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Selection of a suitable data set and model for the estimation of genetic parameters of the weaning weight in beef cattle*

Abstract

The objective of this paper was to select a suitable data subset and statistical model for the estimation of genetic parameters for weaning weight of beef cattle in the Czech Republic. Nine subsets were tested for the selection of a suitable subset. The subsets differed from each other in the limit of sampling criteria. The most suitable subset satisfied these conditions: at least 5 individuals per each sire, 5 individuals per HYS (herd, year, season), 2 sires per HYS, and individuals per dams that have at least one half-sister and two offspring ($n=4\ 806$). The selection of a suitable model was carried out from 10 models. These models comprised some of the random effects: direct genetic effect, maternal genetic effect; permanent maternal environment effect, HYS, sire × herd or sire × year interaction, and some of the fixed effects: dam's age, sex (young bull, heifer × single, twin born), HYS, year, herd. The direct heritability (h_a^2) ranged from 0.06 to 0.17, of maternal heritability (h_m^2) from 0.03 to 0.06. The genetic correlations between the direct and maternal effect (r_{am}) were in the range of -0.15 - 0.42.

Key Words: beef cattle, genetic parameters, animal model, REML, weaning weight

Zusammenfassung

Title der Arbeit: Auswahl des passenden Datenbestandes und statistischen Modells zur Schätzung der genetischen Parameter für das Absetzgewicht bei Fleischrinderrassen in der Tschechischen Republik

Ziel dieser Arbeit war die Auswahl der passenden Datei und des statistischen Modells zur Schätzung der genetischen Parameter für das Absetzgewicht. Für die Auswahl der passenden Datei wurden 9 Dateien getestet. Die einzelnen Dateien unterschieden sich voneinander durch die Grenzen der Selektionskriterien. Die günstigste Datei erfüllte folgende Bedingungen: mindestens 5 Individuen pro Vater, 5 Individuen pro HYS (Herde, Jahr, Saison), 2 Väter pro HYS und die Nachkommen der Mutter, die mindestens eine Halbschwester und mindestens 2 Nachkommen hatte (n=4806). Die Auswahl des passenden statistischen Modells wurde mit 10 Modellen durchgeführt. Die einzelnen Modelle umfassten folgende zufälligen Effekte: direkte, maternale, permanente Umwelt der Mutter, HYS, Interaktion Vater x Herd, Interaktion Vater x Jahr und folgende fixen Effekte: Geschlecht (männlich, weiblich x Einling, Zwillinge), HYS, das Alter der Mutter, Jahr, Herde. Die direkten Heritabilitätsschätzwerte (h_a^2) befanden sich zwischen 0.06 - 0.17 und die maternalen Heritabilitätsschätzwerte (h_m^2) lagen zwischen 0.03 – 0.06. Die genetischen Korrelationen (r_{am}) wiesen Werte von -0.15 – 0.42 auf.

Schlüsselwörter: Fleischrinderrassen, genetische Parameter, Tiermodell, REML, Absetzgewicht

Introduction

Estimation of breeding value and subsequent selection of parental pairs is primarily based on correct estimation of genetic parameters. Applying the BLUP method, which is used for genetic evaluation, it is possible to work with a large and unbalanced data set in an efficient way. However, data structure influences the estimation of genetic parameters and error. For this reason the correct estimation of genetic parameters depends on the data set selected from the basic data and the used statistical model for the given traits under study. Many authors were concerned with the selection of a suitable data set (BRADE and GROENEVELD, 1999; TOSH and WILTON, 1994;

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WOOD et al., 1991; SCHUELER et al., 1996; REINSCH and KALM, 1995; SUMPF and HERRENDOERFER, 1993; PŘIBYL and PŘIBYLOVÁ, 2001).

Growth ability is of great economic importance in the beef cattle breeds. Besides systematic effects, the direct effect, the maternal effect and the permanent environment participate in the growth ability of the animal (JAKUBEC et al., 1998). The selection of an adequate model for the trait analysis includes direct and maternal effects. MEYER (1992), WALDRON et al. (1993) and ROBINSON (1996) investigated a model comprising the genetic direct effect, maternal effect and the effect of the permanent maternal environment. The effect of sire \times year interaction on the correlation between the genetic direct and maternal effect was studied by LEE and POLLAK (1997) and ROBINSON (1996). The sire \times herd interaction was tested by NOTTER et al. (1992).

The objective of this paper was to select a suitable structure of a data set and statistical model for the estimation of genetic parameters for the weaning weight in beef cattle in the Czech Republic.

Material and Method

The complete data set was provided by the Czech Association of Beef Cattle Breeders (www.cschms.cz). The selection of a suitable subset (further "subset") and model for the estimation of genetic parameters was realized in the Charolais breed, the most used beef breed in the Czech Republic during the period of 13 years (1990 – 2003). The calves were weaned at the age of 210 days.

Selection of a suitable set

The set was adjusted in such a way that all considered effects could be estimated. Nine subsets were tested for the selection of the most suitable data structure. The data of subsets were grouped according to HYS (herd, year, and season) and within the HYS were offspring after more than two sires. Each dam had at least two offspring. Subset 9 did not contain any other sampling criteria. The other tested subsets (1 - 8) were adjusted by the following criteria (Table 1).

Set	Minimal number of animals in HYS	Minimal number of animals per sire	Minimal number of dams per dam sires	Sample size (number of animals)
1	10	5	2	2283
2	10	2	2	2584
3	5	5	5	3389
4	5	5	2	4806
5	5	2	2	5162
6	2	5	5	4162
7	2	5	2	5345
8	2	2	2	5691
9		Without sampling		6180

Table 1

Values of sampling criteria and numbers of individuals (Werte der Auswahlkriterien und Anzahl der Individuen)

Recorded were the individual performance and the information of two ancestor generations. Unknown individuals in pedigrees born before 1990 were placed into specific groups of unknown animals. The relatedness of the animals between the subsets was not determined exactly, but in a simplified way step by step. Sires were selected randomly from the subsets and all their offspring were allocated to them according to the HYS. To the latter sires which had offspring in these HYS were allocated again. This procedure was reiterated until the number of individuals remained constant. The rate of relatedness was determined as the ratio of related individuals to the total number of individuals in the given subset.

A suitable subset was chosen on the basis of the residual error and the ratio of the standard error of the heritability to the direct and maternal heritability (further "ratio").

Selection of a suitable model

A suitable model for the estimation of genetic parameters was selected on the results of 10 tested models. The single animal model in beef cattle was used for the parameter estimation according to PŘIBYL (2003)

$$y = Xb + Zu + e$$

Where:

- b the vector of fixed effects that comprised: combined effect of sex and parturition frequency, dam's age, effect of herd, year and HYS
- u the vector of random effects that comprised: a vector of random direct additive genetic effects, m vector of random additive maternal genetic effects, pe vector of random effects of permanent maternal environment, hys vector of random HYS, sh vector of random sire × herd interaction, sy vector of random sire × year interaction and e vector of random residual errors
- X, Z incidence matrix of fixed and random effects

It is assumed that the effects *a* and *m* are correlated, the remaining effects are independent and show a normal distribution with the 0 mean and variance (σ^2).

$$V\begin{bmatrix} \sigma_a^2 & \sigma_{am} \\ \sigma_{am} & \sigma_m^2 \end{bmatrix} \qquad V(sy) = I\sigma_{sy}^2$$
$$V(pe) = I\sigma_{pe}^2 \qquad V(sh) = I\sigma_{sh}^2$$
$$V(HYS) = I\sigma_{HYS}^2 \qquad V(e) = I\sigma_e^2$$

Where:

 σ_a^2 – additive genetic variance of the direct effect, σ_m^2 – additive genetic variance of the maternal effect, σ_{am} – genetic covariance of direct and maternal effect [*Cov*(*a*,*m*)], σ_{pe}^2 – variance of the permanent maternal environment, σ_{HYS}^2 – variance of HYS, σ_{sh}^2 – variance of the sire × herd interaction, σ_{sy}^2 – variance of the sire × year interaction, σ_e^2 – variance of the residual error, *A* – relationship matrix, *I* – identity matrix.

The variance, covariance and standard errors were estimated by the computation programme VCE 5.1 (KOVAČ, 2002). Using the variance and covariance components following parameters were estimated: σ_{gt}^2 – total additively genetic variance [$\sigma_{gt}^2 = \sigma_a^2 + 1.5 \sigma_{am} + 0.5\sigma_m^2$], σ_p^2 – phenotypic variance, h_a^2 – direct heritability, h_m^2 – maternal heritability, h_t^2 – total heritability [$h_t^2 = (\sigma_a^2 + 1.5 \sigma_{am} + 0.5 \sigma_m^2)/\sigma_p^2$] (WILLHAM, 1979). All or only some of the effects were included into the tested models (*sy*, *sh*, and *hys*) were considered either fixed or random). Model I contained the direct effect, maternal effect, the effect of maternal permanent environment and genetic covariance between the direct and maternal effect (MEYER, 1997). Model II (NOTTER, 1992)

and III (MEYER, 1997) contained the same effects as in the Model I, and in addition the sire \times herd interaction and/or sire \times year interaction. Model IV, V, VI and VII comprised the same effects as the models II and III and the fixed effect of herd or year. The so called "random models" (Ia, IIa, IIIa, IV, V, VI and VII) were models in which the effect of HYS was taken as a random variable (PŘIBYL et al., 2003; HAGGER, 1998). Table 2 shows genetic parameters estimated by the appropriate models.

Table 2

Genetic parameters estimated by different models (Genetische Parameter geschätzt mit Hilfe von unterschiedlichen Modellen)

	Ι	Ia	II	IIa	III	IIIa	IV	V	VI	VII
σ_a^2	\checkmark									
σ_m^2	\checkmark									
σ_{am}	\checkmark									
σ^2_{HYS}		\checkmark		\checkmark		\checkmark	\checkmark	\checkmark	\checkmark	\checkmark
σ^{2}_{ne}	\checkmark									
$\sigma^{2_{sh}}$			\checkmark	\checkmark			\checkmark	\checkmark		
$\sigma^{2}_{sy}^{sn}$					\checkmark	\checkmark			\checkmark	\checkmark

 σ_a^2 – additive genetic variance of the direct effect, σ_m^2 – additive genetic variance of the maternal effect, σ_{am} – covariance between the direct and maternal effect, σ_{HYS}^2 – variance of HYS, σ_{pe}^2 – variance of the permanent maternal environmental effect, σ_{sh}^2 – variance of the sire × herd interaction, σ_{sy}^2 – variance of the sire × year interaction

The suitable model was selected by means of the residual error variance and Akaik's information criterion (AIC, BOZDOGAN, 2000).

$$AIC = -2logL(\theta) + 2d$$

Where:

 $logL(\theta)$ – the natural logarithm of the likelihood function d – the number of free parameters in the model

Results and Discussion

Table 1 contains the numbers of evaluated animals selected from the set, number of sires, dams and other effects, weaning weight means and standard deviations. Similar results of weaning weight means and standard deviations in the Charolais were reported by JAKUBEC et al. (2003) (271.98 kg, 33.05 kg respectively).

Selection of a subset

A high rate of relatedness (98 - 99%) was characteristic for all tested subsets. Such a high rate of relatedness was the result of a lot of exchanges of sires between herds during the period of 14 years. To select a suitable subset and model for the estimation of genetic parameters 90 computations of genetic parameters were performed. In graphs the estimated genetic parameters are grouped according to a sampling subset, and within these groups according to the individual models (subset \times model).

Figure 1 represents the ratio of the standard error of direct heritability to the direct heritability and the ratio of the standard error of maternal heritability to the maternal heritability. The direct heritability ratio showed a similar trend in the models for all subsets. The subsets 1 and 2 reached the highest direct heritability ratio. The lowest direct heritability ratio was recorded in the subset 9. Similarly like the ratio of direct heritability. The ratio of maternal heritability was similar as the ratio of direct heritability for the individual models in most subsets. The direct heritability ratio was

higher than maternal heritability ratio. The lowest maternal heritability ratio was found in the subset 8. The increase of sampling criteria, number of animals per HYS and number of animals per sire caused a more suitable structure of the subset. In general the maternal heritability ratio increased if the number of animals in the subset decreased. Exceptions were found in the subset 2, in which the value of maternal heritability ratio decreased, and set 9, which had markedly high values of this ratio due to the low suitability of the data set. These results demonstrate that the direct heritability ratio was not markedly influenced by the data structure or numbers of animals in the subsets. On the contrary, the maternal heritability ratio was mostly negatively influenced by the low number of animals in the set.



Fig. 1: The ratio of the standard error of direct heritability to the direct heritability and the ratio of the standard error of maternal heritability to the maternal heritability (Verhältnis der Standardabweichung der direkten Heritabilität zur direkten Heritabilität und Verhältnis der Standardabweichung der maternalen Heritabilität zur maternalen Heritabilität)

The values of residual variance (Fig. 2) showed an opposite trend compared to the values of direct and maternal heritability ratios. The highest residual variance was found in the subset 9, which had the worst data structure. If the limit of sampling criteria increased, the values of the residual variance decreased. The largest drop was found in the subsets in which the number of individuals per HYS exceeded the minimal limit of 10 individuals (subset 1 and 2) and in the subsets which had the most suitable data structure. With the exception of these two subsets the other subsets had the identical pattern of residual variance; the lowest value of residual variance was estimated by the model IIa. On the contrary to the ratios of direct and maternal

heritability, the values of residual variance were mostly influenced by the structure of the subset (Fig. 1 and 2).

These results indicate that the estimation of genetic parameters was influenced by the number of individuals in the subset whereas the estimate of residual variance depended on the data structure of the subset. If the ratios of direct and maternal heritability were compared, set 2 had the most suitable values, followed by set 3 - 8. TOSH and WILTON (1994) and PRIBYL and PRIBYLOVA (2001) and other authors reported that the higher number of individuals in HYS increased the accuracy of the estimation of genetic parameters. If the number of individuals in HYS was higher than 5, the contribution to the estimation accuracy was negligible. WOOD et al. (1991) published that an increase in the number of half-sibs per sire in several HYS diminished the average variance of prediction error. TOSH and WILTON (1994) recommended a higher number of sires in HYS for a more accurate estimation. Taking into account our results and the results of the above-mentioned authors we can resume that the subset for the estimation of genetic parameters should contain at least 5 individuals per HYS. Our aim is the highest possible number of individuals per sire and a sufficient number of individuals at the same time. Subset 2 did not satisfy the criterion proposed by WOOD et al. (1991), i.e. a sufficient number of individuals per sire. Subsets 3 and 4 satisfied the above mentioned criteria. Subset 4 had an optimal structure: at least 5 individuals per sire, 5 individuals per HYS, 2 sires per HYS and animals per dam that have at least one half-sister and two offspring.



Fig. 2: The residual variance (Restvarianz)

Selection of a suitable model

Fig. 1 and 2 illustrate that the subsets had similar values of variance-covariance components. With respect to the above conclusions subset 4 was analysed in detail.

	Ι	Ia	II	IIa	III	IIIa	IV	V	VI	VII
-2logL	11366.70	11378.44	11271.10	11250.13	11349.73	11357.22	11097.57	11051.15	11409.13	11386.64
AIC	11380.70	11390.44	11285.10	11266.13	11363.73	11373.22	11111.57	11067.15	11423.13	11402.64
- ²	167.24	160.82	73.89	84.44	115.51	108.04	128.25	71.29	166.52	111.91
O _a	(0.83)	(0.80)	(0.68)	(0.76)	(0.79)	(0.74)	(0.73)	(0.58)	(0.82)	(0.77)
σ^2	29.55	75.62	33.76	49.09	27.15	70.39	76.81	56.16	75.99	70.46
0 m	(0.57)	(0.71)	(0.59)	(0.68)	(0.60)	(0.67)	(0.65)	(0.57)	(0.71)	(0.68)
~	1.53	-16.67	20.70	23.93	23.48	7.26	-15.30	9.90	-15.44	7.99
Uam	(0.46)	(0.61)	(0.33)	(0.40)	(0.37)	(0.58)	(0.55)	(0.42)	(0.62)	(0.59)
c ²		469.09		366.78		450.46	298.04	255.20	460.43	445.69
O HAR		(0.68)		(0.59)		(0.64)	(0.49)	(0.44)	(0.67)	(0.64)
σ^2	106.53	97.48	91.81	82.78	97.59	89.59	80.43	80.32	95.61	88.64
O pe	(0.53)	(0.53)	(0.52)	(0.49)	(0.50)	(0.52)	(0.48)	(0.48)	(0.53)	(0.52)
σ^2			152.00	203.48				88.00		
O sh			(0.43)	(0.53)				(0.34)		
σ^2					49.12	54.07				55.73
O sy					(0.27)	(0.26)				(0.26)
σ^2_{gt}	184.30	173.62	121.81	144.88	164.31	154.13	143.70	114.22	181.36	159.12
σ^2	685.37	685.77	669.18	658.06	690.00	689.65	672.65	672.20	682.08	685.95
0 e	(0.57)	(0.56)	(0.45)	(0.55)	(0.53)	(0.52)	(0.54)	(0.42)	(0.56)	(0.53)
σ^2_y	990.22	1472.11	1041.33	1468.56	1002.84	1469.47	1240.88	1233.08	1465.19	1466.36
h^2	0.17	0.11	0.07	0.06	0.12	0.07	0.10	0.06	0.11	0.08
II a	(0.03)	(0.02)	(0.03)	(0.02)	(0.03)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)
\mathbf{h}^2	0.03	0.05	0.03	0.03	0.03	0.05	0.06	0.05	0.05	0.05
n m	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)	(0.02)
h_t^2	0.19	0.12	0.12	0.10	0.16	0.10	0.12	0.09	0.12	0.11
r	0.02	-0.15	0.41	0.37	0.42	0.08	-0.15	0.16	-0.14	0.09
1 am	(0.27)	(0.20)	(0.46)	(0.40)	(0.47)	(0.29)	(0.20)	(0.31)	(0.20)	(0.29)
c^2	0.11	0.07	0.09	0.06	0.10	0.06	0.06	0.07	0.07	0.06
C	(0.02)	(0.01)	(0.02)	(0.01)	(0.02)	(0.01)	(0.02)	(0.02)	(0.01)	(0.01)

Table 4 Genetic parameters and (S.D.) for model I – VII (Genetische Parameter für die Modelle I –VII)

-2logL - the natural logarithm of likelihood function, AIC - Akaike's information criterion, σ_a^2 - additive genetic variance of the direct effect, σ_{m}^2 - additive genetic variance of the maternal effect, σ_{am}^2 - variance of the HYS, σ_{pe}^2 - variance of the permanent maternal environmental effect, σ_{sh}^2 - variance of the sire×herd interaction, σ_{sy}^2 - variance of the residual errors, σ_y^2 - phenotype variance, h_a^2 - direct heritability, h_a^2 - maternal heritability, h_t^2 - total heritability, r_{am} - direct - maternal genetic correlation, c^2 - ratio of permanent maternal environment

Table 3 Description statistics (Beschreibungsstatistiken)

Desemption statistics (Desemption angestatistic)									
	Nubers	Number	Number Number Number		Number of Number of		Average	Standard	
	of	of sires	of dams	of HYS	sire×herd	sire×year	(kg)	deviation	
	animals				interactions	interactions		(kg)	
Set	4806	150	1403	460	540	653	273	40.7	

Table 3 shows the numbers of individuals in the particular classes of subset 4. Estimations of variance-covariance components and genetic parameters by a single-trait animal model in this subset are given in Table 4.

Fixed or random effect of HYS.

In the majority of the models with random HYS (models Ia, IIa, IIIa), compared to models with fixed HYS (models I, II, III), there was a negligible decrease in the direct genetic variance and an increase in the maternal genetic variance. Residual variance showed minimal changes in these models. The inclusion of the fixed effect of herd markedly diminished the variance of HYS (model IV). A further decrease in the HYS variance was observed when the sire \times herd interaction was included into the model (model V). The decrease of the HYS variance was also caused by a reduction of variability between herds. A decrease in the value of residual variance in models IV and V indicates a better suitability of these models which was caused by the including of the random HYS and the fixed effect of herd into the model. In the remaining genetic and environment effects random fluctuations between the models were observed. The inclusion of the fixed effect of year in the model did not influence the estimation of the HYS variance. The models that contained the HYS as a random variable ("random models" - Ia, IIa, IIIa, IVa) had higher values of the phenotypic variance compared to the remaining models. Other authors (MEYER, 1997; ROBINSON, 1996; WALDRON, 1993) pointed out that the use of HYS as a random effect resulted in higher values of correlation between the estimated and actual breeding value. If the HYS was included in the model as a fixed effect, some information was lost. But VISSCHER and GODDARD (1992) stated that in HYS with a small number of individuals (N \leq 12) the inclusion of HYS as non-random into the model might lead to negative correlations between the estimated and actual breeding value because a worse breeding value might be assigned to better sires than to average sires. On the contrary, FREY et al. (1995) concluded that it was possible to estimate the breeding value in boars in small herds more accurately if HYS was included as random effect into the model. If there is an uneven distribution of sires across HYS (breeds of beef cattle) VISSCHER and GODDARD (1992) and HAGGER (1998) recommended the HYS as fixed. If HYS is included as s random effect in beef cattle, wrong estimations of genetic and environment effects may be often found (STRAFFELD, 2004 – personal communication).

Genetic correlations between the direct and maternal effects.

Genetic correlations between the direct and maternal effect were in the range of -0.15 (model Ia and IV) to 0.42 (model III). If the random HYS was included into the model (models Ia, IIa, IIIa), the genetic correlation markedly decreased. This decline was caused by the above-mentioned increase of the maternal variance and decrease the direct genetic variance. If the sire \times herd and sire \times year interactions were included

into the model, the value of r_{am} markedly increased. On the contrary, in models with the fixed effect of herd or year (models IV and VI) the value of r_{am} decreased. These changes are caused by a drop of the direct genetic variance and an increase of the maternal genetic variance. In the models with sire \times herd and sire \times year interactions decreased the value of the direct genetic variance. The values are mostly consistent with the values published by de MATTOS et al. (2000), MEYER (1997), ROBINSON (1996) and WALDROM et al. (1993), who mentioned the values from -0.594 to 0.223. VAN VLECK et al. (1996) reported that correlation coefficients in the breeds might be largely different. In accordance with this finding MEYER (1992) published different values of r_{am} for the breeds Hereford (-0.587) and Angus (0.223). WALDRON et al. (1993) drew the conclusion that breeds with a higher growth ability have generally a lower genetic maternal ability for growth. This statement is supported by our experience in the Charolais which has a high growth rate. CUNDIFF (1972) considered a moderate negative correlation between the direct and maternal effect as logical. For these reasons the models that reached high positive values of correlation between the direct and maternal effect are less suitable for the estimation of genetic parameters.

Sire \times herd and sire \times year interactions.

The estimations of the sire \times herd and sire \times year interactions are derived from a comparison of the relative performance of sires in different herds or years. This is the reason why the number and nature of sires linking the particular herds have a great impact on the accuracy of the sire \times herd and sire \times year interaction estimates in the field tests. The sire \times herd interaction was in the range of 88.00 – 203.48 and the sire \times vear interaction was in the extent of 49.12 - 55.73. The inclusion of the fixed effect of herd into the model lead to a decrease in the sire \times herd interaction. If the fixed effect of year was included into the model, the estimation of the sire \times year interaction was not influenced. Table 4 shows that the inclusion of the sire \times herd and sire \times year interaction in the model resulted in a reduction of the direct genetic effect in all models by 36 - 56% due to the fact, that the interactions size \times herd or size \times year reduce the genetic variability. Similar results were published by BASCHNAGEL et al. (1999), HAGGER (1998), LEE and POLLAK (1997), NOTTER et al. (1992). The inclusion of the sire \times herd interaction into the models I, II, Ia and IIa obviously reduced the value of information criteria (AIC) and residual error, which also documents a better suitability of these models. The comparison of models III and IIIa with the sire \times year interaction (models III and IIIa) did not show a marked decrease in AIC values compared to models without the sire \times year interaction (model I and Ia), and these models reached the highest value of residual variance. Obviously, the addition of the sire \times year interaction into the models did not improve the statistical model markedly. LEE and POLLAK (1997) and NOTTER et al. (1992) accentuated the great importance of the sire \times year interaction especially in populations with a regular immigration of sires. LEE and POLLAK (1997) also concluded that even though this interaction was statistically highly significant, its reason need not be sufficiently known. The interaction size \times year might be caused either by different environment factors or by unidentified sources of covariances between the individuals in the particular environments. These authors also admitted that the inclusion of the sire \times herd and sire \times year interaction might lead to the underestimation of the direct genetic effect, and subsequently to the inaccurate estimation of breeding values. Even if the AIC values and the residual variance indicate a statistical significance of the sire \times herd interaction, the disputableness of the inclusion of the sire \times herd and sire \times year interaction is documented by a high positive correlation between the direct and maternal effect.

Effect of the permanent maternal environment.

The values of the permanent maternal environment effect had the magnitude from 6 to 11% of the total phenotypic variance. These values are valid for about 50% of the total heritability and correspond to the values of the maternal heritability. It can be concluded that the effect of permanent environment has the same influence as the maternal effect. Similar results were published by de MATTOS et al. (2000), MEYER (1992) and MEYER et al. (1993). If the sire \times herd and sire \times year interactions were included, a part of the variability of the permanent maternal environment was reduced. This reduction was not so important if only the sire \times year interaction was included into the model. If the fixed effect of herd was included into the model a decrease of the effect of permanent maternal environment was found. The inclusion of the fixed effect of year into the model led to a negligible decrease in this effect (model VI and VII). The value of permanent maternal environment in model V decreased because the effect of permanent environment comprised also the variability between herds. The inclusion of the herd and sire \times herd interaction did not influence the estimation of the value of the permanent environment.

Direct and maternal effects and heritability coefficients.

The highest values of the direct effect were estimated in the models I, Ia and VI whereas models V and II exhibited the lowest values. These low values were caused by a reduction of the direct effect variability on account of the sire \times herd interaction and fixed effect of herd. Similarly, the inclusion of HYS effect as random resulted in a decrease of the direct effect. On the contrary, the inclusion of the effect of year increased the value of the direct effect. The values of the maternal effect reached the highest values 75.62 in model Ia and the lowest values 29.55 in model I. The maternal effect increased if the random HYS effect was included into the model. The addition of the sire \times herd interaction to the other effects diminished the maternal as well as the direct effect. Fixed effects of herd and year did not have any influence on maternal effect estimations. For the particular models, the estimates of the direct heritability were in the range from 0.06 in the model IV to 0.17 in the model I. The low direct heritability in model IV was mainly caused by the interactions. The inclusion of the HYS effect as a random variable diminished the direct heritability that can be explained by an increase of the phenotypic variance. The magnitude of the maternal heritability estimate ranged from 0.03 for model I to 0.06 for model IV. The models that comprised the interactions and the fixed effect of herd or year reached higher values of the maternal heritability (0.06). The increase of the maternal heritability was produced by an increase of the maternal effect. In the other models similar values were estimated for the maternal heritability. The estimated standard errors corresponded to values cited by other authors (MEYER, 1997; ROBINSON 1996 and WALDRON, 1993), who estimated heritabilities in the range of 0.15 - 0.25 for the direct heritability and 0.16 - 0.4 for the maternal heritability.

Residual variance.

The residual variance ranged from 658.18 (model IIa) to 690.00 (model III). The residual variance is influenced to a larger extent by the sire \times herd interaction (decrease by 3 – 4%) and by the herd effect (decrease by 2%). The impact of the other effects on the residual variance was not so marked. The inclusion of the HYS effect as a random variable into the models led to a slight decrease of the residual variance while the sire \times year interaction resulted in an increase of the residual variance.

Results of this study support the estimation of genetic parameters was significantly influenced by the evaluation method. It is always necessary to use several methods and their mutual assessment.

The results indicated that for the correct genetic parameters estimation the subset should contain a sufficient number of individuals which mostly influence the estimation of genetic parameters. An appropriate structure of subsets has a large impact on the estimation of the residual variance. In agreement with other authors (WOOD et al., 1991; TOSH and WILTON, 1994; PŘIBYL and PŘIBYLOVÁ, 2001) the subset should have a sufficient number of individuals within the HYS effect and a sufficient number of individuals per sire. The data subset 4 satisfied these conditions in the best way. This subset comprised these sampling criteria: at least 5 individuals per each sire, 5 individuals per HYS, 2 sires per HYS and animals with dams which had at least one half-sister and two offspring.

Models including sire × herd and sire × year interactions underestimated the direct genetic effect and were responsible for the significant increase of the of maternal effect and the genetic correlation between the direct and maternal effect. The inclusion of the fixed effect of herd led to a decrease of the sire × herd interaction. The addition of the sire × herd interaction diminishes the value of the information criteria (AIC) and residual error, but the dubiousness of the inclusion of the sire × herd and sire × year interaction indicated a high positive correlation between the direct and maternal effect. In models including the HYS effect as a random variable there is a marked decrease in the correlation between the direct and maternal effect (r_{am}) while the residual error variance did not change.

For these reasons model I, which comprised the fixed effect of dam's age, combined with the fixed effect of sex and frequency of parturition, fixed effect of HYS and random effects (direct individual effect, direct maternal effect, permanent environment and random error) was the most suitable one for the genetic parameter estimation of beef cattle breeds in the conditions of the Czech Republic.

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