Trajectory of body weight of performance tested dual-purpose bulls

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ABSTRACT: 6 508 bulls of dual-purpose cattle at performance-test stations were weighed at intervals of 30 days from birth to 420 days. After all editing a total of 74 558 weight records were available. Live weight was evaluated by orthogonal Legendre Polynomial (LP) of degree 4 and by Linear Spline function (SP) with 5 knots. The fixed effects of test-day-year-station of weighing (TDS) and LP within station-year explain together 97% of variability. Variance components were estimated by REML (REMLF90 programme) taking into account heterogeneous variance during growth. The basic model included fixed effects: TDS, and fixed regression on age (LP_F), and random regression for additive genetic (SP_G) and permanent environmental of the animal (SP_{PE}) effects. Variability of all components increases with age. During the 50–400 day period the heritability is 0.28 on average. Heritability increases with the age of the animal; it is the highest at the end of the period. Correlations for body weights between different ages of the animal are high.

Keywords: cattle; random regression; heritability; genetic correlation; growth curve; linear spline

Czech Fleckvieh (dual-purpose, Simmental type) cattle are used for dairy and beef production, therefore their growth ability is one of the most important traits. The main selection criteria for meat performance of young bulls entering insemination are their own live weight and average daily gain in the period of growth performance test (110 to 365 days of age) at performance-test stations with standardised environment. Nutrition is regulated for daily gain of 1.3 kg in the test and lower value of daily gain before and after the test. Bulls are filled into stations continually all the year round; therefore contemporary groups consist of animals at different phases of growth.

Growth of bulls of Czech Fleckvieh cattle at performance-test stations, including genetic parameters, was analysed by Pulkrábek et al. (1980, 1983, 1984) and Šiler et al. (1981). Přibyl et al. (1986) used a linear model for multi-trait evaluation of body weight, body measurements and body indexes, considering groups of contemporaries, animals and polynomial regression on age in the model. Hyánek and Hyánková (1995) and Nešetřilová (2001, 2005) studied the shape and development of growth curve for Czech Pied cattle. To construct a growth model they examined suitable non-linear functions and estimated their parameters. Hrouz and Gotthardová (2000) used individual non-linear growth curves for the selection of animals of beef breeds. Fitzhugh (1976) analysed a possibility of changing the shape of growth curves.

A Multi-Trait model (MT) with traits defined at the specific age of animals (BIF, 1996; Přibyl et al., 2003) is currently used in many countries for genetic evaluation of growth in beef cattle. Ericsson et al. (1979) used a BLUP method to evaluate average daily gain at performance-test stations of Hereford and Charolais bulls. A similar model was deve-

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loped for Czech Fleckvieh cattle (Konstantinov and Váchal, 1985). Přibylová et al. (2004) elaborated methodology for the breeding value estimation of beef bulls at performance-test stations after weaning at the end of pasture season.

The live weight of the animal at a given age is influenced by its genetic potential and by environment accumulated during the whole history of the animal. The history of systematic environmental effects could be different for each animal, and it is difficult to account for it correctly in the evaluation. Therefore Random Regression (RR) models could be used for genetic evaluation of animals coming from contemporary groups with a large range of ages.

Body weight recorded repeatedly during the animal's life is an example of longitudinal data. RR models are increasingly used for traits with repeated measurements such as milk yield in cattle (Schaeffer et al., 2000), feed intake of pigs (Nielsen and Damgaard, 2004), and body composition (Roehe et al., 2004).

Growth evaluation by RR model is likely to be more precise than that by MT due to the adjustment of both means and variance for age. Nobre et al. (2003a,b) evaluated live weight in a large population of beef cattle by RR model and compared this evaluation with the results obtained by MT model. Differences were large because different parameters were estimated by the two models. Legarra et al. (2004) developed methodology for converting parameters of MT to RR model. In their study cubic Legendre polynomials (LP) seemed to provide a reasonable fit with minimal artefacts.

Rasch and Mašata (2006) compared methods suitable for the estimation of variance components. The estimation of parameters of polynomial functions causes computational problems. Misztal et al. (2000) developed strategy for the estimation of parameters for different TDM. Swalve (2000) reviewed the methodology of TDM. Orthogonal polynomials are a popular choice for models with RR. These polynomials should be of degree 4 or higher (Guo and Schaeffer, 2002). Nobre et al. (2003b) considered the orthogonalisation and stricter convergence criterion (10^{-12} rather than 10^{-10}) which is essential to obtain numerically accurate EPDs from RR by iteration. The dropping of effects with very small eigenvalues from models does not influence the results, but reduces memory and computing time requirements. The reliability of results is influenced by the structure of data set and structure of relationship matrix, which must be handled correctly by fixed and random effects in the model (Veselá et al., 2007).

The polynomial functions frequently have the "border effect" which causes illogical values on the extremes of the observed period. This fact was mentioned in literature for example by Druet et al. (2003), and this is the reason for using another type of function. Faro et al. (1998) used segmented polynomials to model a lactation curve. Methodology of RR and methodology of production growth curve were compared by Varona (2004). Vuori et al. (2006) analysed nonlinear methodology of mixed effects model for Gompertz growth curve. Kor et al. (2006) compared several exponential growth models for goats.

In many cases residual variance is not constant over the course of the curve. This can be solved by weighted analysis or by modelling the curve for the residual. Meyer (2001) described variance by a polynomial function of higher degree to alter variance in dependence on age. The variance function has a part of measurement error and a part of polynomial function. Druet et al. (2003) used an exponential function for residual variance in the model of lactation curve evaluation.

Meyer (1999a,b) and Albuquerque and Meyer (2001, 2002) evaluated genetic and phenotypic covariance functions for different growth stages in beef cattle. They described the structure of covariance between the effects of the animal and animal's permanent environment. Genetic parameters for cows of beef cattle were estimated by Arango et al. (2002). Bohmanová et al. (2003) used RR for description of differences in growth trajectories in seven beef breeds. Meyer (2005) compared several methodologies for the evaluation of longitudinal data using a sample of beef cattle data set. The author recommended B-splines for RR with reduced rank via the principal components. Misztal et al. (2004) suggested Linear Splines (SP) for growth curve to simplify longitudinal analyses. The distance between knots in SP depends on their correlations that should not be below 0.70. If the knots are located sparsely, depressions are visible between some knots on the curve. In a simulation study by Bohmanová et al. (2005) MT and RR models with LP and with SP were compared. Functions for direct genetic and animal's permanent environment, maternal genetic and maternal permanent environment, and residual random effects were used. Four random curves were simultaneously modelled for the growth of each animal and five curves for variance components. RR models with SP were simple to implement and had better numerical properties. Iwaisaki et al. (2005) estimated direct and maternal genetic parameters in beef cattle using MT and RR model with a SP function. The model with spline function may be superior to MT because of better modelling of age in both fixed and random effects.

Heritability and genetic correlations between live weights of bulls at performance-test stations at different ages were analysed by Bouška et al. (2003). Preliminary results of variance components estimation for daily gain curve and breeding value estimation for the growth curve of Czech Pied young bulls were presented by Krejčová et al. (2003) and Přibyl et al. (2004).

The objective of this paper was to analyse live weight of dual-purpose bulls.

MATERIAL AND METHODS

The dataset consisted of 6 508 Czech Fleckvieh bulls – candidates for breeding that were kept at seven performance-test stations from 1971 to 1997. The first available weight of each animal was obtained before 60 days of age when the animals entered the station. Weighing during the test was carried out at about 30-day intervals until approximately 420 days of age. Each bull was weighed 6 times at least. On average, each bull was weighed 11 times. Only those days of weighing (test days) were left in the data set when more than 4 animals were weighed. Close test days with a small number of animals were grouped. Within one test day on average 38 bulls were weighed at the station.

Only the sire relationship was considered because very few dams provided ties. The evaluated bulls were offspring of 253 sires, and each sire had at least 6 sons in the data set. Each bull at performance-test stations had 26 half-sibs on average.

After all adjustments a total of 74 558 weight records were available. Live weight is an analysed trait.

To analyse variability in the course of growth curve, all records were distributed into 20 classes according to age.

Growth of the animal and variability of traits in relation to age were fitted by functions (f) of orthogonal Legendre Polynomials (LP) and Linear Spline (SP), both with 5 parameters.

$$f = p'b$$

where:
b = the vector of regression coefficients
p = the vector of parameters of the function

Age standardisation (as) was performed in LP:

$$as = 2\,((x_i - x_{\min})/(x_{\max} - x_{\min})) - 1$$

where:
x_i = age on the day of weighing
$x_{\min}$ = minimum age
$x_{\max}$ = maximum age

p terms (n-th parameter) in LP were calculated from the formula of Rodriguez (Rektorys, 1963):

$$p_n' = \frac{1}{2^n n!} \frac{d^n}{d(as)^n} (as^2 - 1)^n$$

and standardised for the variability of each parameter close to 1 (Kirkpatrick et al., 1990; Schaeffer et al., 2000) according to this equation:

$$p_n = p'_n \times (2n + 1)^{0.5}$$

After standardisation the first seven parameters of p are:

$p_0 = 1$

$p_1 = as\sqrt{3}$

$p_2 = 0.5(3as^2 - 1)\sqrt{5}$

$p_3 = 0.5(5as^3 - 3as)\sqrt{7}$

$p_4 = 0.125(35as^4 - 30as^2 + 3)\sqrt{9}$

$p_5 = 0.125(63as^5 - 70as^3 + 15as)\sqrt{11}$

$p_6 = 0.0625(231as^6 - 315as^4 + 105as^2 - 5)\sqrt{13}$

p terms in SP express proportional distances of age at test day from the ages at neighbouring knots. It is just a linear interpolation between neighbouring knots; the closer knot has a higher value of the parameter. The sum of neighbouring parameters connected with given age is 1, the values outside are 0. Knots were located equally at the same distance covering the whole age range of 3–420 days. The formulation of SP function was described by De Boor (1993), Bohmanová et al. (2005) or Cantet et al. (2005).

The effects influencing growth of bulls were analysed using SAS/GLM. Simple and weighted analysis was used. "Weight" (w) in the weighted analysis is the relative reciprocal value of variance at age (i), calculated as average variance (V_{aver}) during the whole growth, divided by variance in dependence on time (V_i). Weight at age (i) is

$$w_i = V_{\text{aver}}/V_i$$

where:
V_i = the variance at day (i) modelled by LP

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

model 1 – LP
model 2 – LP + the effect of test-day-year-station (*tds*)
model 3 – LP within the year of test + *tds*
model 4 – LP within the station + *tds*
model 5 – LP within the station × year of test combination (*sy*) + *tds*
model 6 – like (5) + the effect of sire × station combination

Model 5 was used for variance component estimation by REML (REMLF90 programme, Misztal et al., 2002). The estimation was done according to the model equation:

$$y = X_{SY} f_{\mathrm{LP}} + X_{TDS}\, tds + Z f_{SPG} + Z f_{SPPE} + e$$

where:
y = measured values of weight
X_{SY} = the incidence matrix for *SY* classes
f_{LP} = average LP growth curve according to groups of bulls within sy classes (fixed effect)
X_{TDS} = the incidence matrix for *tds* classes
tds = the test-day-year-station effect (fixed effect)
Z = the incidence matrix for animals
f_{SPG} = SP function for the genetic deviation of individual growth curve of the animal (random effect with relationship matrix)
f_{SPPE} = SP function for the deviation of individual growth curve under the effect of permanent environment of the animal (random effect)
e = random residual

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

$$VC_{i,i'} = p_i' \times C\, p_{i'}$$

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 LP parameters at age (i) and (i')
C = the covariance matrix of regression coefficients (b_G) or (b_{PE}) for the genetic or animal's permanent environment effect

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

$$VRE_i = V_e / w_i$$

RESULTS AND DISCUSSION

Table 1 shows averages of body weight at the specific age. Figure 1 illustrates average growth. The growth curve increased almost linearly with age.

Figure 1 shows the real average values of weight for the whole data set and predictions by LP when polynomials of degree 3 to 5 were used. Taking into account the number of observations the degrees of freedom of different models are not important. The fitness of different degrees of LP polynomials was tested by the determination coefficient (R^2) and mean square error (MSE) of the model (Table 2). R^2 is high. Differences between polynomials are small. For further calculations the polynomial of degree 4 was used. The determination coefficient is 95.20%.

Average standard deviations within the age classes are given in Table 1. Standard deviation (SD) of weight is 28.62 kg on average. These values correspond with residual standard deviations (MSE) from Table 2 which express the average for the whole period of observations corrected by the given polynomial. For polynomials of degree 4 the standard deviation of live weight is 28.70 kg.

Table 1. Average values and standard deviations (in brackets) at the specific age and for the whole rearing period

Age days	*n*	Weight (kg)
60	3 072	95 (15.36)
120	4 582	152 (20.68)
180	4 060	224 (28.04)
240	4 050	300 (32.26)
300	4 353	375 (33.24)
360	4 654	447 (34.31)
420	1 157	509 (38.73)
Average*		(28.62)
Measured data	74 558	284 (130.94)

*Within age classes

Table 2. Reliability of weight prediction by different polynomials

Polynomial degree	R^2	MSE
2	95.08	29.04
3	95.19	28.71
4	95.20	28.70
5	95.20	28.69
6	95.20	28.69

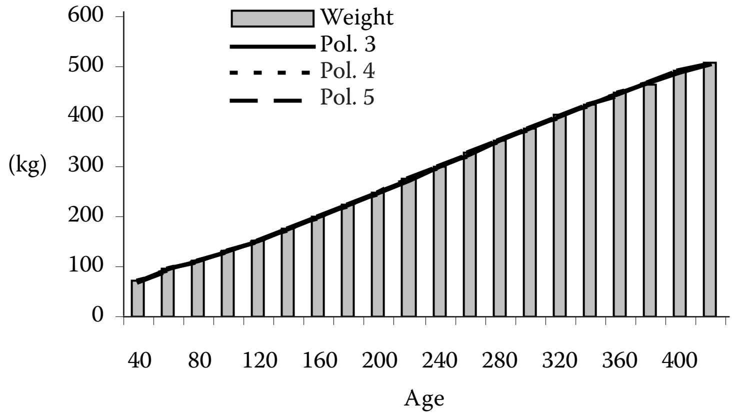

Figure 1. Average growth curve (kg), live weight and prediction by Legendre Polynomials of degree 3 to 5

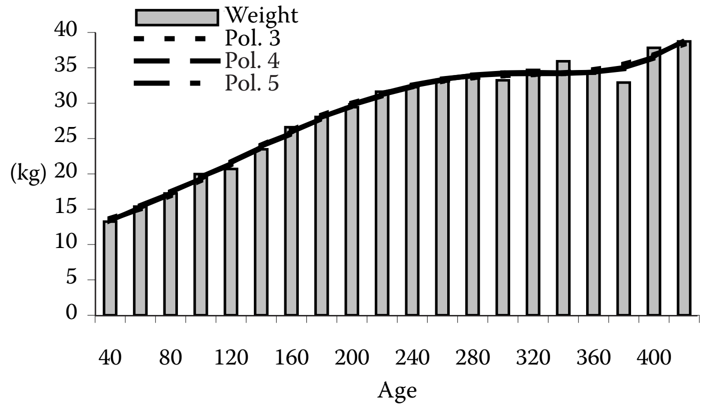

Figure 2. The relation of standard deviation to age – weight (kg) and prediction by Legendre Polynomials of degree 4 to 6

The curve of SD had a varying shape in the course of bull growth, and these variations are documented in Figure. 2. SD of weight slowly increases until the age of about 250 days, is nearly steady until day 360, and it increases again at the end of the observed period.

We tried to find an adequate function that would describe the relation of standard deviation to age. Table 3 shows the values of determination coefficient R^2 and MSE of standard deviation prediction when polynomials of degree 2 to 6 were used. The estimated curve was compared with measured values in Figure 2. Differences between polynomials are small.

The results of the six tested models with different effects were summarised (Table 4). Evaluations were done by "simple" and "weighted" analysis. All effects in the evaluated models were statistically significant. R^2 values of weighted analysis were higher, but the differences were small. These values corresponded with small differences in MSE.

Table 3. Reliability of standard deviation prediction for live weight by different polynomials

Polynomial degree	R^2 (%)	MSE
2	97.33	1.33
3	97.53	1.32
4	98.78	0.96
5	98.90	0.94
6	98.93	0.97

Determination coefficients for body weight are high. The value R^2 is naturally lowest in model 1, where no other effects except LP were considered. R^2 increases with the complexity of the model. Differences between the models for body weight are small. The growth curve explains a major part of variance. model 6 eliminates also a certain part of genetic variance. For this reason model 5 was selected as a basis for genetic analysis.

Table 5 and Table 6 document the components of variance for body weight at the age of one year and on average for the age period of 50–400 days. The results of simple and weighted analysis are similar. The components of variance for weight are numerically corrected "corweight" for all components of variance according to the initial value at the age of 50 days ($Vcor_i = V_i + V_{49} - 2Cov_{(i,\,49)}$). The corrected values are much lower than for live weight. The heritability for corweight is slightly higher than for weight without correction.

Presented values of heritability for cumulative growth are higher than those reported by Meyer

Table 4. Comparison of models with different fixed effects describing the growth of bulls

	Simple analysis		Weighted analysis	
	R^2 (%)	MSE	R^2 (%)	MSE
Model 1	95.20	28.70	96.39	28.66
Model 2	96.41	25.14	97.25	25.36
Model 3	96.56	24.62	97.40	24.68
Model 4	96.43	25.06	97.27	25.26
Model 5	96.61	24.46	97.45	24.47
Model 6	96.97	23.22	97.68	23.39

Table 5. Components of variance for the average of the period 50–400 days and cumulative growth at 365 days of age – simple analysis

Weight (kg^2)	Average of the period		Cumulative growth at day 365	
	weight	corweight	weight	corweight
VG	213	142	455	346
VPE	437	262	598	420
VRE	25	0	25	0
Heritability	0.28	0.32	0.42	0.45

VG = genetic, VPE = permanent environment, *VRE* = residual; corweight = weight corrected for the initial values

Table 6. Components of variance for the average of the period 50–400 days and cumulative growth at 365 days of age – weighted analysis

Weight (kg^2)	Average of the period		Cumulative growth at day 365	
	weight	corweight	weight	corweight
VG	214	149	457	353
VPE	440	286	594	445
VRE	25	19	34	28
Heritability	0.28	0.31	0.42	0.43

(1999b) and Albuquerque and Meyer (2001). Bogdanovic et al. (2002) estimated variance components for growth traits of Simmental bulls. They evaluated weight and gain in different segments of growth. Their coefficients of heritability were also lower than ours (0.29 for lifetime gain).

In body weight we observed an accumulated proportion of genetic component, and much lower accumulation of residual component with the increasing age of the animal (Figure 3). Therefore heritability also increased (Figure 5). The results are in agreement with Meyer (2002).

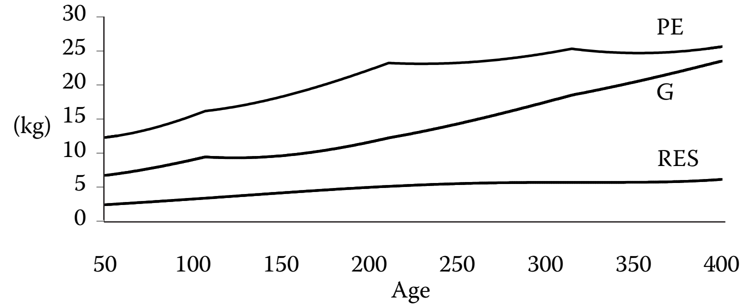

Figure 3. Curves of standard deviations during the growth of bulls – body weight, Genetic (G), Animal's permanent environment (PE) and Residual (RES) components

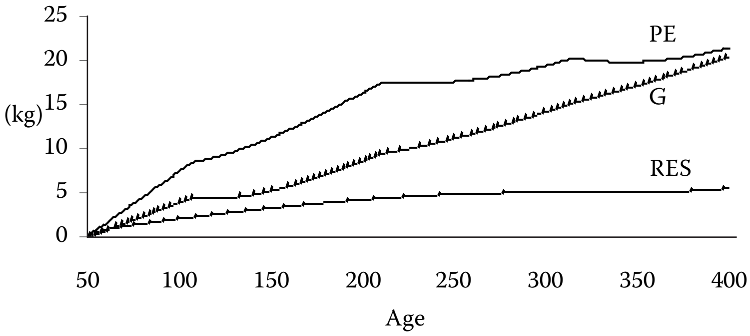

Figure 4. Curves of standard deviations during the growth of bulls – corweight (corrected body weight), Genetic (G), Animal's permanent environment (PE) and Residual (RES) components

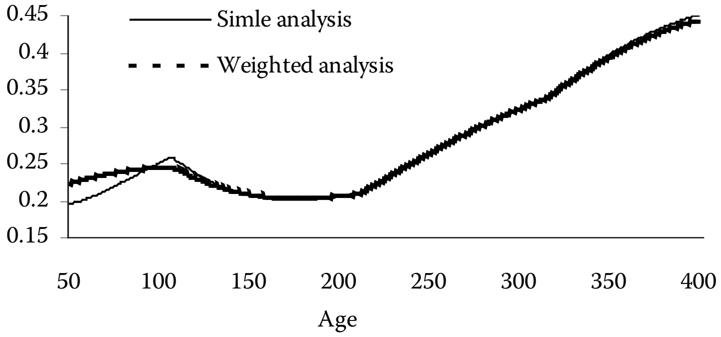

Figure 5. Curves of heritability according to the age of the animal for simple and weighted analysis

The curves of corweight (Figure 4) are similar to those for weight, but on a little lower level.

There were no differences in heritability between the simple and weighted analysis (Figure 5). Heritability slightly decreases from 100 days of age to about 180 days of age and then it increases till the end of the observed period.

Meyer (1999b) reported relatively constant heritability between 100 and 300 days of age. Albuquerque and Meyer (2001) found out the highest maternal and the lowest direct heritability at the age of 150–200 days. Meyer (2001) stated in Hereford that heritability of direct effect decreased in the range of approx. 0.40 to 0.20 from birth to 300 days of age and heritability of maternal effect increased from 0.10 to 0.15 in the same period of age. But Meyer (2002) reported a practically linear increase in heritability with age.

In our case we cannot split the components into direct and maternal parts because bulls are the progeny of selected dam of sire, when each dam has practically only one son in the data set and bulls

Table 7. Phenotype correlations for body weight at different ages in percentage

Age days	60	90	120	150	180	210	240	270	300	330	360	390	420
60	–	89	80	75	68	60	61	59	57	55	53	50	46
90		–	94	88	80	71	70	68	64	62	60	57	53
120			–	93	86	79	77	74	70	67	65	62	58
150				–	94	90	88	85	80	77	74	71	66
180					–	95	93	89	84	81	78	74	69
210						–	95	91	86	82	80	75	70
240							–	95	92	89	87	82	77
270								–	95	94	91	87	82
300									–	96	94	90	84
330										–	96	93	88
360											–	96	93
390												–	96
420													–

Table 8. Genetic (above diagonal) and animal's permanent environment (below diagonal) correlations between body weights at different ages in percentage

Age days	60	90	120	150	180	210	240	270	300	330	360	390	420
60	–	87	79	80	74	64	64	62	60	58	56	54	52
90	93	–	98	91	77	62	61	59	56	55	53	52	50
120	84	97	–	95	82	67	66	64	61	59	58	56	55
150	77	92	98	–	96	87	86	83	79	77	76	74	72
180	70	85	93	99	–	97	95	92	88	86	84	83	81
210	62	77	87	95	99	–	98	95	91	88	87	86	84
240	63	77	86	94	98	99	–	99	97	95	94	92	91
270	62	75	83	91	94	95	99	–	99	98	97	96	94
300	60	71	78	86	89	89	95	99	–	100	99	97	95
330	58	69	76	83	85	86	93	97	99	–	99	98	97
360	57	68	74	81	83	83	90	94	96	98	–	100	99
390	54	65	71	77	79	79	84	89	91	94	99	–	100
420	49	60	66	71	72	72	78	82	83	88	95	99	–

enter into performance-test stations at very young age. Therefore only one overall value of heritability is presented.

Table 7 shows phenotypic correlations between body weights at different ages of the animal. The values range from 46 to 96%. The highest values are between adjacent weightings.

Table 8 shows genetic and animal's permanent environment correlations for body weight at different ages. All are on a high level and higher than phenotype correlations. Presented values are in agreement with Bouška et al. (2003).

CONCLUSION

Heritability increases with the age of animals. Correlations between body weights at different ages are high, decreasing with distance to the intermediate value. Body weight is a cumulative trait which repeats the whole previous history of the animal, therefore the high correlations cannot be overvalued. The main task of performance-test stations is to select sires according to their performance at early age, whose progenies will have good growth till the end of fattening at the age of about 18 months. The final part of the test is therefore more important than previous parts.

Random Regression Models allow bettering the explanation of individual growth of each animal. For body weight it is possible to use models with Linear Splines which are simpler for calculations and sufficiently project the particular components of growth.

In spite of a significant increase in the variability of body weight with age, the results of simple and weighted analysis were similar.

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