

Models for evaluation of growth of performance tested bulls

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ABSTRACT: Before being used for insemination, young bulls of Czech Fleckvieh (CF) are tested for growth at performance-test stations. While at stations, the bulls are weighed monthly. Evaluation included 7 448 bulls with 82 676 records of weight measured from 6 to 520 days of life. In the station-year-period (HYS), which can be prolonged up to 3 months, different groups were tested according to the beginning of growth curve and according to test-days of weighing. Weight analyses were used to handle heterogeneous variability based on age. Legendre Polynomials (LP) with 5 parameters described the average growth curve for HYS classes. Deviations from average curves were decomposed into genetic (G), animal's permanent environment (PE) and residual (RES) components. Functions of (G) and (PE) were tested using LP random regression (RR) methodology with 5 or 3 parameters and Linear Spline (SP) function with 5 knots. Variance increases with the age of the animals. From 100 to 400 days, heritability was nearly the same with a mild depression in the middle of the period. The average was $h^2 = 0.31$ and ended with $h^2 = 0.36$. Results were similar for variance components, heritability, genetic, environmental and phenotype correlations from different models with different LP and SP functions. Higher RES variability occurred only for LP with 3 parameters. For traits like live weight, the RR should have at least 3 parameters and SP function should be used.

Keywords: cattle; random regression; heritability; statistical model; growth curve; bulls

Growth is one of the essential traits to evaluate bulls for selection. Performance data of young bulls allow the selection at an early age. All bulls of Czech Fleckvieh (CF) breed (Simmental type), candidates to insemination, are tested for growth at test stations with standard environment and moderate nutrition. Therefore, the genetic evaluation of young bulls is an important part of selection. Bulls from selected dams and sires are continually placed to stations at an early age (before 60 days). Therefore, the weight testing consists of groups in different phases of growth. During rearing, the bulls are repeatedly weighed. The growth of CF

bulls at test stations, including genetic parameters, was analyzed by Pulkrábek et al. (1984), Přibyl et al. (1986), Hyánek and Hyánková (1995), Bouška et al. (2003) and Nešetřilová (2005).

Vuori et al. (2006) analyzed nonlinear methodology of the mixed effects model for the Gompertz growth curve, and Varona (2004) compared the methodology of Random Regression (RR) and methodology of production growth curve. Nobre et al. (2003) used the RR model to evaluate live weight in a large population of beef cattle. Albuquerque and Meyer (2002), Arango et al. (2002), Bohmanová et al. (2005) and Meyer (2005) evaluated genetic

Table 1. Measured live weights ($n = 82\ 676$)

	Mean	SD	Min	Max
Age days	233	110	6	520
Live weight kg	298	139	40	770
SD of live weight within age class	32		12	48
w	1.003	0.882	0.342	6.259

w = weighted factor

and phenotypic covariance functions for different growth stages in beef cattle. Rasch and Mašata (2006) compared several methods of estimating variance components, the essential part of evaluation.

Příbyl et al. (2007) describes RR methodology of growth evaluation for dual-purpose CF bulls at test stations. Legendre Polynomials (LP) were used to express the dependence of live weight on age for a fixed part of the equation (function within station-year-period (HYS) classes) and Linear Splines (SP) for random parts (the animal and its permanent environmental effects). In contrast to the previously mentioned authors who worked with beef breeds, maternal effect was not included because the bulls are carefully selected; the majority of mothers have only one son in the database, and bulls enter the stations at a very early age. SP function sufficiently described the trajectory of estimated variance components. Heritability was in a moderate value, growing slowly with the age of the animal to the value $h^2 = 0.45$ at 400 days. Genotype, animal's permanent environment, and phenotype correlations between body weights at different ages were high. Though variability significantly increases with the age of the animals, the evaluation of this heterogeneous variance in testing did not influence the results.

Since observations within stations and time periods are limited, some clustering into HYS classes and model tuning are needed. The animals are usually grouped according to the expectation of a similar curve with respect to the systematic effects. However, Krejčová et al. (2007) constructed a fixed regression curve within test-days classes of observations of different animals.

The objective of this paper was to compare models with different classification of systematic environmental factors and different types of RR functions for growth evaluation of young bulls.

MATERIAL AND METHODS

The updated database consisted of 7 448 CF bulls – candidates for breeding, which were kept at seven performance-test stations with regulated nutrition from 1971 to 2005. The first known weight of each animal was obtained before 60 days of age when the animals entered the station. The ages ranged from 6 to 520 days. Weighing occurred in around 30-day intervals. Each bull was weighed 11 times on average. Close test-days within the station with a small number of animals were grouped. Within a one-month period of test-days, testing resulted in 119 observations on average. After all adjustments were made, a total of 82 676 weight records were available. Average daily gain from birth is about 1.19 kg/day. Descriptive statistics of the whole dataset are in Table 1.

The evaluated bulls were offspring of 327 sires, and in the dataset each young bull at the performance-test stations had 22 half-sibs on average. In the older part of the database, only sires in pedigree until the birth year 1990 were considered. In a new part of the database (1/3 of the dataset), the complete 3 generations of ancestors are used. The total number of animals, including the pedigree file, is 13 608.

Genes of related breeds of Simmental family, Red Holstein and Ayrshire (Ayrshire in the 1960s, Red Holstein 1970s, Simmental recently), were also introduced into the CF breed during the history. In the oldest parents' generation ancestors were therefore grouped into phantom parent groups (PPG) of CF and others breeds, in combination with sex and with the year of birth category (< 1971, 1971–1980, ≥ 1981). Animals with more than 50% of CF and related Simmental breeds are considered as CF. In dependence on frequency 11 groups are used. In PPG 86% of sires and 77% of mothers were CF. In the total pedigree file 44% of animals have known

both parents, 43% have one parent and 13% both parents in PPG.

To analyze the variability in the growth curve, all records were divided according to age into 45 ten-day classes. Standard deviations within classes are in Table 1.

Příbyl et al. (2007) describes the methodology of evaluation. The growth of animals and variability of traits in relation to age were fitted by functions (f) of orthogonal Legendre Polynomials (LP) and Linear Spline (SP).

$$f = p'b$$

where:

b = vector of regression coefficients

p = vector of parameters of the function

P terms (n -th parameter) in LP were calculated according to standardized age from the formula of Rodriguez (Rektorys et al., 1963) and standardized for the variability of each parameter close to 1 (Kirkpatrick et al., 1990; Schaeffer et al., 2000). Functions with 3 or 5 parameters were used.

P terms in SP express the proportional distance from neighbouring knots. Five parameters were used. The sum of the values of neighbouring parameters is 1, and the values outside are 0. Knots were located at equal distances, covering the whole age range of 6–520 days.

The fixed effects that influenced growth were analyzed using SAS/GLM and MIXED procedure. Simple and weighted analysis was used to investigate the influence of heterogeneous variability. The “weight” (w) in weighted analysis is the relative reciprocal value of variance at age (i). It is calculated as average interclass variance (V_{aver}) during the whole growth period divided by variance depending on the age of the animal (V_i) modelled by LP. The values of w are adjusted so that their average in the whole dataset will be 1 (sum of weights = number of observations). Range of w for total dataset is in Table 1.

Average growth curves were modelled by LP of degree 4 with parameters p_0, \dots, p_4 . Models with different fixed effects were tested:

Model 1 – LP

Model 2 – LP within the station-year of birth combination (sy) + the effect of months of weighing-year-station combination (tds)

Model 3 – LP within the station-year-3-month period of birth combination ($sy3$) + tds

Model 4 – LP within sy + the effect of 3-month period of weighing-year-station combination ($tds3$)

Model 5 – LP within $sy3$ + $tds3$

Model 6 – LP within $tds3$.

Genetic effects of animal (G) and animal's permanent environment (PE) were added to models 2 – 6 by RR, and these models were used for variance component estimation by REML (REMLF90 programme; Misztal et al., 2002). The estimation was done according to the mixed model equation:

$$y = X_{SY}f_{LP} + X_{tds}tds + Zf_G + Zf_{PE} + e$$

where:

y = measured values of weight

X_{SY} = the incidence matrix for sy or $sy3$ classes

f_{LP} = average LP growth curve according to groups of bulls within sy or $sy3$ classes (fixed effect)

X_{tds} = the incidence matrix for tds or $tds3$ classes

tds = 1-month or 3-month period of test-days of weighing (fixed effect)

Z = the incidence matrix for animals

f_G = function LP or SP for the genetic deviation of individual growth curve of the animal (random effect with relationship matrix)

f_{PE} = function LP or SP for the deviation of individual growth curve under the effect of permanent environment of the animal (random effect)

e = random residual

In model 6 ($X_{SY}f_{LP} + X_{tds}tds$) are substituted by ($X_{tds3}f_{LP}$).

Genetic and environmental components of covariance for live weight were determined by the equations:

$$VC_{i,i'} = p_i C p_i'$$

where:

$VC_{i,i'}$ = genetic ($VG_{i,i'}$) or animal's permanent environment ($VPE_{i,i'}$), covariance of growth trait between age (i) and (i')

$p_i p_i'$ = vectors of parameters at age (i) and (i')

C = the covariance matrix of regression coefficients (b_G) or (b_{PE}) for the genetic or permanent environment effect of the animal

The residual covariance matrix is diagonal. The residual component (VRE_i) was calculated as the ratio of the residual variability (V_e) from the statistical model to the value of weight (w_i) from the function describing the dependence of the trait variability on animal age.

$$VRE_i = V_e/w_i$$

RESULTS AND DISCUSSION

Table 1 shows the measured values. Body weight increases linearly with age, and within the classes standard deviations increase with age as well (from

minimal to maximal values in Table 1). Weighted factor (w) was adjusted so that the average value in the whole dataset would be 1 (not for mediate age).

Statistical parameters of Models 1–6 with only fixed effects are in Table 2. In all models, all effects are statistically significant. The most suitable values are in tables marked.

Average standard deviations within the classes for simple analysis (Table 1) correspond with the error to standard deviations (SD_e) for Model 1, which has only a polynomial function (Table 2). The complexity of the model decreases the SD_e and increases the value of determination coefficients (R^2). The

number of parameters has only a small influence on the results due to a large number of observations. Compared to Model 1, the inclusion of additional systematic effects influences a reduction in SD_e , but the values of determination coefficients in tested models are influenced very little. Differences between Models 2–6 are small. Bayesian information criterion (BIC), which takes account of the number of estimated parameters in the model, is in agreement with the determination coefficient and the reduction of variability.

Weighted analysis resulted in a decrease in residual variability. In contrast to our previous paper (Příbyl et al., 2007), when the weight was equal to

Table 2. Validity of the model with fixed effects

Model	1	2	3	4	5	6
Independent parameters	4	996	1 765	542	1 311	1 190
Simple analysis						
SD_e (kg)	32.20	26.72	26.27	26.75	26.33	26.51
R^2 (%)	94.46	96.28	96.40	96.27	96.39	96.34
BIC	808 758.80	773 146.00	765 831.70	775 826.30	768 714.80	769 495.70
Weighted analysis						
SD_e (kg)	26.20	22.00	21.62	22.04	21.67	21.82
R^2 (%)	95.97	97.16	97.26	97.15	97.24	97.21
BIC	794 789.50	761 475.70	754 344.00	764 115.00	757 129.00	757 813.90

SD_e = residual standard deviation; R^2 = determination coefficient corrected according to the degree of freedom of the model; BIC = Bayesian Information Criterion

Table 3. Models of weighted analysis with added random effects (REML calculations)

Model	2	3	4	5	6
Random LP with 5 parameters					
SD_e (kg)	6.65	6.57	6.91	6.82	6.71
-2logL	625 126.74	618 982.15	631 456.58	625 260.98	625 566.06
AIC	625 228.74	619 084.15	631 558.58	625 362.98	625 668.06
Random LP with 3 parameters					
SD_e (kg)	7.66	7.54	7.92	7.76	7.74
-2logL	635 246.62	629 442.81	642 108.61	634 779.33	633 839.83
AIC	635 284.62	629 482.81	642 146.61	634 817.33	633 877.83
Random SP with 5 knots					
SD_e (kg)	6.60	6.52	6.88	6.76	6.70
-2logL	632 815.55	626 102.39	638 718.20	631 966.50	633 020.47
AIC	632 917.55	626 204.39	638 820.20	632 068.50	633 122.47

-2logL = Log-likelihood multiplied by -2; LP = legendre polynomials; SP = linear spline; AIC = Akaike's Information Criterion

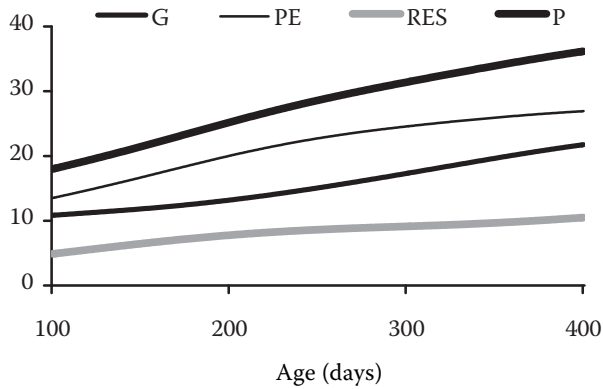


Figure 1a. Standard deviations for phenotype (P), animal's genetic (G) and permanent environment (PE), and residual (RES) components according to LP function with 5 parameters in dependence on the age of animal

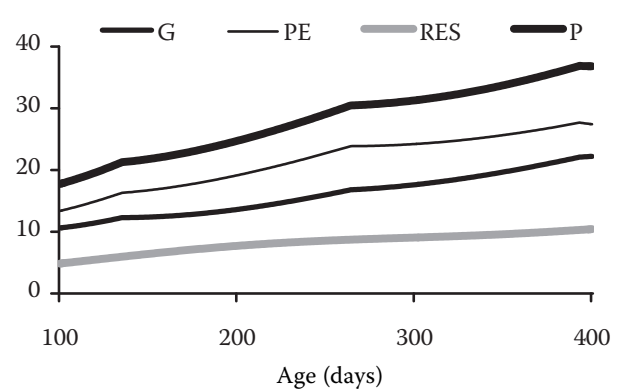


Figure 1b. Standard deviations for phenotype (P), animal's genetic (G) and permanent environment (PE), and residual (RES) components according to SP function with 5 parameters in dependence on the age of animal

1 for mediate age and the weights did not influence the value of residual variability, the weighted coefficient has an average value 1 in this present case (sum of weights = number of observations). In weighted analysis, R^2 is approx. 1% higher than in simple analysis, like in our previous paper. The adjustment of weights (w) for weighted analysis has only a numerical impact and does not influence the comparison of models. The differences between models are similar to those in the simple analysis.

The distribution of station-year of birth (sy) classes into station-year-season of birth ($sy3$) classes has a larger impact (comparison of Models 2:3 and 4:5)

than the length of the test-day-season period of weightings (tds) and ($tds3$) (comparison of Models 2:4 and 3:5). Results of Model 6 correspond with the other models and are dependent on the number of independent parameters. Model 3 is the most suitable, but in practice it could cause a low number of equalities in some tds classes. Model 5 is the second most suitable.

Results from REML calculations of weighted analysis of random animals and their permanent environmental functions are in Table 3. Models 2–6 were tested by LP with 5 and 3 parameters and SP with 5 knots. SD_e are much smaller than those from fixed effects models (compare Tables 2 and 3). LP

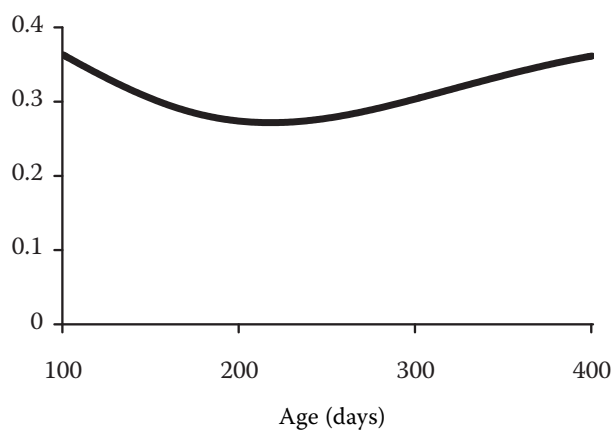


Figure 2a. Heritability of body weight depending on the age of animal for LP function with 5 parameters

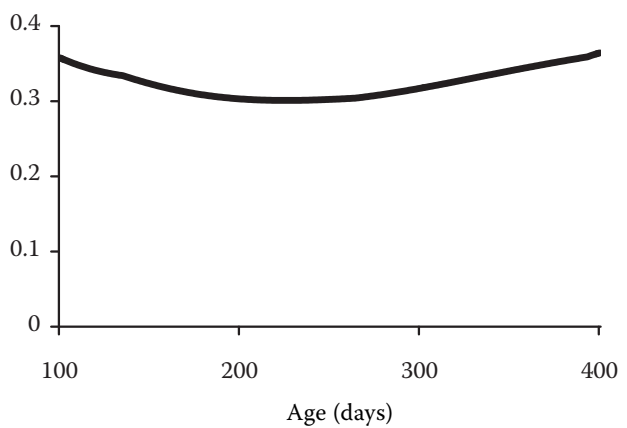


Figure 2b. Heritability of body weight depending on the age of animal for SP function with 5 parameters

models with 3 parameters have higher values of SD_e than do models with 5 parameters. SP models with 5 knots have advantages of up to 1% less SD_e than LP models with 5 parameters.

According to AIC within Models 2–6, LP with 5 parameters are the most suitable models. Cases of SP functions with tested optimal locations of knots could slightly improve the results. In all cases Model 3, which has the highest number of parameters, has the lowest standard deviation. These values also correspond to the most suitable values for likelihood function ($-2\log L$) and information criterions (AIC). This is in agreement with fixed models (Table 2). On the contrary, by adding random effects, Model 2 is the second most suitable.

Conclusions are the same for all types of random functions. Differences between models within the same type of random function are small.

Genetic parameters are calculated from covariance matrices of random effects (results from REML). Trajectories of standard deviations for Model 3 with LP and SP functions, both with 5 parameters, are presented in Figures 1a and 1b. The values of estimated parameters and their trajectories are similar for both types of functions. Visible small edges at the points of knots are on SP. The courses of functions for all tested models are similar.

The tested models also have a similar trajectory for heritability (Figure 2a and 2b). In LP and SP cases with 5 parameters, the course of heritability during the observed period from 100 to 400 days is flat with a small depression at the middle of the

period. Our previous results (Příbyl et al., 2007) had a steeper increase of heritability towards the end of the observed period. The differences could be caused by data in this article that contains updated previous and more complex pedigree information.

The values of heritability were lower than those reported by Iwaisaki et al. (2005), who used SP with 3 knots for the estimation of genetic parameters by beef growth data with maternal effect of Gelbvieh. They compared MTM with a random regression model with an SP function. The range of our values of heritability was in agreement with Bouška et al. (2003), who estimated h^2 values of 0.20–0.46 for the same category of performance tested dual-purpose bulls as our data using a sire model with fixed effect of year and season of bull birth.

Table 4 contains summary statistics of genetic parameters in all tested models and functions applied to random effects models. Each case presents heritability and standard deviation for phenotype, genetic, and animal's permanent environment and residual components in an average observed age period of 100–400 days and at 400 days of age.

Results are practically the same regardless of the model, according to fixed effects and the type of RR functions for random effects. Only the LP models with 3 parameters have higher residual components, but heritability is similar to the other random functions. Models with SP function tend to have a little higher heritability in an average period of 100 to 400 days.

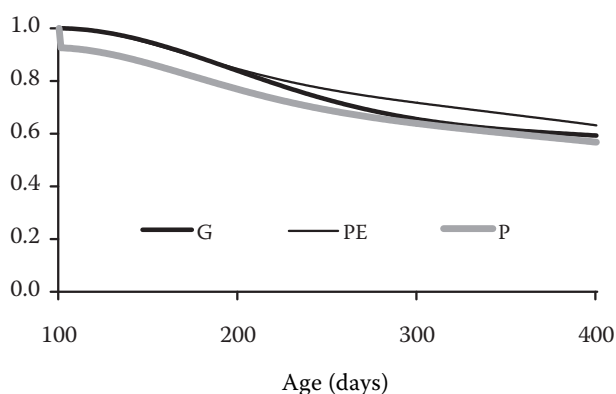


Figure 3a. Phenotype (P), genetic (G), and animal's permanent environment (PE) correlations of body weight at 100 days of age to other ages for model 3 with LP functions with 5 parameters

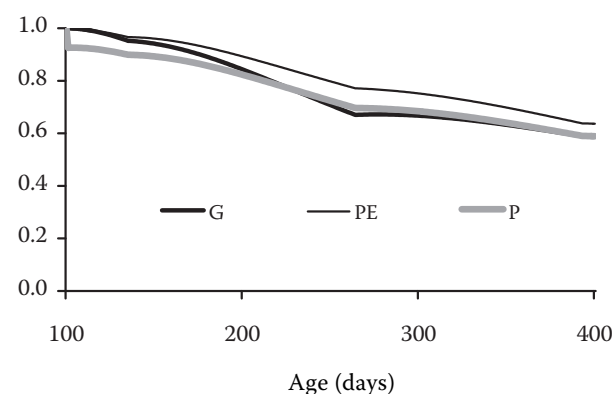


Figure 3b. Phenotype (P), genetic (G), and animal's permanent environment (PE) correlations of body weight at 100 days of age to other ages for model 3 with SP functions with 5 parameters

Table 4. Standard deviations in kg of genetic and environment components in an average observed age period of 100–400 days and at 400 days of age

Model	2	3	4	5	6
Random LP with 5 parameters – average of period					
P	28.30	27.96	28.45	28.01	28.62
G	15.46	15.55	15.49	15.31	16.18
PE	22.18	21.72	22.21	21.82	22.04
RES	8.30	8.23	8.66	8.54	8.41
h^2	0.30	0.31	0.30	0.30	0.32
– age 400 days					
P	36.69	36.17	36.73	36.33	37.11
G	22.05	21.74	21.86	21.87	22.70
PE	27.35	26.93	27.38	26.89	27.33
RES	10.57	10.49	11.02	10.89	10.72
h^2	0.36	0.36	0.35	0.36	0.37
Random LP with 3 parameters – average of period					
P	28.37	28.04	28.49	28.08	28.57
G	15.34	15.58	15.31	15.26	15.78
PE	21.82	21.29	21.86	21.44	21.73
RES	9.60	9.44	9.92	9.72	9.69
h^2	0.29	0.31	0.29	0.29	0.30
– age 400 days					
P	38.48	38.00	38.54	38.12	28.85
G	23.26	22.98	23.07	23.00	23.42
PE	28.10	27.76	28.16	27.76	28.43
RES	12.24	12.04	12.66	12.40	12.37
h^2	0.37	0.37	0.36	0.36	0.36
Random SP with 5 knots – average of period					
P	28.39	28.04	28.53	28.09	28.72
G	15.91	15.97	15.92	15.69	16.70
PE	22.00	21.55	22.04	21.69	21.80
RES	8.27	8.17	8.62	8.47	8.40
h^2	0.31	0.32	0.31	0.31	0.34
– age 400 days					
P	37.31	36.80	37.35	36.94	37.64
G	22.56	22.21	22.33	22.31	22.69
PE	27.78	27.43	27.86	27.38	28.05
RES	10.54	10.42	10.99	10.80	10.71
h^2	0.37	0.36	0.36	0.36	0.36

P = phenotype; G = genetic; PE = animal's permanent environment; RES = residual

For the components of body weight (genetic, animal's permanent environment, and phenotype), correlations between different ages were calculated. For Model 3, LP and SP functions with 5 param-

eters are presented in Figures 3a, 3b, 4a, 4b, 5a and 5b. Figures represent the values of correlations between body weights at the age 100, 250 and 400 days to the ages in the whole interval. There



Figure 4a. Phenotype (P), genetic (G), and animal's permanent environment (PE) correlations of body weight at 250 days of age to other ages for model 3 with LP functions with 5 parameters

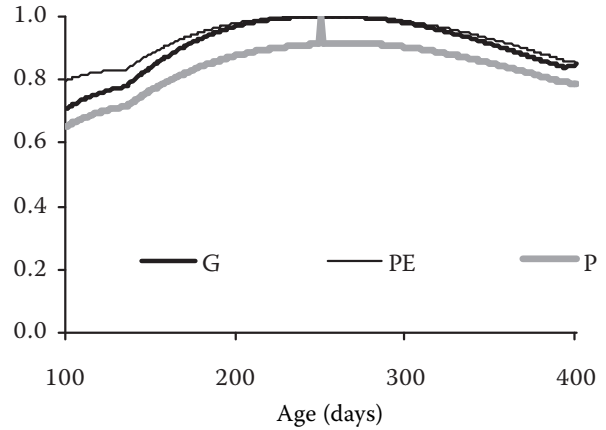


Figure 4b. Phenotype (P), genetic (G), and animal's permanent environment (PE) correlations of body weight at 250 days of age to other ages for model 3 with SP functions with 5 parameters

are visible small edges at the points of knots on lines of correlations for SP function. Correlations for all components are relatively high and have a similar course for both LP and SP functions. The lowest values of correlations are for the phenotype because phenotype variance includes also residual components which are not correlated for different ages. Correlations decrease with distance between ages. Results are similar for all tested models and types of random functions.

The courses of correlation curves related to a given age are in agreement with Legarra et al. (2004). They used LP of third to sixth degree for the fitting of additive genetic, animal and maternal permanent environment effects by data of beef cattle.

Nešetřilová (2005) analysed the growth of young dual-purpose bulls on the basis of multifasic growth model. The model was based on the sum of two logistic functions. The residual variability of the best fitting model was lower than when the com-

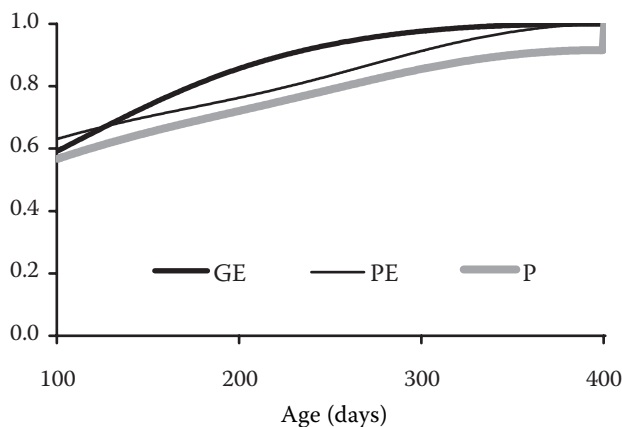


Figure 5a. Phenotype (P), genetic (G), and animal's permanent environment (PE) correlations of body weight at 400 days of age to other ages for model 3 with LP functions with 5 parameters

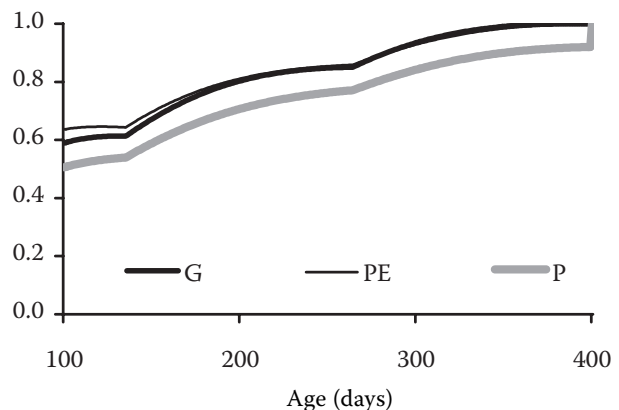


Figure 5b. Phenotype (P), genetic (G), and animal's permanent environment (PE) correlations of body weight at 400 days of age to other ages for model 3 with SP functions with 5 parameters

mon growth model with Gompertz function was used. Vuori et al. (2006) used non-linear growth models with Gompertz function and stated that the linear models were less complicated to solve than the non-linear ones.

After several reviews (Bohmanová et al., 2005; Iwaisaki et al., 2005) the random regression models with SP functions could be simpler and faster to implement than those with LP.

CONCLUSION

The growth curves was spread out into genetic, animal's permanent environment, and residual components. Heritability of body weight was on a moderate level and quite steady during the observed age period from 100 to 400 days.

The tested statistical models showed only small differences in describing the variability and population-genetic parameters. Sufficient numbers of animals in contemporary groups are scarce in practice. However, it is possible to prolong HYS classes up to 3 months.

The number of parameters in the RR function is more important than the type of function. For traits such as live weight, in which the different stages are highly correlated, it is suitable to use SP function for random effects. For describing the growths of bulls, we recommend RR functions with more than 3 parameters.

Editing the database plays a role in estimating genetic parameters. Though the previous paper analyzed a sufficient database with 6 508 bulls and 74 558 weight records, the updated, edited database with 7 448 bulls and 82 676 weight records includes a more complex pedigree and produces slightly different results.

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