Genetic evaluation of daily gains of dual-purpose bulls using a random regression model

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ABSTRACT: Daily gains of 8 243 dual-purpose bulls from 100 to 400 days of age during the years 1971 to 2007 were analyzed by random regression models. Orthogonal Legendre polynomials (LP) of degree 4 were applied to daily gains calculated at 30-day intervals over the test period. Fixed curves were estimated within the station-year-season of birth. The models also included a fixed station-year-season of weighing, animal additive genetic effects and animal permanent environmental effects. The peak daily gain was attained between 230 and 280 days of age, which corresponded to the period of the lowest variance in daily gains. Heritability estimates of daily gain were in the range of 0.014 to 0.043. The reliability of composite trait – cumulative gains over the entire period was 0.87. Genetic correlations between gains at different ages were high for adjacent ages and decreased with increasing difference in ages. Correlations of permanent environmental effects were high for adjacent ages, but became negative for ages that were far apart, indicating the possibility of compensatory growth. The phenotypic correlations were close to zero. The correlations for cumulative daily gains were higher than those for individual daily gains.

Keywords: daily gains; curve; random regression; heritability; correlation; bulls

The growth ability of cattle is commonly judged for genetic purposes or nutritional experiments by body weights at different ages or by average daily gains over specific periods of time (Bartoň et al., 2007). Multi-Trait Animal Models (MT) with traits defined at the specific age of animals (BIF, 1996) are currently used for genetic evaluation. Growth is a complicated trait. Various methods of evaluation were tested. Nešetřilová (2005) studied the shape and development of growth curves for Czech Pied cattle (Czech Fleckvieh) by exponential functions. Vuori et al. (2006) used a linearization of non-linear growth models.

The growth of livestock is intensely biased by the method of rearing, mainly by nutrition in different phases of growth, which produces changes in growth curves and a shift of inflexion point at almost any age (Hrouz and Gotthardová, 2000). Due to these biases the growth curve does not frequently follow a sigmoid shape (Přibylová et al., 2004). Therefore, the traditional exponential growth functions may not be suitable in all cases.

Random regression models (RR) have been used increasingly for longitudinal traits with repeated measures over a set time interval. Schaeffer et al. (2000) described a test day model for the evaluation of milk yield in dairy cattle. RR are characterized by fixed curves that model the phenotypic shape of the yield curve or growth curve, and by random curves that model the variability of animals around the fixed curves. Orthogonal polynomials have been used for the random curves. Random

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curves are needed for the animal additive genetic effects separately from the animal permanent environmental effects. The shapes of the random curves differ from the phenotypic shapes (Zavadilová et al., 2005b).

RR models for growth were studied by Meyer (1999a,b, 2001), and Albuquerque and Meyer (2001), where the weights of beef cattle at different ages were analyzed. They described the structure of covariance for the effects of direct animal, direct permanent environment (PE), maternal and maternal PE. Nobre et al. (2002) compared RR evaluations with results from an MT model and found large differences between the models. They concluded that growth analyzed by an RR model may be more exact than by an MT model because all weights are considered directly with their corresponding covariances.

Records of body weights at different ages show high correlations between each other because weight at age (x) includes the previous weight at age (x–1) (Bouška et al., 2003; Přibyl et al., 2007a). These values must not, therefore, be overestimated. The phenotypic correlations between growth increments in different intervals are very low, almost negative (Krejčová et al., 2007a), which suggests a possibility of growth compensation. However, these correlations remain hidden by the evaluation of body weight or gain over a long period. Thus, the gain over one period is not highly related to the growth in a previous period, as weights would be. Live weight is a cumulative trait and involves the entire history of the animal including systematic effects of external environmental and internal genetic and non-genetic factors. It is not possible to separate out the effects of environment retroactively at the moment of evaluation correctly. It turned out consequently that live weight is not an entirely suitable trait for the evaluation of animal growth. The evaluation of daily gains over short consecutive periods of time, which are in reality the derivatives of growth curve, may be more suitable than using weights at given ages or average daily gains over a long period.

Czech Fleckvieh cattle (Simmental type) are used for both dairy and beef production, and therefore their growth ability is an important economic trait. Bulls are performance-tested at test stations under standard nutrition and management prior to being selected for artificial insemination.

Bogdanovic et al. (2002) estimated variance components for weights and gains in different periods for Simmental bulls. The evaluation of live weight of Czech Fleckvieh bulls at performance-test stations by RR was described by Přibyl et al. (2007a, 2008). Gains over 50-day intervals were studied by Krejčová et al. (2007a,b) and Mielenz et al. (2007), comparing RR and MT models at the same time.

The objective of this paper was to evaluate daily gains for repeated consecutive 30-day intervals using different RR models for Czech Fleckvieh bulls.

MATERIAL AND METHODS

Data consisted of 8 243 Czech Fleckvieh bulls, the progeny of 349 sires, performance-tested from 1971 to 2007 at seven test stations. The bulls were the progeny of highly selected mothers and sires of sires from the entire national population. Therefore, each mother usually had only one son at the stations. The pedigree included three generations of ancestors, giving a total of 16 488 animals.

Bulls enter test stations throughout the year usually at 2 months of age, and are selected for use in artificial insemination (AI) at 14 months. Thus, bulls of all ages, between 2 and 14 months, are present at the test station at any given time. For some animals records even from the date close to that of birth are also available. Weights of bulls for evaluation are available from the age of 6 to 520 days. The official period of the performance test is from 110 days to 365 days of age. Weighings were done at 30-day intervals. On average, each bull was weighed 11 times. Daily gains were computed by linear interpolation from two consecutive weights.

Nutrition was regulated for a maximum daily gain of 1.3 kg. The individual consumption of nutrients was not recorded. The general methodology for the stations was similar for the entire period and all stations. Some changes in technology, feeding systems, and operation of the station tests occurred during these 36 years.

The evaluation was for the entire observed period from 6 to 520 days. The polynomial curves show generally rather high variability and no logical values at the beginning and at the end of the observed period. The results are therefore formulated for a part of growth curve without boundary values. In this case from 100 to 400 days of age only, which is close to the official test period.

The standard deviations of daily gains changed over the age range, so that a weighted analysis had to be performed, using weights equal to the ratio of the average variance divided by the variance at age i (Přibyl et al., 2007a). Variance at age i was predicted by an LP of degree 9 with gains grouped in 10-day age intervals.

The best phenotypic curves for daily gains were found by comparing 7 different fixed effects models (GLM/SAS, 2005). A Legendre Polynomial (LP) of degree 4 (i.e. 5 parameters) was used in conjunction with other factors as follows:

(1) LP only;
(2) LP + TDS (station by month in the middle of two weighings);
(3) TDS + LP × YB (YB: year of birth);
(4) TDS + LP × S (S: station);
(5) TDS + LP × YSB (YSB: year-season of birth);
(6) TDS + LP × SYSB (SYSB: station-year-season of birth);
(7) LP × *TDS*3 (*TDS*3: station-year-3-month interval of weighings).

For the reasons already mentioned, that calves enter the stations at a very early age, that there are only weak ties among mothers, and that each mother has practically only one son at a station, the maternal effects were not therefore considered in evaluation.

After determining the best fixed curve functions for daily gains, an RR model was applied to the data as follows:

$$y_{iojk} = TDS3_i + \sum_{m=0}^{n} \beta_{om}\phi_m(t_{ojk}) + \sum_{m=0}^{n} \alpha_{jm}\phi_m(t_{ojk}) + \sum_{m=0}^{n} \gamma_{jm}\phi_m(t_{ojk}) + e_{iojk} \qquad (n = 1, ..., 4)$$

where:

y_{iojk} = gain k of animal j ranking into subclass for fixed regression SYSB o measured within class $TDS3$ i
$TDS3_i$ = fixed effect of station × year × 3-month season of weighing i
t_{ojk} = standardized age in interval (–1, 1)
$\phi_m(\cdot)$ = parameters of Legendre polynomial of degree 4 (with m = 0, ..., 4)
β_{om} = m^{th} fixed regression coefficient within class SYSB o
α_{jm} = m^{th} random regression coefficient of the additive genetic effect of animal j, polynomial for the individual growth curve of the animal (G) (random effect with additive relationship matrix)
γ_{jm} = m^{th} random regression coefficient of the permanent environment effect of animal j, polynomial for a deviation in the growth curve under the effect of the permanent environment of the animal (PE)
e_{iojk} = random residual

A three-month season was chosen in order to maintain sufficient numbers of records within contemporary group subclasses. Contemporary groups were examined using two different methods. Firstly, groups were formed by year and month of birth within stations or across stations. Secondly, groups were formed by date of weighing regardless of age at weighing. Either l-month or 3-month seasons within stations were examined. In the first case the assumption is that animals born at the same time experience the same nutrition and management throughout their lives, but in the second grouping, contemporaries are all animals at one point in time experiencing the same nutrition and management effects. Edits of data were made so that there were at least 5 animals per contemporary group (25 on average). In total there were 79 796 daily gain observations.

Estimates of the genetic (G) and permanent environmental (PE) covariance matrices and the residual variances were obtained using the REMLF90 programme of Misztal et al. (2002). Estimates of genetic and environmental components for each day during the test period were obtained by

$$VC_{i,i'} = p_{t'}\, C\, p_{t'}$$

where:

$VC_{i,i'}$ = genetic ($VG_{i,i'}$) or the animal's permanent environment ($VPE_{i,i'}$), covariance of growth trait between age (t) and (t')
$p_{t'}, p_{t'}$ = vectors of parameters $\phi_m(\cdot)$ at age (t) and (t')
C = covariance matrix of regression coefficients (α) or (γ) for the genetic or permanent environment effect of the animal

Cumulative components until the times (i) and (i') ($CVC_{i,i'}$) were calculated according to the sum of the vectors of parameters from the age of bulls 100 days to the given age:

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

The residual variances were estimated as the ratio of the REML estimate of the residual variance times 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.

RESULTS AND DISCUSSION

Besides the testing of the growth ability of bulls, the purpose of performance-test stations is the

Table 1. Average values and standard deviations at the specific age and for the entire rearing period

Age (days)	*n*	Gain (kg)	SD (kg)	Min. (kg)	Max. (kg)
65	771	0.827	0.241	–0.040	1.609
125	2 551	1.175	0.358	–0.226	2.667
185	2 484	1.285	0.319	–0.059	2.531
245	2 507	1.298	0.320	–0.161	2.724
305	2 388	1.248	0.318	0	2.633
365	1 710	1.097	0.350	–0.409	2.613
425	566	0.910	0.411	–0.192	2.571
Measured data	79 796	1.188	0.353	–0.409	2.724

rearing of healthy and well-developed animals that are able to work in breeding for many consecutive years. Therefore, it is not possible to feed the bulls *ad libitum*. Nutrition at test stations (our dataset) is formulated to give a gain restricted to the maximum of 1.3 kg/day. The same conditions in terms of nutrition for all the bulls in the test are ensured in this way.

Means and standard deviations from daily gains at a few selected ages are given in Table 1. The shape of the daily gain curve is given in Figure 1, and the trends in standard deviations by day of age are given in Figure 2. The minimum values of gain, listed in Table 1, show even negative values. Therefore, the growth of the same animal fluctuates and is sometimes suspended. Also, production recording for daily gain in short intervals has considerable errors, which are compensated over a longer period.

Peak gains (close to 1.3 kg/day) were observed between 230 and 280 days of age. The curve of standard deviations was fitted by a Legendre polynomial of degree 9 in order to determine the weight factors for the analyses. Variability of daily gain is higher around the beginning of the official test period. Then it decreases approximately up to 250 days of age, and later it increases again. Depression in variability is at the moment of maximum daily gain (compare Figures 1 and 2). This means that the limitation of nutrition does not allow the best animals to grow according to their genetic potential and can cause a decrease in variability. This depression in

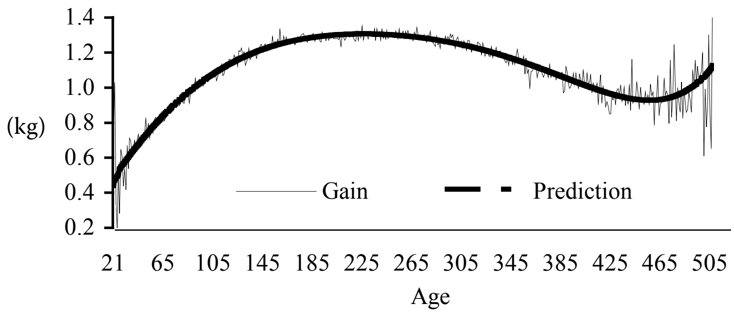

Figure 1. The curve of average daily gain (kg) and prediction by Legendre polynomials of degree 4

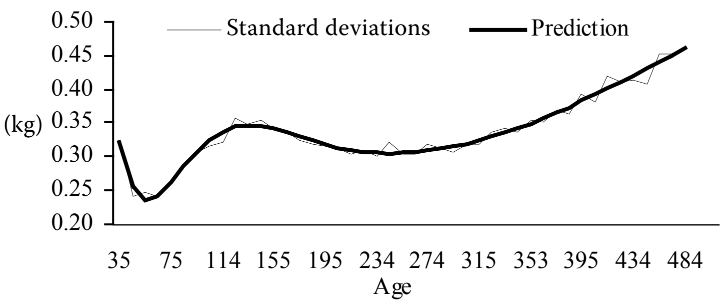

Figure 2. The relation of standard deviation of gain to age and prediction by Legendre polynomials of degree 9

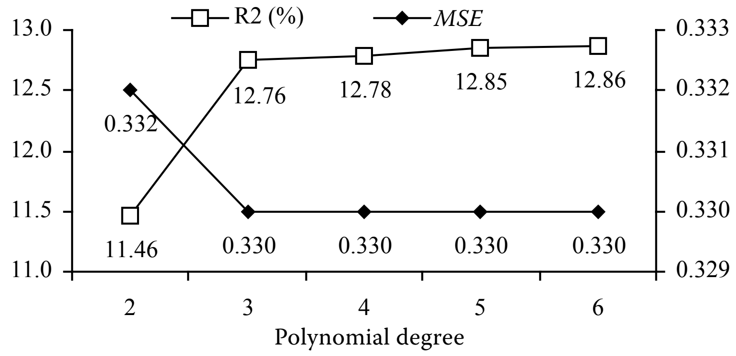

Figure 3. Reliability of daily gain prediction by different polynomials

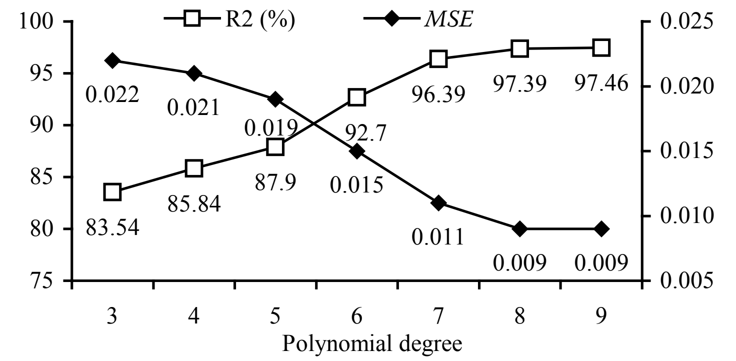

Figure 4. Reliability of standard deviation prediction for daily gain by different polynomials

variability occurs simultaneously at the moment of the inflection point of the growth curve.

Different degrees of LP were studied, but degree 3 or higher gave similar *R*-squared values (13%) for predicting mean daily gains (Figure 3). Thus, degree 4 was selected for the final analyses. Standard deviations were predicted the most accurately (97%) by LP of degree 9 (Figure 4).

Fixed effects models

The *R*-squared values and Mean Squared Errors for seven fixed effects models are given in Table 2. Even when the best models are used, determination coefficients are relatively low. The model with the highest *R*-squared values (and the lowest *MSE*) was the model with station-year-month of weighing contemporary groups and fixed curves nested within station and year-season of birth (35.43% in weighted analysis). The weighted analysis has higher determination coefficients by about 2% than the simple analysis and similar improvement of *MSE*. The comparison of models is identical to that in the simple analysis. Model 7, which has a lower number of parameters, was suggested as a suitable model by Krejčová et al. (2007a). From this study, Model 6 was chosen for the estimation of

Table 2. Comparison of models with different fixed effects describing the growth of bulls

	Simple analysis		Weighted analysis	
	R^2 (%)	*MSE*	R^2 (%)	*MSE*
Model 1	12.78	0.330	14.69	0.324
Model 2	25.58	0.306	27.44	0.301
Model 3	28.81	0.300	30.57	0.294
Model 4	26.79	0.304	28.63	0.298
Model 5	30.32	0.297	32.00	0.292
Model 6	33.91	0.291	35.43	0.286
Model 7	29.08	0.300	30.39	0.295

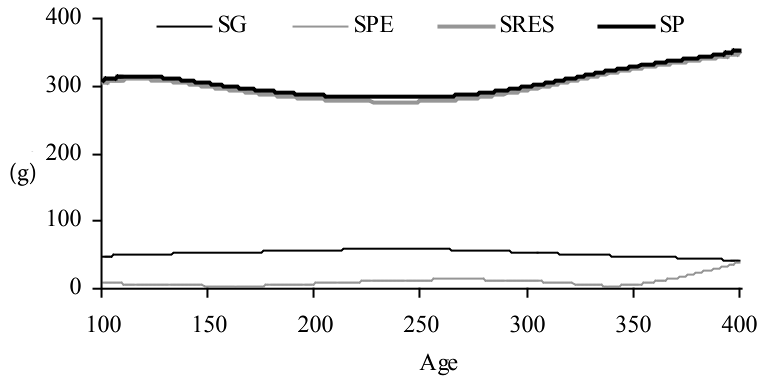

Figure 5. Curves of standard deviations during the growth of bulls, genetic (SG), animals' permanent environment (SPE), residual (SRES) and phenotypic (SP) components

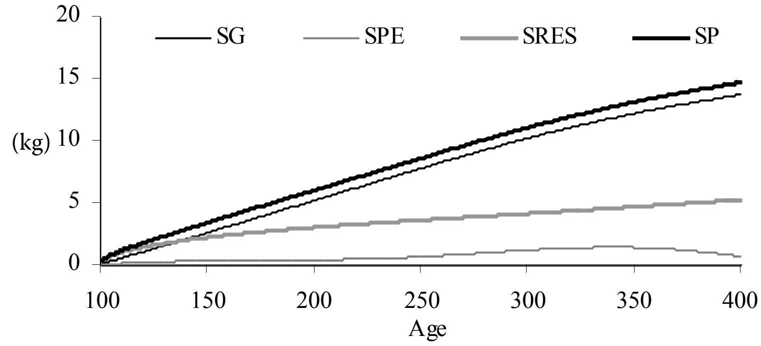

Figure 6. Cumulative curves of standard deviations during the growth of bulls, genetic (SG), animals' permanent environment (SPE), residual (SRES) and phenotypic (SP) and components

genetic parameters, but due to small numbers in some station-year-month of weighing subclasses, this effect was replaced by station-year-3-month weighing subclasses.

Estimation of covariance parameters

This model corresponds to the principles of the test-day model used for milk production (Zavadilová et al., 2005a). Preliminary LP and linear spline (SP) functions for the evaluation of daily gains were compared by Přibyl et al. (2006). Although the general level of genetic parameters in the cited paper was similar for LP and SP functions, due to the low correlations between knots, SP produced less smooth curves. Therefore, only LP was used in this work.

Estimates of genetic, permanent environment, residual, and total phenotypic standard deviations by day of age are shown in Figure 5, over a period of 100 to 400 days of age. Boundary values of the curve gave the typical upward trends seen in most analyses (Meyer, 2001; Druet et al., 2003). From 100 to 400 days each component is fair1y stable, but low compared to the residual SD. Averages

Table 3. Standard deviations of components of variance for the average of the period 100–400 days and cumulative growth at 400 days of age

	Average of the period		Cumulative gain at 400 days of age (kg)
	daily gain (g)	cumulative gain (kg)	
SG	52.66	7.46	13.68
SPE	10.45	0.71	0.68
SRE	300.74	3.43	5.23
SP	305.67	8.30	14.67
Heritability	0.03	0.73	0.87

SG – genetic; SPE – permanent environment; SRE – residual; SP – phenotype

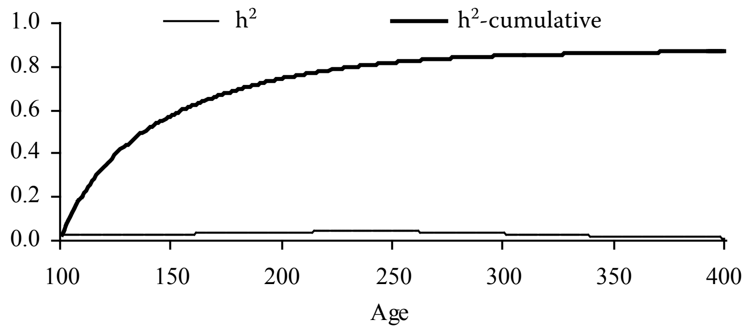

Figure 7. Relation of genetic to phenotype components for daily gain (heritability) and cumulative gain (reliability)

over the period for each component are given in Table 3.

Estimates of heritability of daily gains were very low, averaging about 0.03. The peak heritability estimates were at 100 and 270 days of age, with a rapid decrease at the end of the rearing period (Figure 7). The value of heritability for daily gains is much lower than for live weight calculated from the same data (Přibyl et al., 2007a). This appears to be a general phenomenon. Substantially lower heritability for short segments in comparison with cumulative production for the entire period was also detected in egg production of laying hens (Wolc et al., 2007).

Estimates of parameters for cumulative gains from 100 to 400 days were calculated from the RR estimated covariance matrices, as indicated in the Material and Methods section. Standard deviations of genetic, permanent environment, residual, and phenotypic effects are shown in Figure 6 and Table 3. Cumulative gains can be considered to be a linear combination of daily gains (composite trait – selection index), and the variance of cumulative gains depends on the covariances between adjacent ages. Correlations between genetic effects at different ages are high, but correlations between residual effects at different ages are zero. Thus, the environmental and residual components are only a small part of the total variability of cumulative gains.

The ratio of the genetic variance of cumulative gains to the total variability of cumulative gains was high (Figure 7). This ratio can be considered as the reliability of the composite trait. The curve of this interclass coefficient has the typical shape of dependences of reliability on the quantity of information. This value approached 0.90, which is much more than the heritability of live weight at 400 days of age (Přibyl et al., 2007a). The same kinds of ratios were used by Zavadilová et al. (2005a) in a study of test day milk yields. Daily yields had lower heritability than the cumulative lactation yield derived from the RR covariance matrices in the same manner as here. However, the differences were small. The reason for this is that the contribution of the permanent environmental effects was negligible for cumulative gains, but was greater than that of genetic effects for milk production.

Components of correlations of daily gains between different ages

There are functional dependences and predeterminations of efficiency between daily gains at different ages by the previous state of animals. Different components of daily gains in different phases of the growth curve are differently correlated with each other. Figures 8 a,b,c show genetic, PE, and phenotypic correlations of daily gains at 100, 250, and 400 days of age, respectively, with daily gains at all other ages being tested.

The genetic potential persisted over a longer period; correlations of the genetic component are high and regularly decrease with age distance in all cases (Figure 8), but reach no negative values.

The correlation of the effect of PE related to 100 days of age reaches highly negative values in the middle of the observed period (Figure 8a). At the end of the observed period it increases sharply again to highly positive values. This means that an animal growing well at the beginning of the period decelerates in the middle of the period due to the permanent environmental effect in comparison with the contemporary one, and grows well again at the end of the period. One reason for this may be that under the restriction of nutrients animals growing faster in the initial phase use later a higher

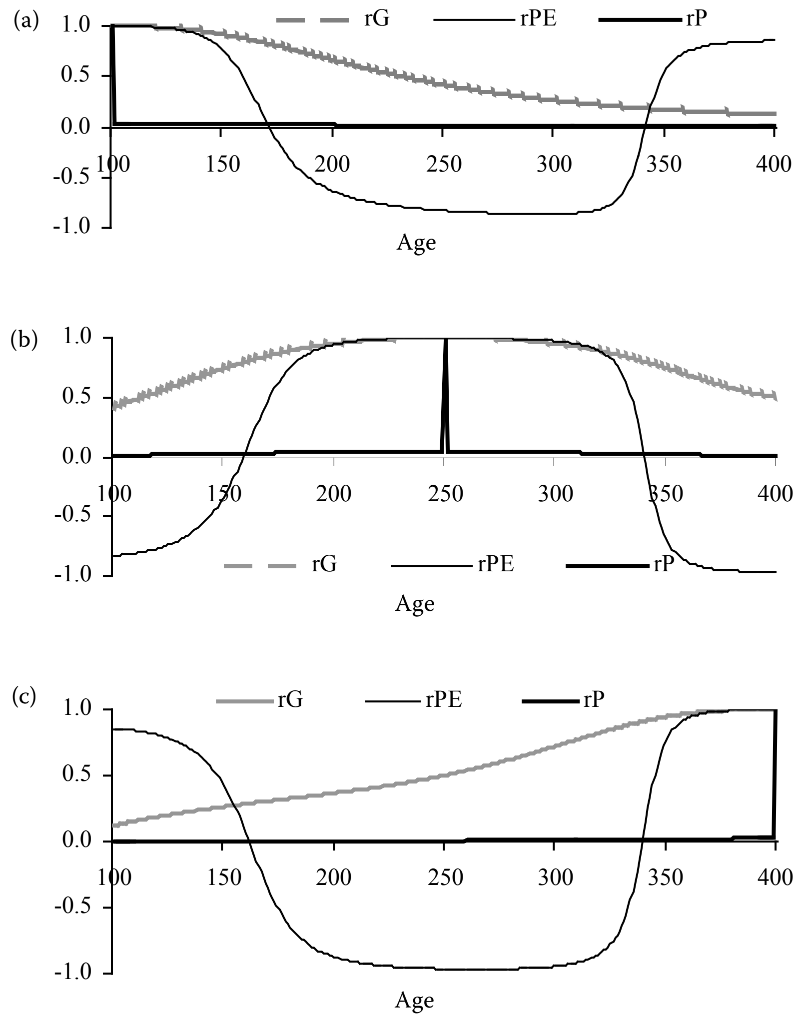

Figure 8a. Correlations of daily gains to (a) 100 days of age, (b) 250 days of age, (c) 400 days of age

proportion of nutrients for the maintenance, and only a smaller part of feed ration is released for weight gain. During rearing there are therefore environmental compensations for growth. This means that at the beginning of the period inferior bulls could reach a higher intensity of growth later, particularly those bulls beginning with rapid growth, and who stopped in the middle of the period for some reasons, and thereby the production (live weight) of all animals was later balanced on the same level. After the bulls lagging behind caught up with the other bulls, all the animals got into a comparable condition again, and the permanent environmental correlations turned from negative to positive values. Therefore the selection decision according to the phenotype value can be false.

Phenotypic correlations involved the genetic, PE and the residual component, collectively. The resulting correlation was practically zero. According to the phenotype correlations, the daily gains in different phases of growth appear independent, which is not true in reality.

Correlations of PE in relation to the age of 250 days (Figure 8b) show negative values at the beginning and at the end of the observed period. The picture of correlation for PE is reciprocal to values in Figure 8a. Those animals growing well in the middle of the period were not growing at the beginning and at the end of the period due to their permanent environment.

The correlations of the PE related to day 400 (Figure 8c) have similar courses to the correlations to day 100 (Figure 8a). Negative values were determined in the middle of the time interval. The genetic component has an opposite trend to that in Figure 8a.

Figure 9 show genetic, PE, and phenotypic correlations of cumulative gains at 100, 250, and 400 days of age, respectively, with cumulative gains at all other ages being tested.

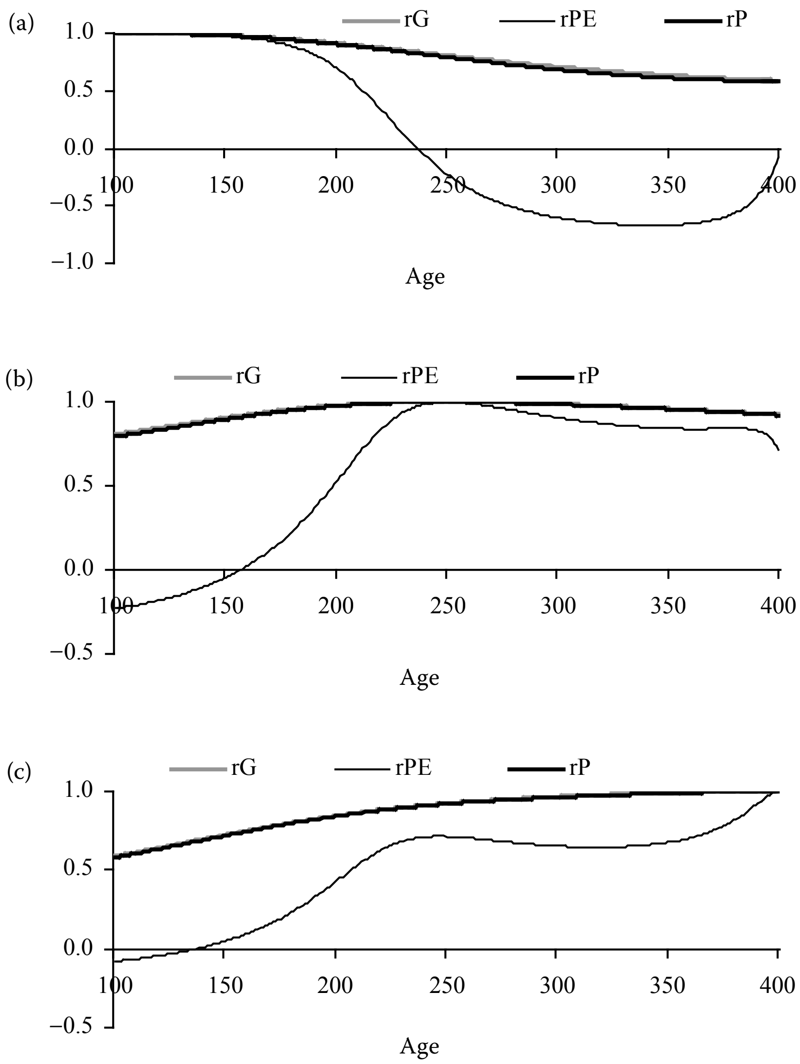

Figure 9a. Cumulative correlations of daily gains to (a) 100 days of age, (b) 250 days of age , (c) 400 days of age

The values of correlations both for genetic and phenotype components are high and decrease slightly with time. The levels of correlations are similar to correlations to live weight (Přibyl et al., 2007a, 2008). It follows from the magnitude of cumulative components of variance (Figure 6) that mostly the genetic component is involved in the phenotypic variance of the composite cumulative index.

Correlations of PE of cumulative gain (Figures 9a to 9c) decrease to negative values with increasing distance. Contrary to daily gains (Figures 8a to 8c), the correlation persisted longer at the same positive values, and the negative values were shifted to further records and did not reach such extremely negative values. In the case of correlations related to day 250 and 400 (Figures 9b and 9c), the negative values of the correlations occurred at the beginning of the period. From the second half they reached middle to high positive values.

CONCLUSION

Figures 1 and 2 of the course of gains and their standard deviations in relation to age show that a lower standard deviation is simultaneously observed in the period of the highest gain. It can be assumed that bulls with the genetic ability for a higher gain are "stopped" at this point by their feeding ration, and all animals grow similarly regardless of their abilities. Consequently, the influence of rearing conditions is very high. To facilitate the growth of animals in accordance with their genetic predispositions without any restriction on the part of the rearing environment is not practically possible, and the animals are almost always under some restrictions.

Contemporary groups were best defined by station-year-season of weighing, and fixed regressions were best fitted within station-year-season of birth.

Daily residual effects, including the error of recording, have a large impact on daily gains in short intervals, so that the heritability of daily gains is low. The heritability of cumulative gains to different ages, calculated from the RR estimated covariance matrices, is much higher than for daily gains and live weight, whereas this ratio reflects the reliability of the composite trait rather than heritability.

Genetic correlations between gains at different time intervals are high and decrease with the distance between the intervals. Correlations of an animal's permanent environment represent functional non-genetic dependences of growth in the particular phases. During growth there are environmental compensations for growth. The resulting phenotype correlations between gains at different intervals are close to zero. Without the breakdown of growth into causal genetic and non-genetic internal dependences between the phases of growth and external components of daily gains, it is very difficult to evaluate the real genetic capability of the animals correctly.

REML calculations require more iterations for daily gains than for body weights at different ages. Polynomial functions of variance components show borderline deviations from the common trend.

The presented methodology has been used for routine evaluation of young bulls since 2007 (Přibyl et al., 2007b). Genetic progress in a population of dual-purpose breeds is strongly influenced by the use of international sires in the position of sires of sires, selected according to several criteria. Only some of them were previously tested at the evaluated stations. Therefore, genetic improvement in the growth potential was low in the past.

Future research activity should be focused on the validation of methodology by evaluation of independent data sets which cover different systems of fattening, prolonging the observed period to a higher age of the animals, and which include maternal and non-additive genetic effects, and which test other types of functions, including nonlinear splines.

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