Selection of a suitable definition of environment for the estimation of genotype × environment interaction in the weaning weight of beef cattle

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ABSTRACT: Genotype by environment interactions for weaning weight in beef cattle were tested using several definitions of environments. Four breeds of beef cattle (Hereford, Aberdeen Angus, Beef Simmental, and Charolais) were represented. The environments were defined according to five criteria: altitude, production areas, economic value of the land, less favourable areas, and performance levels of a breed within herds. Ten mixed models were compared including the effects of direct and maternal genetics, herd-year-season, maternal permanent environmental, breed, environment, genotype × environment interaction, sex of calf, and age of dam. The suitability of the models was tested by Akaike's Information Criterion, likelihood ratio test, and magnitude of the residual variance. The most suitable definitions of environment were less favoured areas and herd levels of performance. Estimates of direct heritability ranged from 0.07 to 0.19. Genotype × environment interactions should be included in a genetic evaluation model for interbreed comparisons of beef cattle in the Czech Republic.

Keywords: environment; beef cattle; genetic parameters; REML; maximum likelihood

Knowledge of the genotype × environment (G × E) interaction is important for the optimum use of particular genotypes in different production and breeding systems, especially for beef cattle which are kept in both intensive and extensive environments. The adaptation of breeding systems in beef cattle was studied by Krupa et al. (2005) and Veselá et al. (2007). G × E interaction is defined as a change in the relative value of the performance of two or more genotypes in two or several different environments. When comparing two different genotypes, the magnitude and statistical significance of this interaction is related mainly to the distinctness of genotypes or environment. In fact, such an interaction is assumed to exist whenever two or more genotypes occur in two or several environments.

Two approaches are used to study G × E interaction: either G × E interaction is included in the evaluated model or phenotype expression of the same trait in different environments is classified as two different production traits (Falconer, 1970). To apply these two approaches to the evaluation of G × E interaction, the environments should be divided into classes of a given environmental effect. The selection of a suitable approach to the classification of G × E interaction was studied e.g. by Fernando (1984) and Mathur and Schlote (1995). A definition on the basis of a high number of levels with increasing values, i.e. reaction norm, may be another method (Kolmodin et al., 2002).

According to Lin and Togashi (2002), the definitions of G × E interaction can be divided into

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Supported by the Ministry of Education, Youth and Sports of the Czech Republic (Project No. MSM 6046070901) and by the Ministry of Agriculture of the Czech Republic (Project No. MZe 0002701401).

breed × environment interaction (between-breed interaction), which was investigated e.g. by Křížek et al. (1992), Brown et al. (1993) and Sandelin et al. (2002), and individual × environment interaction (within-breed interaction), which was studied e.g. by Notter et al. (1992), De Mattos et al. (2000).

Production characteristics of all beef cattle animals are under routine ICAR recording across breeds in the Czech Republic. The objectives of this paper were to select a suitable definition of environment and to test the existence of G × E interaction for weaning weight at 210 days of age in beef cattle breeds under the conditions in the Czech Republic. Genotype was determined by the most frequent breeds of beef cattle, and five different definitions of environment were tested.

MATERIAL AND METHODS

G × E interaction was estimated for weaning weight at 210 days of age in the most frequent breeds of beef cattle kept in the Czech Republic during a period of 16 years (1990–2005).

The data were edited so that the components of variance between all the considered effects would be estimable (Vostrý et al., 2007). The data set included:

(1) Sires that had at least 5 offspring with tested performance.
(2) Herd × year × season (HYS) had at least 5 individuals.
(3) Sires that had offspring in at least two HYS.
(4) HYS which had progeny of at least two sires.
(5) Mothers that had at least two offspring and at least one half-sister.

The two most numerous breeds of medium body frame – Hereford (HE) and Aberdeen Angus (AA) – and the two most numerous breeds of large body frame – Beef Simmental (BS) and Charolais (CH) – were used for the estimation of G × E interaction. Each breed was represented by individuals with a gene proportion of 88 to 100% of the given breed. The total set consisted of 19 760 individuals.

Environments

Environment was classified according to these criteria:

(1) Economic value of agricultural lands (hereinafter the economic value):
  (a) low prices – average price maximally 1.5 Kč/m;
  (b) medium prices – average price from 1.5 to 3.0 Kč/m;
  (c) high prices – average price more than 3.0 Kč/m.
(2) Altitude:
  (a) mountain – altitude above 600 m a.s.l.;
  (b) foothills – altitude from 450 to 600 m a.s.l.;
  (c) lowland – altitude up to 450 m a.s.l..
(3) Production areas:
  (a) forage production – annual temperatures 5–6°C, precipitation above 700 mm, steeply sloping and stony lands;
  (b) cereal production – annual temperatures 5–8.5°C, precipitation 550–700 mm;
  (c) sugar beet production – annual temperatures 8–9°C, annual precipitation 500–650 mm.
(4) Areas according to LFA: Categorisation of farm land resources from the aspect of less favourable areas (LFA):
  (a) mountain – above 600 m a.s.l. or 500 to 600 m a.s.l., with steeply sloping lands – in more than 50% of lands the gradient is higher than 7°;
  (b) barely cultivable land – low productivity of farm land, barely tillable soils and soils with reduced production potential;
  (c) productive – with high productivity of farm land.
(5) Levels of performance of breeds achieved within a herd (hereinafter the herd level) (Kolmodin et al., 2002). Environment was divided into classes of herd levels according to average performance achieved in the particular HYS within breeds. HYS were ranked according to the average live weight achieved by breeds, and herd levels were composed so that about 33% HYS of the given breed would be in each level:
  (a) high-level herd;
  (b) medium-level herd;
  (c) low-level herd.

The definition of environment and the testing of the existence of G × E interaction were performed by mixed models using the MIXED maximum likelihood procedure in the SAS statistical package (SAS, 2004) respecting Rasch and Mašata (2006):

Model 1

$$y_{ijklmno} = \mu + \mathrm{Sex}_i + FB_j + \mathrm{Age}M_k + \mathrm{Breed}_l + \mathrm{Env}_m + \\ + hys_{mn} + \mathrm{sire}_{lo} + (\mathrm{Breed} \times \mathrm{Env})_{lm} + e_{ijlkmno}$$

Model 2 corresponded to Model 1, but it did not include the effect of interaction $(\text{Breed} \times \text{Env})_{lm}$

where:

y_{ijklmo} = weaning weight at 210 days of age
μ = general mean
Sex_i = fixed effect of sex (either young bull or heifer)
FB_j = fixed effect of litter size (either single or twin-born)
$\text{Age}M_k$ = fixed effect of mother's age
Breed_l = fixed effect of breed
Env_m = fixed effect of environment
sire_{lo} = random effect of sire within breed
hys_{mn} = random effect of HYS within environment
$(\text{Breed} \times \text{Env})_{lm}$ = interaction between breed (Breed_l) and environment (Env_m)
$e_{ijklmno}$ = random error

The effects of HYS and sire were considered as random because of the high number of levels of these effects (HYS – 1 270 levels and sire – 602 levels).

Models 1 and 2 were used for the definition of a suitable environment only for further analysis. Therefore these models do not use relationships among sires, and no genetic variance is assumed.

The selection of a suitable definition of environment was made on the basis of the number of sires with offspring in different environments related to the total number of sires (hereinafter the numbers of connecting sires), and the number of offspring of connecting sires related to the total number of individuals in the database, achieved values of residual variance (σ^2_e), and Akaike's information criterion (AIC). G × E interaction was tested on the basis of statistical significance of G × E interaction by a comparison of the values of residual variance and AIC between the model with G × E interaction (Model 1) and the model without G × E interaction (Model 2). The ratio of connecting sires to their offspring in the entire database is crucial for testing the existence of G × E interaction.

The values of AIC were calculated from this equation (Bozdogan, 2000):

$$\text{AIC} = -2\log L(\theta) + 2d$$

where:

$\log L(\theta)$ = the logarithm of the value of likelihood function
d = the number of free parameters in the model

Estimation of genetic parameters for the testing of genotype × environment interaction.

The estimation of genetic parameters was carried out using a single-trait animal model by the REML method. Definitions of environment for the estimation of genetic parameters and G × E interaction effect were based on a previous investigation.

Different models were tested (Table 1), based on the animal model used for the estimation of breeding value in the Czech Republic (Přibyl et al., 2003).

$$V\begin{bmatrix} a \\ m \end{bmatrix} = A \otimes \begin{bmatrix} \sigma^2_a & \sigma_{am} \\ \sigma_{am} & \sigma^2_m \end{bmatrix}$$

$$V(pe) = I\sigma^2_{pe}$$

$$V(\text{HYS}) = I\sigma^2_{\text{HYS}}$$

$$V(\text{G} \times \text{E}) = I\sigma^2_{\text{G} \times \text{E}}$$

$$V(e) = I\sigma^2_e$$

The effects a and m are assumed to be correlated with each other, and the remaining effects are independent. The particular effects are also assumed to show normal random distribution with zero mean and variance (σ^2):

Table 1. Models

Model	Age M, Sex	HYS	YS	*a, m, pe*	Breed	Env	G × E
I	F	F		R	F		R
Ia	F	F		R	F		
II	F	R	F	R	F		R
IIa	F	R	F	R	F		
III	F	F		R	F	F	R
IIIa	F	F		R	F	F	

Age M – effect of mother's age; sex – effect of the combined effect of sex (young bull, heifer) + litter size (single, twin-born); HYS – effect of HYS; YS – effect of year × season; breed – effect of breed; Env – effect of environment; *a* – direct effect of the individual; *m* – maternal effect of the individual; *pe* – effect of the permanent maternal environment; G × E – effect of genotype × environment; F – fixed; R – random where:

σ_a^2 = additive genetic variance of direct effect
σ_m^2 = additive genetic variance of maternal effect
σ_{am} = genetic covariance of direct and maternal effect ($Cov(a, m)$)
σ_{pe}^2 = variance of the effect of permanent maternal environment
σ_{HYS}^2 = variance of HYS effect
$\sigma_{\mathrm{G \times E}}^2$ = variance of the effect of genotype × environment interaction
σ_e^2 = variance of the effect of residual error
A = relationship matrix
I = identity matrix

The computation programme VCE 5.1 (Kovač et al., 2002) was used for the estimation of variance-covariance components and their mean errors. The following population parameters were derived from the estimated variance-covariance components:

σ^2_y = phenotype variance ($\sigma_y^2 = \sigma_a^2 + \sigma_m^2 + \sigma_{am} + \sigma_{pe}^2 + \sigma_{G \times E}^2 + \sigma_e^2$) (Willham, 1979)

h_a^2 = coefficient of direct heritability ($h_a^2 = \sigma_a^2/\sigma_y^2$)

h_m^2 = coefficient of maternal heritability ($h_m^2 = \sigma_m^2/\sigma_y^2$)

c^2 = the ratio of variance of permanent maternal environment to phenotype variance ($c^2 = \sigma_{pe}^2/\sigma_y^2$)

G × E^2 = the ratio of variance of genotype × environment interaction to phenotype variance (G × E^2 = $\sigma_{\mathrm{G\times E}}^2/\sigma_y^2$)

r_{am} = genetic correlation of direct and maternal effect ($r_{am} = \sigma_{am}/(\sigma_a \times \sigma_m)$)

The suitability of the model was tested by AIC and by the Likelihood Ratio test (LR, Kaps and Lamberson, 2004), which is based on a comparison of the values of the likelihood function of two models.

$$\chi^2 = -2\log\frac{L(reduced)}{L(full)} = 2(-\log L(reduced) + \log L(full))$$

where:

χ^2 = the value of *chi*-squared test
L(reduced) = the value of the likelihood function of a reduced model – model without G × E effect
L(full) = the value of the likelihood function of a full model – model with G × E effect

RESULTS AND DISCUSSION

Selection of a suitable definition of environment

Table 2 shows that both Models (1 and 2) reached the same values of residual variance for all definitions of environment. The only exception was the definition according to herd level, which had lower values. Model 2 reached slightly higher values of residual variance. The highest suitability evaluated by AIC was the environment according to herd level and economic value. On the contrary, definitions according to altitude and LFA were the least suitable if the AIC value was used. The lower values of AIC and residual variance for Model 1 indicate the effect of G × E interaction. The values of connecting sires and their offspring, similar to those of residual variance, did not demonstrate any marked differences between the environments. An exception was the definition according to herd level, when the values of connecting sires and their offspring reached twofold values compared to the other definitions of environment. These high values were caused by the creation of herd level classes.

Table 2. Significance of models evaluated according to the definitions of environment by means of a mixed model

	Altitude	Production areas	Economic value	LFA	Herd level
F < Pr	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Numbers of connecting sires	37%	37%	42%	37%	74%
Offspring of connecting sires	54%	47%	58%	54%	90%
σ_e^2 – Model 1	958.25	958.54	957.29	957.68	954.12
σ_e^2 – Model 2	958.72	958.64	958.47	958.75	954.51
AIC – Mode 1	195 091.20	195 035.50	195 030.60	195 102.40	193 343.50
AIC – Mode 2	195 157.60	195 181.60	195 105.40	195 166.00	193 393.10

F < Pr – statistical significance of the effect of genotype × environment interaction; σ_e^2 – residual variance; AIC – Akaike's information criterion

Table 3. The correlation between the definitions of environment

	Altitude	Production areas	Economic value	LFA	Herd level
Altitude	1.000	0.338	0.657	0.652	0.166
Production areas		1.000	0.263	0.121	0.111
Economic value			1.000	0.438	0.166
LFA	sym.			1.000	0.118
Herd level					1.000

Table 3 shows the values of the correlation which evaluates the overlapping of definitions of environment. By this correlation the identity of the inclusion of individuals in the particular areas according to different definitions of environment was evaluated. The highest values of correlation were estimated between definitions according to LFA, altitude (0.652), and economic value (0.438). A high correlation was also calculated between environmental definitions according to altitude and economic value (0.657). The consideration of altitude and the average price of land in LFA methodology caused the high values of correlation between the above-mentioned definitions. The high value of correlation between definitions according to economic value and altitude is influenced by the fact that the value of agricultural land declines with higher altitude. The lowest values of correlation were observed between the definition according to herd level and the other definitions of environment. The low correlation between the herd level and the other environments is explained by the absence of any relation between the achieved performance level in herds and the other aspects of classification. As the definitions of environment had identical values of residual variance, AIC, proportion of connecting sires and their offspring, and due to the existence of a high correlation between definitions, it is possible to further consider only the definition of conditions according to herd level and LFA. The definition according to LFA was selected because it is currently used for the allocation of support to farmers in the Czech Republic and comprises both the altitude and the economic value of land.

Models 1 and 2 provided the identical value of residual variance for all definitions of environment (Table 2). The fixed effects included in the mixed model were statistically highly-highly significant ($P < 0.0001$) in all cases. Hence, the addition of the effect of G × E interaction does not improve the explanation of variability. The greater suitability of Model 1 is indicated by the values of AIC, which were lower in all definitions of environment for Model 1 than for Model 2. G × E interaction was estimated as statistically highly significant ($P < 0.0001$) in all definitions of environment (Table 2).

Figure 1 illustrates the LSM values estimated for breeds in localities defined according to LFA methodology (G × E interaction). The lowest values in the mountain area, which represents the least

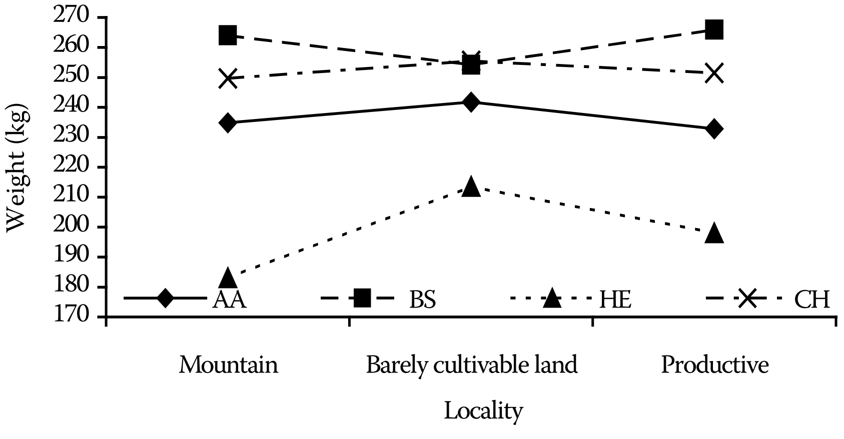

Figure 1. LSM values according to breeds and locality in relation to LFA methodology

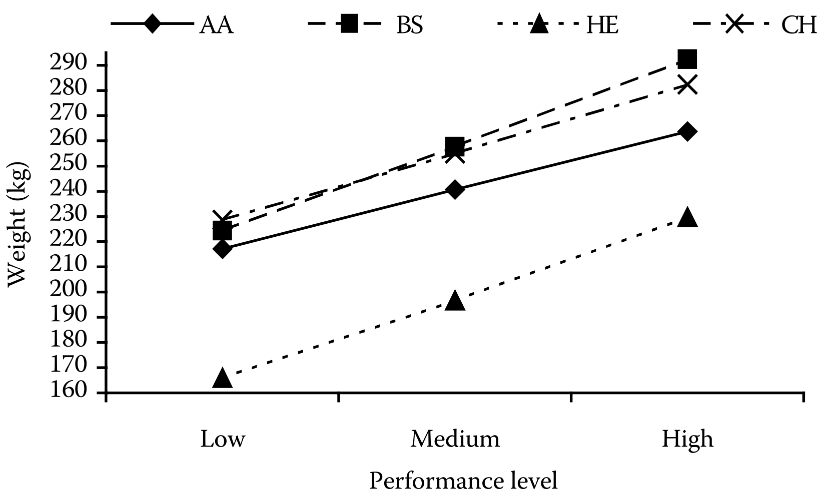

Figure 2. LSM values according to breeds and performance level

intensive one of the areas, were determined in the HE breed while the BS breed had the highest values. In the barely cultivable locality, differences in the expected values between breeds are reduced. In this locality we anticipate the most suitable conditions for beef cattle production due to the higher yields of pastures and less dense stocking of land. In productive localities, which are less suitable for cattle production due to the highest stocking of land, the expected value drops in the majority of breeds except the BS one. Higher values of the BS breed may be caused by the higher lactation performance of cows of this breed that allows calves to obtain sufficient nutrients in less favourable nutrition conditions.

Figure 2 shows the LSM values estimated for breeds at the particular herd levels (G × E interaction). The HE breed had the lowest value at all herd levels. The AA, BS and CH breeds had relatively identical values on a low herd level. Differences between the HE and AA breeds decrease with increasing herd level. On the other hand, differences in performance between the BS, CH and AA breeds increase and a slight change in the ranking occurs between the BS and CH breeds. This change between the BS and CH breeds may be caused again by the higher lactation performance of the BS breed.

These conclusions demonstrate that weaning weight may be influenced by G × E interaction. The inclusion of interaction in the model did not affect the estimation of residual variability, but it did influence the AIC value, and interaction was found to be a statistically significant effect. The effect of interaction is expressed either as covariance when a change in environment influences differences between the expected values of genotypes or partly as a change in the ranking of genotypes with similar values.

The results correspond to the definition of G × E interaction according to Lynch and Walsh (1998). The method was used in sheep breeds kept in Norway (Steonheim et al., 2004) and in the Brahman breed and other meat breeds for weaning weight or adult weight (Brown et al., 1993 and Sandelin et al., 2002). Hyde et al. (1998) confirmed the occurrence of interaction for the Charolais breed under conditions in the USA, Canada, Australia, and New Zealand.

For accurate estimations of the interaction of G × E, models which included covariance between genotype and environment were also tested. These models showed no meaningful results.

Genotype × environment interaction in the definition of environment according to LFA methodology

Further testing of interaction was performed by the estimation of genetic parameters. Table 4 shows the variance-covariance components and genetic parameters with mean errors calculated by the method of the single-trait animal model for the definition of environment according to LFA methodology.

Genotype × environment interactions. Models with G × E interaction (Models I, II, III) had slightly higher residual variance compared to models without this interaction (Models Ia, IIa, IIIa). The

Table 4. Estimations of genetic parameters and their mean errors for Model I–VIIa within the definition of environment according to LFA methodology

	I	Ia	II	IIa	III	IIIa
–2 log*L*	43 199.97	43 210.37	42 891.65	42 948.63	43 199.97	43 210.37
AIC	43 213.97	43 222.37	42 907.65	42 962.63	43 213.97	43 222.37
σ^2_a	197.19 (0.32)	200.80 (0.33)	245.96 (0.36)	256.50 (0.35)	197.19 (0.33)	200.80 (0.33)
σ^2_m	25.87 (0.17)	26.68 (0.15)	30.91 (0.16)	32.648 (0.17)	25.88 (0.17)	26.68 (0.15)
σ_{am}	7.60 (0.15)	6.54 (0.13)	20.17 (0.15)	21.48 (0.15)	7.60 (0.14)	6.54 (0.13)
σ^2_{HYS}			449.17 (0.34)	469.15 (0.35)		
σ^2_{pe}	163.71 (0.21)	163.02 (0.20)	161.40 (0.22)	159.33 (0.21)	163.71 (0.21)	163.02 (0.20)
$\sigma^2_{\mathrm{G \times E}}$	105.58 (1.33)		55.20 (0.41546)		105.69 (1.38)	
σ^2_e	647.08 (0.21)	645.48 (0.21)	621.02 (0.21)	615.98 (0.20)	647.08 (0.22)	645.48 (0.21)
σ^2_y	1 147.03	1 042.51	1 583.82	1 555.09	1 147.16	1 042.51
h^2_a	0.17 (0.02)	0.19 (0.01)	0.16 (0.01)	0.17 (0.01)	0.17 (0.02)	0.19 (0.01)
h^2_m	0.02 (0.01)	0.03 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)	0.03 (0.01)
r_{am}	0.11 (0.11)	0.09 (0.09)	0.23 (0.09)	0.24 (0.09)	0.11 (0.10)	0.09 (0.09)
c^2	0.14 (0.01)	0.16 (0.01)	0.10 (0.01)	0.10 (0.01)	0.14 (0.01)	0.16 (0.01)
$\mathrm{G \times E}^2$	0.09 (0.05)		0.04 (0.01)		0.09 (0.05)	
e^2	0.56 (0.03)	0.62 (0.01)	0.39 (0.01)	0.40 (0.01)	0.56 (0.04)	0.62 (0.01)
LR(*P*<)	0.137		<0.0001***		0.202	

σ^2_a – additive genetic variance of direct effect; σ^2_m – additive genetic variance of maternal effect; σ_{am} – covariance between direct and maternal effect; r_{am} – genetic correlation between direct and maternal effect; σ^2_{pe} – variance of permanent maternal environment; σ^2_{HYS} – variance of HYS effect; σ^2_e – variance of random error; σ^2_y – phenotype variance; h^2_a – coefficient of direct heritability; h^2_m – coefficient of maternal heritability; c^2 – ratio of permanent maternal environment; $\mathrm{G \times E}^2$ – coefficient of the effect of genotype × environment interaction; e^2 – ratio of residual variance; –2 log*L* – likelihood function; AIC – Akaike's information criterion; *LR* – *P*-value of the ratio of likelihood function

most marked difference was observed in Models II and IIa, where HYS is considered as a random effect. The value of G × E interaction is reduced to the greatest extent by direct effect and by the effect of breed. The reduction of the above-mentioned components of variance corresponds to the nature of G × E interaction because the effect of breed is taken as a genetic effect. Besides these effects, G × E interaction in the other models is also reduced by HYS effect. The inclusion of the effect of G × E interaction in the model does not influence either the variance of maternal effect or the variance of the effect of permanent maternal environment. On the other hand, G × E interaction decreases the value r_{am}. A decrease in r_{am} is caused by a decrease in the value of variance of the direct effect of G × E interactions. A comparison of AIC values between the identical models with G × E interaction (Models I, II, III) and models without this interaction (Models Ia, IIa, IIIa) shows that the models with G × E interaction had lower values of AIC, which proves the suitability of the inclusion of G × E interaction. The LR values indicated a statistical significance of G × E interaction only in Model II ($P < 0.0001$). In the other Models (I, III) G × E interaction was statistically insignificant ($P = 0.137, 0.202$). G × E interaction explained from 4% (Model II) to 9% (Models I and III) of the total phenotype variability.

Fixed or random effect of HYS. A decrease in residual variance was determined in models with random effect HYS (Models II and IIa) compared to the other models (Model I, Ia, III, IIIa). However, in the former models there was an increase in direct and maternal effect and also in the value r_{am}. The increase of direct and maternal effect and genetic correlation (r_{am}) indicates the lower suitability of random effect HYS. The use of fixed HYS was also recommended by Visscher and Goddard (1992) and Hagger (1998).

Genetic correlations between direct and maternal effects. All models had low positive values of r_{am} estimation. These positive values are caused by the low value of the estimation of maternal effect. The estimations of r_{am} were not statistically significant with respect to their standard errors. The lowest values were computed for Model IIIa (0.09), whereas models with random HYS had the highest values (Models II, IIa) (0.23–0.24).

Direct and maternal heritability coefficients. The values of the coefficient of direct heritability in the set for the estimation of G × E interaction ranged from 0.16 (Model II) to 0.19 (Model Ia). These differences between the models are caused to the greatest extent by the value of phenotypic variance. The value of phenotypic variance is mostly influenced by inclusion or non-inclusion of random effects (HYS and G × E interaction) which were considered as fixed effects in other models. The values of direct and residual variance are identical in the models compared, differing from each other in these effects. Models with G × E interaction had lower values of direct heritability due to the absence of variance of direct effect. On the other hand, identical values were estimated for the coefficient of maternal heritability in most models. The exceptions were Models I and Ia. Coefficients of maternal heritability had low values in all models, and they did not reach statistical significance similar to r_{am} when their standard errors were compared.

Genotype × environment interaction in the definition of environment according to herd level

Table 5 shows the estimations of variance-covariance components and genetic parameters with mean errors performed by the method of the single-trait animal model for the definition of environment according to herd level.

Genotype × environment interactions. Compared to the other models (Models Ia, IIa, IIIa), models with G × E interaction (Models I, II, III) had the same residual variance in most models. The value of residual variance increased only in models with random HYS and G × E interaction (Model II), indicating the lower suitability of G × E interaction in these models. Model IIa with random HYS and without G × E interaction had the lowest value of residual variance. Only slight decreases in the values of residual variance were recorded in the other models. The addition of G × E interaction does not improve the explanation of total variability, but rather, there is only an exchange of values between the components. On the contrary, the inclusion of G × E interaction in the model reduced the variance of direct effect. The greatest difference was determined in Models II (191.47) and IIa (256.50). A marked change in the values of direct effect was also observed in Models I and Ia. The inclusion of G × E interaction in the model also decreased the component for HYS. The addition of random effect HYS increased G × E interaction (Model I vs. II). The reduction of the variance of direct effect through G × E interaction (in Models I and II) corresponds to the definition of G × E interaction. G × E interaction also causes an increase in the value r_{am} (Models I and II). This increase is due to a marked decrease in direct effect and a slight decrease in maternal effect. Similarly like the maternal effect, the effect of permanent maternal environment reacts by a slight decrease to the presence of the effect of G × E interaction. Comparison of AIC values between the models with G × E interaction (Models I, II and III) and those without this interaction (Models Ia, IIa and IIIa) shows that the models with G × E interaction had lower AIC values. These lower AIC values demonstrate the greater suitability of models with G × E interaction. Statistical significance of G × E interaction in Models I and II was confirmed by LR ($P = < 0.0001$ and < 0.0001). The significance of G × E interaction was not proved in the remaining Model (III). G × E interaction explained from 3% (Model III) to 39% (Model II) of the total phenotype variance. The values of residual variance components and selection criteria (AIC, LR) confirm the occurrence of the effect of G × E interaction.

Fixed or random effect of HYS and genetic correlations between direct and maternal effects. The inclusion of random HYS effect resulted in an increase in r_{am} that was caused by a decrease in direct effect in these models, except in Model IIa. In this model the increased value r_{am} was caused by an increase in maternal effect. All the models had low positive values r_{am}, which were influenced by the low value of maternal effect. When HYS was included as a random effect (Model II), the estimated values of direct and maternal effect were lower compared to the other models. On the other hand, the highest values of direct and maternal effect were estimated in Model IIa. The inclusion of HYS as a random effect could lead to an erroneous

Table 5. Estimations of genetic parameters and their mean errors for Model I–VIIa within the definition of environment according to herd level

	I	Ia	II	IIa	III	IIIa
$-2\log L$	47 289.80	47 427.77	41 271.78	42 948.63	47 276.81	47 283.53
AIC	47 303.8	47 439.77	41 287.78	42 965.63	47 290.81	47 295.53
σ^2_a	187.46 (0.32)	198.52 (0.32)	191.47 (0.29)	256.50 (0.35)	187.16 (0.29)	187.64 (0.31)
σ^2_m	23.76 (0.14)	24.54 (0.15)	24.38 (0.15)	32.65 (0.17)	23.79 (0.15)	24.01 (0.14)
σ_{am}	9.61 (0.13)	6.50 (0.13)	22.95 (0.12)	21.48 (0.14)	9.60 (0.13)	9.71 (0.12)
σ^2_{HYS}			78.70 (0.08)	469.15 (0.35)		
σ^2_{pe}	156.66 (0.19)	157.08 (0.21)	168.35 (0.20)	159.33 (0.21)	156.66 (0.19)	156.76 (0.18)
$\sigma^2_{\mathrm{G \times E}}$	450.49 (3.36)		730.60 (3.89)		30.72 (0.40)	
σ^2_e	636.98 (0.20)	636.32 (0.20)	649.46 (0.20)	615.98 (0.20)	637.15 (0.20)	637.24 (0.20)
σ^2_y	1 464.95	1 022.96	1 865.92	1 555.09	1 045.07	1 015.35
h^2_a	0.13 (0.02)	0.19 (0.01)	0.10 (0.01)	0.17		
(0.01)	0.18 (0.01)	0.18 (0.01)				
h^2_m	0.02 (0.005)	0.02 (0.01)	0.01 (0.003)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)
r_{am}	0.14 (0.10)	0.09 (0.09)	0.34 (0.10)	0.24 (0.09)	0.14 (0.10)	0.14 (0.09)
c^2	0.11 (0.01)	0.15 (0.01)	0.09 (0.01)	0.10 (0.01)	0.15 (0.01)	0.15 (0.01)
$\mathrm{G \times E}^2$	0.31 (0.08)		0.39 (0.06)		0.03 (0.02)	
e^2	0.43 (0.05)	0.62 (0.01)	0.35 (0.04)	0.40 (0.01)	0.61 (0.02)	0.63 (0.01)
LR(*P*<)	<0.0001***		<0.0001***		0.513	

σ^2_a – additive genetic variance of direct effect; σ^2_m – additive genetic variance of maternal effect; σ_{am} – covariance between direct and maternal effect; r_{am} – genetic correlation between direct and maternal effect; σ^2_{pe} – variance of permanent maternal environment; σ^2_{HYS} – variance of HYS effect; σ^2_e – variance of random error; σ^2_y – phenotype variance; h^2_a – coefficient of direct heritability; h^2_m – coefficient of maternal heritability; c^2 – ratio of permanent maternal environment; G × E^2 – coefficient of the effect of genotype × environment interaction; e^2 – ratio of residual variance; $-2\log L$ – likelihood function; AIC – Akaike's information criterion; *LR* – *P*-value of the ratio of likelihood function

assessment of direct and maternal effect and genetic correlation (r_{am}). These conclusions are consistent with the results published by Hagger (1998) and Visscher and Goddard (1992). A comparison of r_{am} and their mean errors shows that all estimations of r_{am} were statistically insignificant again.

Direct and maternal heritability coefficients. The coefficients of direct heritability ranged from 0.09 (Model II) to 0.19 (Model Ia). The inclusion of G × E interaction contributed to a decrease in the coefficient of direct heritability. This decrease was caused by the above-mentioned decrease in the direct effect through G × E interaction. The remaining differences were due to different phenotype variance. Different values of phenotype variance were not caused by different estimations of variance components but by the inclusion of some random effects which were considered as fixed effects in the other models. Identical values were again estimated for direct and residual variance in the models compared, differing in these above-mentioned effects. On the other hand, the coefficient of maternal heritability had identical values in most models. These identical estimates of maternal heritability coefficients are explained by the low value of maternal effects. The estimates of maternal heritability coefficients were statistically insignificant in most models when their standard deviations were compared.

In both methods of G × E interaction classification (according to LFA and herd level), the estimations of residual variance reached similar values in all the models used. These results indicate that the addition of the effect of G × E interaction does not improve the explanation of variability, only that the values are exchanged among the components.

The values of direct heritability coefficient for the most part corresponded to those reported by other authors (Waldron et al., 1993; Robinson, 1996; Meyer, 1997), who estimated the values of direct heritability coefficients in the range from 0.15 to 0.40.

Genetic correlations (r_{am}) estimated in our study had low positive values which for the most part are consistent with the those published by Waldron et al. (1993), Robinson (1996), Meyer (1997), and De Mattos et al. (2000) (from –0.594 to 0.223). Van Vleck et al. (1996) stated that correlation coefficients in particular breeds might differ considerably from each other. In agreement with this finding, Meyer (1992) published different estimates of r_{am} for the Hereford (–0.587) and Angus (0.223) breeds.

The values of variance components and selection criteria (AIC, LR) in the definition of environment according to LFA methodology and herd level confirm the existence of G × E interaction. The within-breed interaction was not demonstrated in a previous paper (Vostrý et al., 2007).

The results of this paper showed that the assignment of different breeds to specific environments is questionable under conditions in the Czech Republic. Furthermore, the routine evaluation of animals across all breeds kept in the Czech Republic and all environments also seems to be questionable. The evaluation of animals within breeds could yield more reasonable results.

CONCLUSION

The most suitable definition of environment is that according to herd level. This definition had the most suitable values of residual variance, determination coefficient or AIC, and number of connecting sires and their offspring. The definition of environment according to LFA was also recommended because in this methodology both the altitude and the economic value of farm land are considered and also because it is currently used for the allocation of support to farmers.

The weaning weight of beef breeds kept in the Czech Republic is influenced by G × E interaction. G × E interaction was statistically highly significant in the given model. The inclusion of interaction in the model did not change the value of residual variance, but it influenced the AIC value.

The most suitable model for the estimation of G × E interaction and genetic parameters in the definition of environment according to LFA and herd level was Model Ia, which comprised the fixed effect of mother's age, the combined effect of sex and litter size, the fixed effect of HYS, and random effects: direct genetic effect of the individual, direct maternal effect, effect of permanent environment, G × E interaction, and the effect of random error.

The values of variance components and selection criteria (AIC, *LR*) indicated that G × E should be taken into consideration in evaluation of the weaning weight of beef cattle.

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Received: 2007–10–04
Accepted after corrections: 2008–03–21

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