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E-mail address of the author: pribyl.josef@vuzv.cz

Relation of own growth of sires of bulls to sons in progeny test stations

J. Pribyl[1], H. Krejcova[1], J. Pribylova[1], N. Mielenz[2], J. Kucera[3] and M. Ondrakova[3],
[1]Inst.Anim.Sci. , Uhrineves, 104 00, Czech Republic, [2]Martin-Luther Univ. , Halle-Wittenberg, 06001-06132, Germany, [3]Czech Fleckvieh Breeders Assoc., Prague, 170 41, Czech Republic

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Abstract: Live weights and daily gains of 8 243 performance tested young sires of Czech Fleckvieh (dual purpose) till the age 400 days were analysed using Random Regression (RR) and Single Trait Animal Models. Evaluations were for entire period and for daily gains in various consecutive monthly intervals. Systematic environmental effects explained a higher proportion of variability in the RR for gains in short consecutive intervals (GSCI) than for other definitions of growth. The expected average reliability of estimated Breeding Values (BV) of young animals was similar for all methods from 0.42 to 0.46, but the rankings of animals differed. Determination (r^2) of BV between methods ranged from 0.64 to 0.94. Within-method correlations of BV of parents with progeny according the data from performance-test stations were highest for the GSCI. Correlations of BV of sires for own growth at performance-test stations with the BV of net gain of groups of progeny at progeny-test stations with the final live weight around 600 kg and age 500 days were according the method of sires evaluation from 0.26 to 0.38. Preferred method was according GSCI. This method also allows include more data in the evaluations, and separate the growth curve into genetic and non-genetic parts.

Keywords: *Growth, daily gains, random regression, correlations, variances*

INTRODUCTION

The growth of animals of different categories and different species is usually evaluated on the basis of recorded live weights at different ages or by average daily gains over specified periods, assuming linearity. Single- or multiple-trait animal models (AM) have been used most frequently for genetic evaluation. Assumption of linearity is frequently not valid. Animals follow different growth patterns (Krejčová et al. 2008) due to different environments, management restrictions, and compensation from changing environments. Animals with high growth potential are negatively affected by unfavourable environmental factors more than animals with poor growth capability.

Growth can be evaluated using repeated weighings of each animal and model the growth trajectory. Different linear and nonlinear growth curves have been used (Hyánek, Hyánková 1995, Nešetřilová 2005, Vuori et al. 2006). Evaluation of longitudinal data has been attempted using Random Regression Animal Models (RR), which account for systematic environmental factors and also genetic and non-genetic factors, including functional dependencies between repeated measurements on the same animal (Legarra et al. 2004, Bohmanová et al. 2005, Meyer 2005 and Přibyl et al. 2007, 2008). Live weights of cattle at different ages are highly correlated, because weight is a cumulative trait, and the subsequent weight includes previous weights at younger ages. Live weights accumulate the history of systematic external and internal factors which are difficult to separate accurately at the moment of evaluation. Besides the evaluation of live weights, daily gains from one age to another can be fit by an RR (Krejčová et al. 2007).

OBJECTIVES

The purpose of this paper was to compare different expressions of growth for the genetic evaluation of animals in a case of restriction of nutrients.

MATERIAL AND METHODS

The live weights of young bulls at performance-test stations, taken at 1-month intervals from approximately 1 to 17 months on age, were used for the study. Bulls of different ages are present in the test station at any given time. Nutrition was regulated for a maximum daily gain of 1.3 kg.

The weights at 1-month intervals were designated as W1m. Gains from month to month were calculated as the difference between two consecutive weights and were designated as G1m. In addition, gains for the period from 100 to 400 days of age (designated as Gp) were calculated. From the analysis of W1m, the difference of live weight at age 400 and 100 days (designated as W1mD) was calculated. Finally, let W400 designate the live weight at 400 days of age.

The data consisted of bulls with more than two weighings, with more than 4 paternal half-sibs and with more than 4 contemporaries in the station-year-3month season of birth classes (SY3), and station-year-3month season of weighing classes (TDS3). After editing, there were 8 243 bulls within 303 TDS3 classes, representing the progeny of 349 sires. The number of observations per animal differed according to the trait under evaluation (Table 1).

Table 1: Data sets for Random Regression (RR) and Single Trait Animal Models (AM) analysis

Trait and Methods	Animals with records	Animals in pedigree	Records	Mean	StdDev
Gp g/d	7 461	15 065	7 461	1 217.27	121.21
G1m. g/d	8 243	16 488	79 796	1 188.23	352.74
W400 kg	7 461	15 065	7 461	499.14	42.42
W1m kg	8 243	16 488	79 796	290.02	130.16

G – Daily gain (g/day); W – Live weight (kg);
1m – Repeated average daily gains or weights in 1-month consecutive intervals between weighings;
Gp – Average daily gain from 100 to 400 days of age;
W400 – Live weight at 400 days of age;
StdDev – Average standard deviation of records;

The monthly gains and weights were analysed using a random regression (RR), while Gp and W400 were analysed with a single-trait animal model (AM).

For the RR model the analysis was done according to the following equation:

$$\mathbf{y} = \mathbf{X}_{SY3}\,\mathbf{f}_{LP} + \mathbf{X}_{TDS3}\,\mathbf{tds} + \mathbf{Z}_{\mathbf{G}}\,\mathbf{f}_{G} + \mathbf{Z}_{\mathbf{PE}}\,\mathbf{f}_{PE} + \mathbf{e} \quad ,$$

where: $\mathbf{y}$ – measured values of monthly weight or gain
$\mathbf{X}_{SY3}$ – the incidence matrix for station-year-3month season of birth (**SY3**) classes
$\mathbf{f}_{LP}$ – average growth curve according to groups of bulls within **SY3** classes (fixed effect)
$\mathbf{X}_{TDS3}$ – the incidence matrix for station-year-3month season of weighing **(TDS3)** classes
tds – the vector of station-year-3month season of weighing classes (fixed effects)
$\mathbf{Z}_{\mathbf{G}}$, $\mathbf{Z}_{\mathbf{PE}}$ – incidence matrices for the animal
$\mathbf{f}_{G}$ – the function for the genetic deviation of the individual growth curve of the animal (random effect with additive relationship matrix)
$\mathbf{f}_{PE}$ – the function for the deviation of the individual growth curve under the effect of the permanent environment of the animal (random effect)
$\mathbf{e}$ – random residuum

In the case of longitudinal analysis of daily gains (G1m) Legendre Polynomials were used for $\mathbf{f}_{LP}$, $\mathbf{f}_G$ and $\mathbf{f}_{PE}$ effects. In the case of live weight (W1m) Linear Spline functions were used for $\mathbf{f}_G$ and $\mathbf{f}_{PE}$. All the functions had 5 parameters. A detailed description of the methodology is in Krejčová et al. (2008) and Přibyl et al. (2007, 2008a, b).

In the case of single traits (Gp and W400), a linear model with only one fixed effect (**sy3)** and additive animal genetic effects (**a**) with relationship matrix was used.

$$\mathbf{y} = \mathbf{X}_{SY3}\,\mathbf{sy3} + \mathbf{Z}_G\,\mathbf{a} + \mathbf{e}$$

Calculations of RR were done for the period from 6 to 520 days of age of the bulls. The polynomial curves show generally rather high variability and no logical values at the beginning and the end of the observed period. The results are therefore formulated for a part of the growth curve without boundary values from 100 to 400 days of age only.

Variance components were estimated by REML (REMLF90 program, Misztal et al. 2002). Heterogeneous variability in the course of growth was handled by weighted analysis. Coefficients of weights for weighted analysis were relative reciprocal values of the variance of a trait at a given age. The variance components for Gp and W400 from AM analysis were available directly from REML calculations. For traits from RR analysis (G1m, W1m and W1mD) the variance components were derived from the covariance matrix of random regression coefficients.

Estimates of genetic (G) and permanent environmental (PE) components for each day during the test period were obtained by

$$VC_{t,t'} = \mathbf{p}_t{}^{\prime}\,\mathbf{C}\,\mathbf{p}_{t'} \qquad ,$$

where: $VC_{t,t'}$ – genetic ($VG_{t,t'}$) or the animal's permanent environment ($VPE_{t,t'}$), covariance of growth trait between age (t) and (t')

$\mathbf{p}_t$, $\mathbf{p}_{t'}$ – vectors of parameters of curves at age (t) and (t')

C – the covariance matrix of regression coefficients for the genetic or permanent environment effect on the animal

Values for cumulative gain have the abbreviation ending "cel". Cumulative (co)variance components up to the times (j) and (j') ($CVC_{j,j'}$**)** were calculated according to the sum of the vectors of parameters from the age of bulls 100 days to the given age.

$$CVC_{j,j'} = \left(\sum_{t=100}^{j} p_t\right)' C \left(\sum_{t=100}^{j'} p_t\right)$$

The residual (RE) variances were estimated as the ratio of the average REML estimate of the residual variance to the weight factor depending on the age. The residuals for each day of age were assumed to be independent of all other days of age, and therefore the overall residual variance was the sum of the estimates for each day.

Breeding values from RR of daily gain or live weight for animal (i) at age (t) were

$$BV(t)_i = \mathbf{g}_i{}'\mathbf{p}_t \,,$$

where: $\mathbf{g}_i$ – the vector of genetic regression coefficients for animal (i) from the function $\mathbf{f}_G$

The breeding value of cumulative gains is just the sum of daily breeding values for a period from 100 to 400 days of age.

For animals with production records (not for ancestors in the pedigree), correlations of breeding values (BV) between the different methods of evaluation were calculated for the traits of cumulative gains, live weights, and differences in live weight. For each method of evaluation, correlations between progeny and parents that reflected the Mendelian sampling and prediction error were calculated (Schaeffer et al. 1996). The correlations of BV of sires' own growth at performance-test stations with the net gain of groups of sons at progeny-test stations were also calculated. The BV of tested progenies was taken from the official national evaluation.

RESULTS AND DISCUSSION

The fixed effects included in the models were tested prior to this study by GLM/SAS procedures and were statistically significant for all evaluated traits and statistical models (Přibyl et al. 2007, Krejčová et al. 2008).

Components of variance

Covariance components were calculated for daily gains, cumulative daily gains, live weight, and difference in live weights. Table 2 shows standard deviations for separate components according to the trait and method of evaluation.

I. Daily gains (g/day)

All components changed with the age of the animal. Table 2 shows only average values over days 100 to 400. ST-AM gave higher genetic components (G) than the RR models and lower residual components (SRE). Phenotypic variability changed with residual variability. Heritability in the RR models was much lower than that for a long, 300-day period, evaluated by ST-AM (Gp). Differences in heritability were caused by differences in residual variability, the genetic components between methods were more similar.

Table 2: Standard deviations of variability components and heritability. SG is the genetic component, SPE is the permanent environmental component, SRE is the residual component, and SP is the total phenotypic SD

	Gp	G1m	W400	W1m	W1mD
Daily gain, average during the period from 100 to 400 days of age (g)					
h^2	0.36	0.03			
SG	**58.99**	**52.66**			
SPE		10.45			
SRE	78.42	300.74			
SP	98.13	305.67			
Cumulative gain from 100 to 400 days of age and live weight at 400 days of age (kg)					
h^{2}cel	0.36^b	0.87	0.36	0.34	0.34
SGcel	**17.70**^{b}	**13.68**	21.64	21.86	**17.70**
SPEcel		1.39		29.03	23.14
SREcel	23.52^b	5.23	28.63	10.12	8.98
SPcel	29.44^b	14.66	35.89	37.72	30.48

cel – Cumulative values from 100 to 400 days of age;
^{b} – Average daily gain multiplied by 300;
W1mD – Deviation (weight at 400 days of age – weight at 100 days of age) calculated from the RR model;

II. Cumulative gains from 100 to 400 days of age (kg)

The values of standard deviations for cumulative components have the ending "cel". ST-AM for gains from 100 to 400 days of age (Gp) and deviations of weight according to RR (W1mD) have much higher genetic components (SGcel) than the cumulative gains at 400 days of age according to the RR models for gains in short interval (G1m). The cumulative values according to RR for gains at 400 days of age for permanent environment (SPEcel) and random environment (SREcel) were very low. The accumulation in the RR models for gain was much higher for the genetic component

(SGcel). This accumulation is practically the selection index with summation of everyday breeding values (economic values constant = 1). The components of variance express variability of the index in this case. The RR models for daily gains yielded much lower cumulative phenotype standard deviations (CPcel) than ST-AM for gain over a long period and than evaluations of live weight. This documents that systematic environmental effects in the RR models for gain in short consecutive intervals explain the much higher proportion of variability than in ST-AM for a simple trait covering a long period.

The values of (h^2cel) in RR for gain represent the ratio of components after linear combination of traits into the complex selection index. It is not a question of the heritability of a simple trait, but rather the reliability of a composite trait.

III. Weight at 400 days of age

Our selection criterion was live weight at the age 400 days. Covariance components for live weight develop notably with the age of the animal (Přibyl et al. 2007, 2008).

The heritability of live weight, deviation of live weight and daily gain according to the simple trait (Gp) for the period from 100 to 400 days yielded similar values. The values of heritability were comparable with those reported by other authors (Pulkrábek et al. 1983, Kirkpatrick et al. 1990, Bouška et al. 2003).

Variability of cumulative breeding values

Cumulative breeding values (BV) were calculated from recorded traits (Table 1) by the RR and AM methods. Standard deviations of cumulative BV are summarised in Table 3. The highest values were for evaluation of weight, lower for evaluation of a difference in live weight and daily gain over a long interval (BVW1mD, BVGp) and the lowest for evaluation of short consecutive intervals of gain. Standard deviations of breeding values for all animals included in the pedigree file were smaller than for animals having production records. The ratios of this variability (V_{All}/V_{Prod}) were the highest for the RR models of gains (BVG1m). The RR models maintain a higher variability of parents in the pedigree file, which should correspond to the higher precision of genetic evaluation of parents without production records.

Table 3: Standard deviations of cumulative breeding values (BV) and of production records in kg at 400 days of age and the ratio of variability

Variable	SD of BV		Ratio	SGcel	Ratio
	All	Prod	V_{All}/V_{Prod}		V_{Prod}/V_G
CG [b]		36.92			
BVGp	9.78	11.70	0.71	17.70	0.44
BVG1m	8.02	8.94	**0.82**	13.68	0.43
W400		42.78			
BVW400	11.84	14.01	0.71	21.64	0.42
BVW1m	**12.42**	**14.33**	0.76	**21.86**	0.43
BVW1mD	10.37	12.04	0.76	17.70	**0.46**

[b] – Average daily gain in kg from Table 1 multiplied by 300;
All – All animals in pedigree file;
Prod – Animals with production records only;
V_{All}/V_{Prod} – Ratio of variability of BV of all animals and only animals with production records;
V_{Prod}/V_G – Ratio of variability of BV of animals with production records and variability genetic;

The differences between standard deviations of breeding values (SD) in Table 3, according to the method of evaluation, correspond to the differences between genetic standard deviations for cumulative traits (SGcel) from Table 2. Although methods differed in the variability of breeding values, the ratio of variability V_{Prod}/V_G was quite similar for all methods, ranging from 0.42 to 0.46. The ratio of variability V_{Prod}/V_G represents the average reliability of breeding value estimation.

The standard deviations of BV of daily gains calculated by RR were in a smaller proportion from standard deviations of measured cumulative records (CG), about 1/4, compared to standard deviations of BV of live weight from live weight records (W400), about 1/3. Systematic environmental effects in the RR model for gain accounted for a higher proportion of variability than in ST-AM.

Correlations among cumulative breeding values (only animals with production records)

Correlations between BV were calculated only for animals with production records and are summarised in Table 4. All the correlations were highly significantly different from zero. Particular methods handle environmental factors and dependences between growths in different phases differently. Therefore, the similarity between methods is only partial.

The correlation between production records of weight at 400 days of age (W400) and gain from 100 to 400 days of age (CG) was 0.89. ST-AM for gain (BVGp) yielded correlations with the methods according to RR for gain 0.88. The correlation of breeding values of live weight evaluated by the AM (BVW400) and RR (BVW1m) methods was 0.94. Daily gain for the entire period of 100-400 days of age evaluated by ST-AM (BVGp) and for the same interval evaluated by RR for weight (BVW1mD) was correlated at 0.92. ST-AM of weight and ST-AM of gain for the entire period gave a correlation of 0.90. Production records of weight (W400) and production records of gain for the entire period (CG) yielded higher correlations with evaluation by ST-AM than with evaluation by the RR models.

Table 4: Correlations of BV for cumulative values at 400 days

	BVGp	BVG1m	W400	BVW400	BVW1m	BVW1mD
CG	0.79	0.65	0.89	0.70	0.64	0.72
BVGp	1	0.88	0.73	0.90	0.83	0.92
BVG1m		1	0.61	0.80	0.83	**0.94**
W400			1	0.80	0.77	0.69
BVW400				1	**0.94**	0.84
BVW1m					1	0.90

Parents – progeny correlations (Mendelian sampling) of cumulative breeding values

Correlations of BV for cumulative growth between generations are influenced by Mendelian sampling and by the error of evaluation. Mendelian sampling was similar in our study for all methods; therefore, differences between methods in parent – offspring correlations depend mainly on the reliability of BV estimation of both groups of animals. Parent – progeny correlations of BV for cumulative growth are summarized in Table 5.

Table 5: Correlations of cumulative BV of parents with progeny (animal-A, sire-S, dam-D)

	All animals in pedigree file					Only if sire has production records	
	Sires	N_S	N_{SD}	Correlation		Correlation 2	
				A x S	A x (S+D)/2	A x S	A x (S+D)/2
BVGp	1 582	13 218	7 806	0.72	0.91	0.27	0.65
BVG1m	1 670	15 018	9 000	**0.81**	**0.95**	**0.52**	**0.83**
BVW400	1 582	13 218	7 806	0.69	0.90	0.42	0.72
BVW1m	1 670	15 018	9 000	0.73	0.91	0.45	0.76
BVW1mD	1 670	15 018	9 000	0.76	0.92	0.42	0.77

N_S – Number of progeny with known sire; N_{SD} – Number of progeny with both parents known;
Correlation 2 – Two runs, the first only with sires without progeny, the second with complete data set, sires from the first run, progeny + dam from the second;

Three generations of ancestors were available. The methods differ partly in the number of sires (Sires), in the number of progeny with known sires (N_S), and also in the number of progeny with both parents known (N_{SD}).

The correlations between sires and sons were from 0.69 to 0.81. The highest were for RR of daily gain, lower for RR of weight, and the lowest for the ST-AM methods. Correlations between the averages of both parents with their sons were much higher (from 0.90 to 0.96). In a case of restriction only to sires with production records the lower numbers of animals were evaluated. Correlations were lower than for correlations using all animals in the pedigree file. In all cases the rank of methods was similar.

Correlation with progeny at progeny-test stations

The objective of the study was to determine the best prediction method for the growth potential of future progeny. Table 6 shows the correlations of BV of sires according to own growth at performance-test stations and BV according to net gain of groups of their sons at progeny-test stations. The sons were slaughtered at live weight of about 600 kg and 500 days of age. From the file of BV of progeny test only sires with 11 or more progeny were taken. The set comprised 387 sires (bulls in our database of performance test). Correlations ranged from 0.26 to 0.37. The RR methods for gain in short consecutive intervals were better for the prediction of net gain of progeny than the other methods. The lowest values of correlations were for evaluation of sires according to their own live weight. The magnitudes of correlation coefficients should depend on the selected data sample, but the tendency of comparison of methods prefers the RR evaluation of daily gains in short, repeated consecutive intervals.

Table 6: Correlations of BV according to the own performance test of sire with BV according to sons in progeny-test. 387 performance-tested sires were evaluated. The minimum number and average number of progeny per sire are 11 and 11.79

BVGp	BVG1m	BVW400	BVW1m	BVW1mD
0.33	**0.37**	0.30	0.26	0.30

CONCLUSIONS

The comparison of methods was on the basis of cumulative daily gains from 100 to 400 days of age or live weight at 400 days of age. The evaluation of daily gains by RR allows different growth curves for each animal and yields BV for each day during the growth period. However, in this case a greater number of parameters must be estimated for each animal. The cumulative value is, in reality, a selection index with the same weights placed on all combined traits (all partial BV).

Some methods yield similar reliability, but they partly differ in the selection of animals. The reliability of prediction of the results of one method by another one is the square of correlations between the methods. Determination (r^2) between methods ranged from 64 to 94%.

Methods differed in the prediction of genetic variability. The RR models for daily gain in short consecutive intervals showed the lowest genetic variability. The genetic component of variability for live weight or daily gain over a long interval probably includes some artefact that also covers the non-genetic part deriving from the accumulation and compensation in consecutive periods of growth. The methods differed in phenotypic variability. The RR models for daily gain of short consecutive intervals gave the lowest phenotypic variability. Therefore, the RR models for daily gains over short consecutive intervals better deal with the systematic influences of external and internal environments during the entire period of growth of the animals.

The results of BV from the RR models differed more from production records than the results of BV from ST-AM. The RR model allowed the evaluation of the largest number of animals by exploiting all the available records of the animal. Correlations between parents and offspring were the highest for the RR methods for gain in short consecutive intervals. The variability of parents without their own individual production records in the pedigree file in comparison with animals with production records was also proportionately higher for these procedures.

Correlations of breeding values according to two independent data sets – own growth of sires at performance-test stations and progeny test with sons at progeny-test stations – favoured RR evaluation of growth according to daily gain in short, repeated consecutive intervals.

The best overall results were for the evaluation of growth according to daily gains in repeated consecutive intervals. Simple evaluation of growth according to the final weight or daily gain over a long interval is not entirely correct. The results seem to be generally acceptable for all species and categories of animals.

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