Changes over time in genetic parameters for growth in bulls and assessment of suitability of test methods

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ABSTRACT: Objectives of the study were to examine alternative measures of growth potential of bulls in testing stations, determine whether genetic parameter estimates of such traits changed over time, and examine whether existing methods for performance testing were appropriate. Records from 1980 to 2010 of 44 425 Fleckvieh bulls in Czech progeny testing stations were analyzed. The following traits were examined: weight at the beginning of the test (150th day of age), weight at the end of the test (530th day of age), gain from birth to the beginning of the test, and gain during the test. Fixed effects in five multi-trait animal models were station-year-season groups, linear and quadratic regressions on age, and regression on heterozygosity (proportion of an individual's loci with alleles from different ancestor breeds). Random effects included additive genetic, permanent environment, and residual variances. Separate analyses were conducted in four consecutive time periods (1980–1987, 1988–1992, 1993–1997, and 1998–2010). Across these time intervals, estimates of additive genetic variance decreased for all of the traits, while estimates of residual variances increased. In consequence, heritability estimates for all of the traits decreased over time. This decrease was most apparent for gain during the test, for which heritability declined by more than 50% over the course of the study. Results demonstrate that over three decades, the system of testing came into conflict with genetic improvement of the breed, possibly because the measured traits changed genetically over the course of selection. Regular analysis of the recorded data, re-estimation of genetic parameters in relation to time, and appropriate modification of existing methods of rearing/fattening in station tests are required. When such inspections are neglected, data from the testing stations may not accurately reflect genetic merit of individual animals.

Keywords: gain; genetic analysis; progeny test; Fleckvieh; genetic variation during time

Meat production has an important role in the breeding of dual-purpose cattle breeds. For genetic evaluation of meat yield, several types of information can be used, including data from performance testing stations, records from progeny tests (station or field), and measurements taken at slaughter. Reliability and usefulness of results is dependent upon testing environments and procedures. Field tests may provide substantial numbers of records, but data may be less reliable than from testing stations due to greater variation in management. Alternatively, testing stations may provide more uniform management and more reliable recording but produce fewer records. Organization and rearing conditions of any test should allow the expression of genetic variance in the population. Several sources of information are available for the evaluation of meat production in the Czech Republic: performance testing stations, progeny testing stations, and field testing in which data are collected on commercial cattle farms (the SEUROP system). Progeny testing stations were designed to estimate genetic merit for growth of progeny-tested sires (Czech Fleckvieh) and have standardized terms and methodological procedures (see www.cestr.cz/files/pokyny_a_formulare_pk/metodika_masa.pdf). The analytical method for evaluation is the multi-trait animal model, the traits being net gain (calculated

as carcass weight divided by age), SEUROP carcass conformation score (grades S to P according to muscularity) with five fatness classes (1 – lean, 5 – very fat), and meat percentage. These methods were established in accordance with Schild et al. (2003) and other directives (www.zar.at/article/archive/1159).

Alternative procedures to quantify growth are weight at a certain age versus gain over a certain period of time. In both cases, proper evaluation of growth is problematic. Weight is cumulative over time, and it is difficult to properly account for the influence of systematic environmental effects and of compensatory growth (higher growth at a later time in response to environmentally limited growth in a former). As described by Vostrý et al. (2012), gain over an extended period of time is also subject to such influences. For these reasons, it is necessary to proceed very carefully in choosing a genetic evaluation protocol.

Nešetřilová (2005) described the growth curve for Czech Fleckvieh cattle up to 1400 days of age by a multiphase growth model, Veselá et al. (2011) estimated the genetic parameters of beef cattle production traits in the SEUROP system, and Vostrý et al. (2012) described growth evaluation of beef bulls in performance testing stations.

Testing procedures similar to those in the Czech Republic have been described for Swiss dual-purpose cattle (Schleppi et al., 1994) and German Simmental cattle (Engellandt et al., 1999). Bogdanovic et al. (2002) evaluated the performance tests for Simmental bulls and found that selection based on an individual performance test was particularly important for traits of medium (i.e. growth) to higher heritability. In their study daily gain during different time periods (before the test, during the test, and over the lifetime) and weight (at the beginning of the test, monthly during the test, and at the end of the test) were evaluated.

Ducháček et al. (2011) reported that average breeding values of the Angus cattle population changed over the course of time, presumably reflecting cumulative response to selection and change in genetic merit.

The main focus of our work was to evaluate suitability of testing methods for present populations of cattle that may differ distinctly from their ancestral population when the testing method was established. When the same methodology and testing procedures are used for a very long time (1980–2010 in the present study), it may be that the biological determinants of traits as well as their genetic and environment variance have changed. If so, testing conditions may no longer be optimum.

MATERIAL AND METHODS

We evaluated records from 44 425 Czech Fleckvieh bulls in progeny testing stations (PTS). The data were edited in the following manner: station-year-season classes (SYS) with fewer than five bulls and fewer than three sons per sire were removed. Small station-year-season of birth classes (SYSb) and station-year-season of weighing classes (SYSw) were merged to achieve a minimum of 25 animals per class for that effect. If the level of a class within station could not be determined for the following season, that SYS class was excluded. Finally, outliers (i.e. more than 3 standard deviations from mean) of individual subsets described below were excluded.

After these edits were accomplished, the remaining data file included 41 449 bulls tested between 1980 and 2010. These bulls were the offspring of 3902 Czech Fleckvieh sires. The total number of animals included in the four-generation pedigree was 157 523.

The following traits were evaluated: weight at the start of the test (150th day of age), weight at the end of the test (530th day of age), gain from birth to 150 days of age, and gain during the test (150–530 days). Genetic analyses for these traits were conducted using five multi-trait (MT) animal models.

To better model the outcomes of testing over time, the complete data set was separated into 4 time periods (1980–1987, 1988–1992, 1993–1997, and 1998–2010) for evaluation. These particular time periods were chosen so that approximately equal numbers of bulls were in each group.

The general linear model for REML analyses, including random effects in matrix notation, was as follows:

$$y = \mathbf{X}b + \mathbf{Z}u + e$$

where:

y = vector of observations for two weights or two gains

$\mathbf{X}$, $\mathbf{Z}$ = matrices of explanatory variables assigning performance records to fixed and random effects, respectively

b, u = estimated unknown vectors of fixed and random effects

e = vector of random residual effects

In the MT models we assume that the random effects show normal random distribution with zero average and variances:

$$\mathrm{Var} \begin{Bmatrix} \boldsymbol{u1} \\ \boldsymbol{u2} \\ \boldsymbol{e} \end{Bmatrix} = \begin{Bmatrix} \mathbf{I} \otimes \mathbf{P} & 0 & 0 \\ 0 & \mathbf{A} \otimes \mathbf{G} & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{I} \otimes \mathbf{E} \end{Bmatrix}$$

where:
$\boldsymbol{u1}$ = vector of random permanent environment effects of animals with records
$\boldsymbol{u2}$ = vector of additive genetic effects
$\boldsymbol{e}$ = vector of random residual effects
$\mathbf{I}$ = identity matrix
$\mathbf{P}$ = (co)variance matrix for permanent environmental effects
$\mathbf{A}$ = numerator relationship matrix
$\mathbf{G}$ = (co)variance matrix for additive genetic effects
$\mathbf{E}$ = diagonal matrix of residual variances

Effects included in the models are described in Table 1. We did not use model with repeatability because of better fit of the genetic parameters in multi-trait model (Mielenz et al., 2007). Each animal was weighed twice in its common permanent environment. After the evaluation of the models and on the basis of Akaike's information criterion (AIC), variance component estimation, heritability estimates, and studies available in the literature, one model for each trait was chosen as the most suitable.

SYSb and SYSw assessed the net impact of environmental conditions early in life and of testing station, respectively, on variance for each trait. The regression on age characterizes the growth curve from birth to 530 days of age.

Table 1. Effects included in the evaluation

Model	SYSw	SYSb	Age	Age^2	Het	Individual	Pe
1	x	x	x	x		x	
2	x	x	x	x	x	x	
3	x	x	x	x	x	x	x
4	x		x	x	x	x	
5	x		x	x	x	x	x

fixed effects: SYSw = bulls group for the station-year-season effect (3 months) by date of weighing, SYSb = bulls group for the station-year- season effect (3 months) by date of birth, Age = age at weighing, Age^2 = age × age, Het = heterosis effect – regression on heterozygosity
random effects: Individual = genetic effect of the individual with relationship matrix of four generations, Pe = permanent environment effect of the individual

Fitting a regression on heterozygosity is an attempt to account for the effect of heterosis in those bulls with some non-Fleckvieh ancestry and was modelled as the regression of each trait on the expected proportion of each bull's loci with alleles from different ancestor breeds (Hickey et al., 2007). This accounting was deemed necessary because in the 1980's other cattle breeds including Ayrshire, Red Holstein, and Montbeliarde, were crossed into Czech Fleckvieh in an attempt to increase milk production and improve body constitution. Although Czech Fleckvieh cattle are now relatively homogeneous, early observations were subject to heterosis effects, which if unaccounted for, could affect results of our analyses.

To calculate genetic parameters using the REML method, the REMLF90 program was used (Misztal et al., 2002).

RESULTS AND DISCUSSION

During the time span of this study, both the number of testing stations and the number of bulls tested in these stations changed. The largest number of bulls was tested in 1987 (2758), and stations were used most intensively from 1985 to 1991. Thereafter the number of animals being tested gradually decreased; 1208 bulls were tested in 2000 and 724 in 2004 (data not shown). There was no overall trend in observed values of weight and growth traits across time (Table 2), with average values remaining at similar levels throughout the study. The noticeable difference in the age of the animals at the end of the test in the last time period was due to a change in methodology (the test was prolonged).

The genetic parameters obtained from the individual multi-trait models are summarized in Tables 3 and 4 (for weight) and Tables 5 and 6 (for gain).

Weight. Model 4 resulted in the highest heritability estimate for weight at both the beginning and at the end of the test (Table 3), primarily because model 4 resulted in the highest estimate of additive genetic variance while maintaining a residual variance value similar to that of the other models. In model 3, the residual variance was reduced by the inclusion of the permanent environmental effect, but this model also had the lowest value of additive genetic variance for weight at 150 days of age. Mohiudin (1993) and Bogdanovic et al. (2002) both reported a higher

Table 2. Summary of the average values for the entire data set (standard deviation in parentheses)

	Data set	1980–1987	1988–1992	1993–1997	1998–2010
n	41 449	10 663	10 673	9 710	10 379
WB (kg)	165.5 (23)	163 (24)	166 (24)	162 (23)	171 (22)
WT (kg)	554 (62)	528 (51)	537 (59)	558 (56)	595 (60)
GB (g/day)	836 (154)	818 (160)	835 (154)	813 (150)	877 (115)
GT (g/day)	1 075 (143)	1 041 (124)	1 020 (134)	1 128 (141)	1 118 (139)
AGEb (day)	150 (3)	150 (3)	150 (3)	150 (4)	150 (3)
AGEe (day)	511 (15)	500 (4)	514 (15)	501 (5)	529 (8)
HET	0.37 (0.28)	0.3 (0.31)	0.44 (0.27)	0.41 (0.24)	0.34 (0.24)

WB = weight at the start of the test, WT = weight at the end of the test, GB = gain before the test, GT = gain during the test, AGEb = age at the beginning of the test, AGEe = age at the end of the test, HET = average heterosis

heritability for weight at the end of testing than results obtained in this study (0.3 vs. 0.25).

Heritability for the weight at the start of the test was slightly higher in our data than the value of 0.25 reported by Bogdanovic et al. (2002); Koots et al. (1994), Gregory et al. (1995), Bennett and Gregory (1996), and de Matos et al. (2000) reported results that were similar to those of Bogdanovic.

The genetic correlation between start and end of test weights varied only from 0.5 to 0.54 for the four models (Table 4). Correlations among permanent environment effects were low, and residual correlations varied from 0.42 to 0.46. The highest value of the residual correlation was observed when the permanent environment effect was added into the model (model 5 versus model 4). A direct comparison of the models using AIC was possible only for models with the same fixed effects. Therefore, only models 2 and 3 (or models 4 and 5 for gain) could be compared, and model 2 was more appropriate according to this criterion.

Bouška et al. (2003) reported that genetic correlations between weights at 110, 210, 300, 330, 365, and 420 days at performance testing stations ranged from moderate to high. The lowest genetic correlation was between the 110th and 420th day, with a value of 0.4. In their experiment, the genetic correlation between the weight at the beginning and the end of the test was 0.5.

Gain. All models resulted in higher heritability estimates for gain from birth to start of the test than for gain during the test (Table 5). Models 1, 2, and 3 (first group) had nearly the same value for both heritability coefficients. The heritabilities were higher in models 4 and 5 (second group) than in those of the first group. Similar results were observed between these two groups for all of the variances.

Additive genetic variance for daily gain from birth to start of the test for the first group of models was approximately by 900 g[2] greater than that for the second group. Residual variance was lower in the second group compared to the first but by only 250 g[2]. Overall, gain during the test had lower values for all the variances than did the gain up to the beginning of the test. With respect to the gain prior to the test, genetic variance was higher in the second than in the first group of models, whereas

Table 3. Genetic parameter estimates for weight traits – entire data set using different models (M1–M4))

	WB				WT			
	M1	M2	M3	M4	M1	M2	M3	M4
σ^2_a	102	96	95	113	578	572	572	623
σ^2_e	293	296	269	290	1849	1855	1659	1846
σ^2_{pe}	–	–	27	–	–	–	196	–
h^2	0.26	0.24	0.24	0.28	0.24	0.24	0.24	0.25

WB = weight at the start of the test, WT = weight at the end of the test, σ^2_a = additive genetic variance, σ^2_e = residual variance, σ^2_{pe} = permanent environment variance, h^2 = heritability coefficient

Table 4. Correlations between weight at the beginning and at the end of the test, between gain from birth to start of the test and gain during the test, and the Akaike's information criterion (AIC) for each model

	Weight				Gain				
	M1	M2	M3	M4	M1	M2	M3	M4	M5
r_a	0.50	0.54	0.54	0.53	0.11	0.12	0.11	0.07	0.07
r_e	0.43	0.43	0.46	0.42	0.04	0.03	0.03	0.03	0.02
r_{pe}	–	–	0.10	–	–	–	0.09	–	0.09
AIC	857 157	856 916	856 922	864 596	1 079 514	1 079 494	1 079 451	1 103 122	1 103 128

r_a = genetic correlation, r_e = residual correlation, r_{pe} = permanent environment correlation

residual variance for gain during the test was lower in the second group than in the first group.

Heritability for gain during the test in the current experiment (Table 5) was lower than the heritability estimate of 0.32 reported by Bogdanovic et al. (2002). Heritability for gain prior to the test reported by Bogdanovic et al. (2002) was lower than that in our experiment (0.22 vs. 0.27).

In their work with Czech Fleckvieh breeding bulls in performance stations, Bouška et al. (2003) reported heritability values for average daily gain during test ranging from 0.2 to 0.59, depending on the length of the test. Low values were observed at the beginning of the test, and high values were observed at the end of the test.

Genetic, residual, and permanent environment correlations for gain (Table 4) were very low compared with the analogous correlations for weight (Table 4).

Table 5. Genetic parameter estimates for gains – entire data set and models M1–M5

	M1	M2	M3	M4	M5
GB					
σ_a^2	3 855	3 823	3 841	4 739	4 739
σ_e^2	13 305	13 321	11 470	13 060	11 220
σ_{pe}^2	–	–	1 843	–	1 841
h^2	0.23	0.22	0.22	0.27	0.27
GT					
σ_a^2	3 052	3 037	3 047	3 892	3 892
σ_e^2	11 640	11 650	9 611	11 380	9 347
σ_{pe}^2	–	–	2 032	–	2 029
h^2	0.21	0.21	0.21	0.26	0.26

GB = gain before the test, GT = gain during the test, σ_a^2 = additive genetic variance, σ_e^2 = residual variance, σ_{pe}^2 = permanent environment variance, h^2 = heritability coefficient

Bouška et al. (2003) demonstrated that as the interval between weight measurements increased, the genetic correlation between the gains decreased. The long intervals between weighings in our study may account for the low observed correlations.

Based on results presented above, model 4 was chosen to evaluate animal weight during various time periods. For gain, model 4 had results that were very similar to those of model 5, but model 4 was chosen because it had a lower AIC value.

Heritability estimates across four time intervals. As show the results for model 4 in Table 6, across time intervals (1980–1987, 1988–1992, 1993–1997, and 1998–2010), additive genetic variance and heritability estimates gradually decreased, whereas residual variances increased for both weight traits. This trend was particularly evident for the weight at the end of the test. Residual correlations among weights did not show a uniform trend; there was a decline from the first to the second and third intervals, after which levels in the fourth interval returned to those in 1980–1997. In contrast, the genetic correlation between weight at the beginning versus the end of the test increased by almost 50% across the four time intervals. In the multi-trait model, total variance can be compensated by correlations between traits. Due to the decline in the additive genetic variance and the increase in the genetic correlations between weights the same model equation was chosen (i.e. model 4 in Table 1) and used for two single-trait models. No compensation was found when comparing the results of the single-trait (ST) and MT models (results not shown).

The results for gain traits using model 4 showed similar trends to those for the weight analyses. That is, across time intervals and for both gain traits, additive genetic variances and heritability estimates gradually decreased from interval 1 through interval 4, while residual variances in-

Table 6. Genetic parameter estimates for weight traits (model 4)

Period	WB			WT			Correlation	
	σ_a^2	σ_e^2	h^2	σ_a^2	σ_e^2	h^2	r_a	r_e
1980–1987	135	290	0.32	697	1272	0.35	0.39	0.47
1988–1992	130	286	0.31	692	1490	0.32	0.51	0.40
1993–1997	92	256	0.27	475	2011	0.19	0.51	0.37
1998–2010	97	316	0.24	625	2579	0.20	0.66	0.46

WB = weight at the start of the test, WT = weight at the end of the test, σ_a^2 = additive genetic variance, σ_e^2 = residual variance, h^2 = heritability coefficient, r_a = gentic correlation, r_e = residual correlation

Table 7. Genetic parameters for gain traits (model 4)

Period	GB			GT			Correlation	
	σ_a^2	σ_e^2	h^2	σ_a^2	σ_e^2	h^2	r_a	r_e
1980–1987	5 928	12 960	0.31	5 667	7 471	0.43	−0.02	−0.03
1988–1992	5 021	13 140	0.28	3 957	9 512	0.29	−0.03	0.04
1993–1997	4 009	11 420	0.26	3 510	13 710	0.20	0.01	0.03
1998–2010	4 114	14 140	0.23	2 857	14 400	0.17	0.32	0.13

GB = gain before the test, GT = gain during the test, σ_a^2 = additive genetic variance, σ_e^2 = residual variance, h^2 = heritability coefficient, r_a = gentic correlation, r_e = residual correlation

creased (Table 7). The decrease in heritability of gain during the test was very noticeable, whereas the decrease in heritability was more gradual for gain from birth to start of the test. The genetic correlation between gain prior to start of the test and gain during the test was essentially zero. Only in the most recent time interval did the genetic correlation reach a value of 0.318. Even in this period, various single trait models showed the same results as the multiple trait model.

As shown in Figure 1, heritability estimates (h^2) distinctly decreased over time for all traits. The h^2 values calculated for the weight at the end of the test were almost identical in the last two intervals. The largest decrease was for heritability
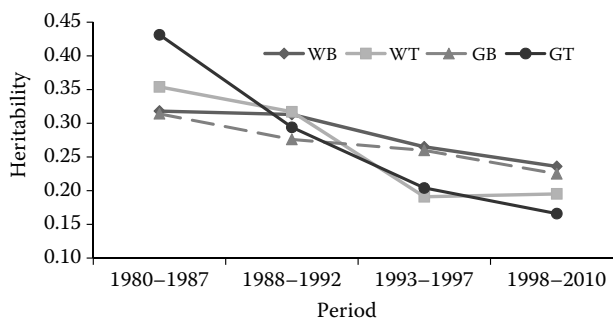

Figure 1. Heritability estimates for weight and growth traits in four time intervals spanning 30 years

of gain during the test, which decreased by more than 50%, from 0.43 to 0.17.

The routine model in use is the multi-trait animal model but with different traits. Prediction of breeding values for sires is carried out outside the Czech Republic and breeding values of bulls evaluated in this experiment are not accessible for comparison.

CONCLUSION

Five animal multi-trait models were tested. The chosen model included fixed effect of station-year-season group of weighing classes, linear and quadratic regressions on age, regression on heterozygosity (proportion of an individual's loci with alleles from different ancestor breeds), and random effect of additive genetic variance.

Over the years, the development of cattle breeds can conflict with original setup of testing. In fact, these situations can result in evaluation of different traits in every period. When the regular analyses of data and changes of test setup are underestimated, the results from the testing stations may not reflect the true genetic foundation of the individuals. Selected individuals may therefore not adequately represent the quality of base popula-

tion, and average genetic values of individuals in tests can be artificially shifted compared to the true values of the entire population.

The results of this study indicate a need for regular analyses of recorded data and estimation of genetic parameters run repeatedly over time. When deficiencies in the test method are discovered, appropriate modification of the existing organization of rearing/fattening in the testing stations is required.

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