^2 – coefficients of maternal heritability $[h_m^2 = \frac{\sigma_m^2}{\sigma_y^2}]$ (14)

c^2 – the ratio of the animal permanent environment variance to phenotype (15)
variance $[c^2 = \frac{\sigma_{pe}^2}{\sigma_y^2}]$.

The suitability of multiple-trait models was tested on the basis of estimated values of residual variance (σ_e^2) and Akaike information criterion (AIC, Bozdogan 2000):

$AIC = -2logL(\theta) + 2d$ (16)

where $logL(\theta)$ is the the natural logarithm of likelihood function and d is the the number of free parameters in the model.

The suitability of a model was also tested by expressing the ratio of the residual component to animal additive genetic variance components by means of the coefficient k:

$k = \frac{\sigma_e^2}{\sigma_a^2}$ (17)

The suitability of models was also tested by the likelihood ratio test (Kaps & Lamberson 2004), which is based on a comparison of the values of likelihood function of two models:

$\chi^2 = -2log \; \frac{L(reduced)}{L(full)} = 2[-logL(reduced) + logL\,(full)]$ (18)

where χ^2 is the the value of *chi*-squared test, $L(reduced)$ is the value of the likelihood function of a reduced model – model without effect of permanent environment of animal, $L(full)$ is the value of the likelihood function of a full model – model with effect of permanent environment of animal.

The estimates of variance components, computed by the multiple-trait model, were compared with the estimates of variance components obtained for average daily gains on identical data by the single-trait animal model (Single – Trait AM-BLUP, STAM) in accordance with Přibylová *et al.* (2004).

Breeding values (BV) were estimated by the BLUPF90 computation programme (Misztal *et al.* 2002).

Results and discussion

Values of AIC, residual variance and likelihood ratio test

The main objective was to assess ADGT using the other traits as informations. In general, relatively small differences were observed among the evaluated models.

Table 1 shows estimates of genetic and environmental variance components, residual variance, and AIC and likelihood ratio test for the particular models. The values of AIC can be compared only for models I vs. II, due to the inclusion of a different number of fixed effects in the other models. The models II comprising the effect of the animal permanent environment showed a lower value for the test criterion AIC compared to the other model (I). This indicates statistical significance of the random effect of the animal permanent environment.

Table 1
AIC, estimates of genetic and environmental variance and error probability for LRT

		AIC	σ_a^2	σ_m^2	σ_{peM}^2	σ_{peA}^2	σ_e^2	P<(LRT)
Model I	W0		4.097	1.078	0.837		10.930	
	W120	245 528	93.300	61.850	76.360		304.600	
	WW		189.800	125.500	129.300		659.600	
	ADGT		13 860.000				34 430.000	<0.0001
Model II	W0		4.114	1.093	0.833	7.109	3.809	
	W120	245 287	93.460	61.740	76.460	225.700	78.860	
	WW		189.400	125.800	129.300	613.700	46.120	
	ADGT		13 970.000			729.500	33 600.000	
Model III	W0		4.123	1.089	0.835	7.046	3.867	
	W120	245 340	93.700	61.520	76.520	229.300	75.080	
	WW		189.100	125.600	129.400	609.800	50.120	-
	ADGT		14 200.000			782.300	33 680.000	
STAM	ADGT		14 270.000				33 940.000	

As documented in Table 1, over all traits very similar values were observed for estimates of genetic and environmental variances in the different models. The only exception was AGDT, for which different values of direct genetic variance (σ_a^2) and of animal permanent environmental variance (σ_{peA}^2) were estimated. The highest value of σ_a^2 was estimated in model III. The inclusion of the random effect of the animal permanent environment in the model increased the value of σ_a^2. The omission of the fixed effect of HLCO also markedly increased the values of σ_a^2 and σ_{pe}^2 (model III). These higher values of σ_a^2 and σ_{peA}^2 (model III) document that the fixed effect of HLCO reduces the variability of these two effects.

Compared to AIC values, the values of residual variance (σ_e^2) showed a similar trend for all models. The highest values of all traits were estimated in Model I. On the contrary, a marked decrease in residual variance was observed in models containing the animal permanent environment (models II and III), when the value of residual variance was reduced by the random effect of the animal permanent environment. The greatest decrease in σ_e^2 was determined in weight at 120 days of age and weight at 210 days of age. The omission of the fixed effect of HLCO led to a minute increase in the value of σ_e^2 in weight at 210 days of age and average daily gains (model III).

Statistical significance of the random effect of the animal permanent environment was confirmed by LRT in the model comprising this effect (models II) when compared with the other model (Table 1).

Coefficients of heritability and genetic correlations

It follows from Table 2 that in the identical traits the particular models showed negligible deviations of coefficients of direct and maternal heritability (h_a^2, h_m^2), genetic correlations of direct and maternal effect (r_a, r_m), and correlations between direct and maternal effect (r_{am}). Nephawe *et al.* (2006) estimated in beef bulls higher values of heritability coefficients for weight at 210 days of age (0.22) and AGDT (0.31). The table also documents that the estimation of h_a^2 value decreases with increasing age. A similar trend was described by Meyer (2000). The estimated coefficients of direct heritability showed similar values to those reported by other authors (Waldron *et al.* 1993, Robinson 1996, Meyer 1997, Szabó *et al.*

2008, Vostrý *et al.* 2009), who estimated heritability coefficients in the range of 0.15 to 0.57. The higher value of h_a^2 for average daily gains estimated by the single-trait may be caused by the pre-selection of bulls to a rearing facility (Schenkel *et al.* 2004). The omission of the effect of HLCO, which reduced a part of the genetic variability, resulted in an increase in h_a^2.

Table 2
Estimates of direct and maternal heritability h^2 (diagonal) and correlations between effects (above diagonal)

MTAM	Model 1	W0-*a*	W120-*a*	WW-*a*	ADGT-*a*	W0-*m*	W120-*m*	WW-*m*
Model I	W0-*a*	**0.262**	0.440	0.406	−0.162	−0.631	−0.112	0.010
	W120-*a*		**0.188**	0.893	0.212	−0.309	−0.530	−0.365
	WW-*a*			**0.181**	0.203	−0.302	−0.457	−0.374
	ADGT-*a*				**0.287**	0.356	0.126	0.217
	W0-*m*					**0.069**	0.349	0.284
	W120-*m*						**0.125**	0.959
	WW-*m*							**0.120**
Model II	W0-*a*	**0.252**	0.441	0.408	−0.142	−0.633	−0.112	0.005
	W120-*a*		**0.174**	0.894	0.232	−0.310	−0.531	−0.367
	WW-*a*			**0.172**	0.214	−0.305	−0.462	−0.375
	ADGT-*a*				**0.289**	0.328	0.112	0.202
	W0-*m*					**0.067**	0.349	0.288
	W120-*m*						**0.115**	0.963
	WW-*m*							**0.114**
Model III	W0-*a*	**0.253**	0.440	0.406	−0.111	−0.633	−0.115	0.004
	W120-*a*		**0.175**	0.894	0.261	−0.307	−0.527	−0.359
	WW-*a*			**0.171**	0.237	−0.303	−0.462	−0.371
	ADGT-*a*				**0.292**	0.329	0.144	0.244
	W0-*m*					**0.067**	0.351	0.289
	W120-*m*						**0.115**	0.963
	WW-*m*							**0.114**
STAM					**0.296**			

The markedly higher value of r_a between weight at 120 days of age and weight at 210 days of age can be explained by the fact that similar environmental conditions influence these traits to a greater extent than the formation of birth weight, in which mainly the dam's internal environment plays a crucial role. No greater changes in the values of r_a between the particular traits were recorded for the tested model. Model III, without the inclusion of the fixed effect of HLCO, was the only exception in which higher values of r_a, compared to the other models were estimated between average daily gains and weight at 120 days of age, and between average daily gains and weight at 210 days of age. This higher value of r_a is caused by the estimation of the higher value of σ_a^2 for average daily gains. The results of the present paper are consistent with those of Nephawe *et al.* (2006), who, however, estimated higher values of r_a between weight at 210 days of age and average daily gains (0.47). Lower estimations of r_a between pre-weaning weight and average daily gains compared to r_a between the particular weights are caused by a correlation between the particular weights. Body weight at different ages generally shows a high correlation with other weights because the weight at age (*x*) comprises weights at preceding ages (*x*-1) (Přibyl *et al.* 2007). These results are consistent with the conclusions of Liu & Makarechian (1993), who also reported that from the genetic aspect, body weights were significantly influenced by the value of preceding body weight

but had no influence on daily gains reached in the test. It is so because pre-weaning weights influence other traits than average daily gains.

The two remaining traits had an identical value of h_m^2. Variability in birth weight was therefore influenced by direct genetic effect for the most part, which was reflected in higher values of h_a^2. In the remaining weights, when the dam influenced the newborn animal by her maternal characteristics to a larger extent, an increase in h_m^2 up to 65 % of the value of h_a^2 was recorded. The coefficients of h_m^2 showed similar values to those reported by the above-mentioned authors (Waldron *et al.* 1993, Robinson, 1996, Meyer 1997, Szabó *et al.* 2008, Vostrý *et al.* 2008, Vostrý *et al.* 2009), who published the values of h_m^2 in the range of 0.03-0.4.

The higher value of rm between weight at 120 days of age and weight at 210 days of age can be explained by the fact that the dam's maternal characteristics are fully expressed between the traits weight at 120 days of age and weight at 210 days of age, while birth weight is influenced by the direct effect of a newborn animal.

Genetic correlation between direct and maternal effect (r_{am}) was negative for particular weights (birth weight, weight at 120 days of age and weight at 210 days of age). The values of h_a^2 and h_m^2 corresponded to this high negative value of r_{am}. These values of ram for pre-weaning weights were consistent with the values reported by the above-mentioned authors (Waldron *et al.* 1993, Robinson, 1996, Meyer 1997, Szabó *et al.* 2008, Vostrý *et al.* 2008, Vostrý *et al.* 2009) (−0.594-0.223). Konstantinov & Brien (2003) considered the high negative values of r_{am} as a potential expression of sire×year interaction or sire×herd interaction. However these authors also stated that the real value of r_{am} could assume negative values. Cundiff (1972) reported that moderate negative correlations between direct and maternal effect correspond to the biological constitution of these effects because negative relationships between direct and maternal effects control and balance direct and maternal effects for growth, thus preventing the animal species from inadequately increasing body weight and body framework size on one hand and milk production on the other. The influences of sire×year interaction or sire×herd interaction on the growth abilities of beef cattle were not demonstrated in the Czech Republic (Vostrý *et al.* 2007).

The estimations of r_{am} between the tested models did not differ substantially. Model III was again an exception, in which higher values of r_{am} between average daily gains vs. weight at 120 days of age and average daily gains vs. weight at 210 days of age were estimated. These higher values of r_{am} were caused by the higher value of the estimation of σ_a^2 in average daily gains.

Animal permanent environment

The influence of the animal permanent environment (σ_{pe}^2) (Table 3) was the most important random effect for pre-weaning growth. The highest influence of this effect was estimated in weight at 210 days of age. The lowest relative value of this effect was estimated in average daily gains. Such a considerable decrease in the relative value of σ_{pe}^2 in average daily gains, compared to the other pre-weaning weights, is caused by the fact that these are different traits. It may also be due to the influence of different environmental conditions which during the test counteract the conditions acting in the course of rearing.

Table 3
Estimates of coefficients (diagonals) and correlations (above diagonals) of animal permanent environmental effects

Traits	Model I				Model II			
	W0	W120	WW	ADGT	W0	W120	WW	ADGT
W0	**0.436**	0.194	0.135	0.536	**0.432**	0.193	0.136	0.523
W120		**0.421**	0.905	0.371		**0.428**	0.901	0.476
WW			**0.556**	0.059			**0.553**	0.163
ADGT				**0.015**				**0.016**

Table 4
Coefficient k (σ_e^2/σ_a^2)

MTAM	k-W0	k-W120	k-WW	k-ADGT
Model I	2.668	3.265	3.475	2.484
Model II	0.926	0.844	0.244	2.405
Model III	0.938	0.801	0.265	2.372
STAM				2.378

The omission of the fixed effect of HLCO led to a marked increase in the value of r_{peA} between average daily gains and weight at 120 days of age and average daily gains and weight at 210 days of age (Table 3). The high value between birth weight and average daily gains is explained by the fact that birth weight is mainly influenced by direct genetic effect similar to that of average daily gains, while in the other weights (weight at 120 days of age and weight at 210 days of age), the maternal effect is also expressed to a greater extent. The estimations of r_{peA} showed an opposite trend between average daily gains and pre-weaning weights (birth weight, weight at 120 days of age and weight at 210 days of age) when compared with r_a.

Coefficient k

While in direct heritability coefficients identical values were estimated by the tested models, in coefficient *k* (Table 4), which is used for the estimation of BV in the solution of a system of equations, large differences were determined among the tested models. Similar to that in σ_e^2, lower values of *k* were estimated by models comprising the random effect of the animal permanent environment (σ_{peA}^2) (model II vs. I). The lowest values of coefficient k for weight at 120 days of age and average daily gains were estimated by tested model III, which included the random effect of σ_{pe}^2 and from which the fixed effect of HLCO was omitted. Coefficient *k* estimated by the single-trait model had lower values compared to the tested models. Lower values of coefficient *k* are more suitable for the estimation of BV because a larger part of the variability is included in direct genetic effect rather than in random error. The comparison of coefficients *k* estimated by the tested models documents that model III, which comprised the random effect of the animal permanent environment and from which the fixed effect of HLCO was omitted, showed the highest suitability for the estimation of genetic parameters and subsequently of breeding value among the tested multi-trait models.

In conclusion, bulls for performance test stations undergo pre-selection. The evaluation of bull testing along with a field test using a multi-trait AM may diminish the influence of pre-

selection of bulls for testing on the evaluation of average daily gains. The results document that the multi-trait model, also comprising pre-weaning growth, may be more suitable for more precise evaluation of the growth ability of beef bulls at performance test stations. Model III was the most suitable for genetic evaluation of the growth of beef bulls, since in addition to routinely used models, it included the random effect of the animal permanent environment and from which the fixed effect of HLCO was omitted.

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