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Relationship between direct and maternal genetic effects on weaning weight of Limousin and crossbred beef calves

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Abstract: Population genetic parameters, direct and maternal breeding value, genetic trend in the weaning weight of Limousin beef cattle calves were estimated in the period 1992–2019. Data of 19 764 calves (15 437 purebred Limousin and 4 327 crossbred) were computed. Crossbred calves were sired by Limousin breeding bulls from Simmental dams. Calves in question came from 37 herds and from 240 sires in Hungary. DFREML and MTDFREML software was used for the estimation of population genetic parameters, BLUP animal model for breeding value estimation. Weighted linear regression model was used for describing genetic trends. The maternal heritability (h_m^2 ± SE = 0.29 ± 0.03; 0.32 ± 0.10) was approximately half of the direct heritability (h_d^2 ± SE = 0.63 ± 0.05; 0.68 ± 0.12). The direct maternal covariance is negative, the direct maternal genetic correlation coefficients (r_{dm} ± SE = −0.80 ± 0.03 and −0.96 ± 0.07) are strong negative. The Spearman rank correlation between direct and maternal breeding value in purebred population is moderate and negative ($r_{rank} = -0.33$; $P < 0.01$), in crossbred population it is strong and negative ($r_{rank} = -0.99$; $P < 0.01$). According to direct and maternal breeding values of sires the genetic trend of the weaning weight of purebred and crossbred Limousin calves appeared stagnant during the examined period (b = +0.01 kg/year to +0.19 kg/year).

Keywords: heritability; direct maternal correlation; breeding value; genetic trend

In beef cattle the weaning weight (WW) of calves is a trait of great importance as it reflects the nursing ability of their mother; moreover, it is the end product, the income of beef cow. Weaning weight within breed, beside the growth potential of a calf, mostly depends on the milk production of their mother. That is why the beef cow must have a sufficient milk production for supplying the calf. Since measuring the milk production of a beef cow is not easy, WW of calf could be the selection criterion. According to MacNeil et al. (2006), selection based on the maternal breeding value (BV) for preweaning gain may be nearly as effective in changing the milk production as direct selection. When improving WW of calves by the selection process of sires, special attention should be paid not only to the direct genetic effect but also to the maternal genetic effects of sires. The efficiency of selection

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for this trait depends, among others, on the genetic merit, the level of heritability. According to several literature sources the heritability of WW of beef calves is low and moderate (Koury Filho et al. 2010; Chud et al. 2014). Montaldo and Kinghorn (2003) found that direct heritability was medium while maternal heritability was close to zero in a multibreed population. According to Albuquerque and Meyer (2001), direct heritability estimates varied between 0.12 and 0.28, while maternal heritability estimates were from 0.01 to 0.14 in Nellore breed. Tilki et al. (2008) reported the value 0.15 for direct, and 0.06 for maternal heritability in the Brown Swiss population. Martinez et al. (2016) published the value between 0.24 and 0.47 for direct heritability and between 0.15 and 0.21 for maternal heritability in the Brahman Zebu population. Boligon et al. (2018) reported direct and maternal heritability for weaning traits of Nellore herd 0.21 ± 0.03 and 0.13 ± 0.01, respectively. The above-mentioned publications confirm that the heritability values of WW trait are low or moderate and indicate that direct heritability values are generally higher than the maternal heritability.

Many publications contain data for the relationship between direct and maternal genetic effects. Tilki et al. (2008) found that genetic correlation between these two effects (r_{dm}) was strong and negative (–0.92). According to Penasa et al. (2012) the direct-maternal genetic correlations in the birth weight trait of Brown Swiss population were moderately low (r_{dm} = –0.02 and –0.31). Martinez et al. (2016) published that the correlation between direct and maternal effects on WW of beef calves was high and negative (r_{dm} = –0.59 to –0.76). Previous studies for Limousin breed (Lengyel et al. 2004; Szabo et al. 2012) indicated also medium negative (r_{dm} = –0.53 to –0.62) direct and maternal correlations.

It is supposed that the negative relationship between direct and maternal genetic effect may appear in the relationship between the direct and maternal breeding value of breeding animals, as well as in the genetic trend resulting from selection based on direct or maternal BV.

Since few test results have been published in this regard, the aim of our study was to estimate the weaning weight direct and maternal breeding value of Limousin sires, the relationship between them, and the genetic trend based on the two kinds of breeding values.

MATERIAL AND METHODS

During the study variance, covariance components, heritability, direct and maternal correlation, direct and maternal breeding value and genetic trend in the weaning weight of Limousin calves in Hungary in the period 1992–2019 was evaluated.

Database

The database of the Association of Hungarian Limousin and Blonde d'Aquitaine Breeders for weaning results (age at weaning and weaning weight) was used for this study. Data of 19 764 calves (15 437 purebred Limousin and 4 327 crossbred) were computed. Crossbred calves were sired by Limousin breeding bulls from Simmental dams. Calves in question came from 37 herds and from 240 sires. The structure of the database is seen in Table 1.

Estimation of population genetic parameters

With the best linear undebiased prediction (BLUP) animal model estimation the following population

Table 1. The structure of the evaluated database

Used database	Database 1 (purebred)	Database 2 (crossbred)
The study period (birth year date of calves)	1992–2019	1992–2014
Number of herds	37	23
Age of cows (year)	2–16	2–16
Breed of dams (cows)	LIM	HS
Breed of sires	LIM	LIM
Number of sires	240	98
Genotype of calves	LIM	HUS × LIM (F_1)
Number of calves	15 437	4 327
The average progeny number per sire	64.3	44.2
Age at weaning (day)		
Mean ± SD	219.1 ± 46.3	218.6 ± 54.0
Range	100–365	100–365
Weaning weight (kg)		
Mean ± SD	223.5 ± 48.1	216.8 ± 43.7
Range	120–400	120–400

HUS = Hungarian Simmental; LIM = Limousin genetic parameters, covariance and variance components were determined: additive direct genetic variance (σ_d^2), maternal genetic variance (σ_m^2), direct-maternal genetic covariance (σ_{dm}), maternal permanent environmental effect (σ_{pe}^2), residual variance (σ_e^2), phenotypic variance (σ_p^2), direct heritability (h_d^2), maternal heritability (h_m^2), direct-maternal genetic correlation (r_{dm}), the ratio of the permanent environmental variance to the phenotypic variance (c^2) and the ratio of the residual variance to the phenotypic variance (e^2). The total heritability (h_T^2) was calculated using the following formula (Willham 1972):

$$h_T^2 = (\sigma_d^2 + 0.5\ \sigma_m^2 + 1.5\ \sigma_{dm})/\sigma_p^2 \qquad (1)$$

Using the BLUP model, two matrices were created. One of these was the pedigree matrix and the other was the database matrix. The pedigree matrix of relatives included pedigree data for full sibs, half sibs, sires, dams, and grandparents. The database matrix contained fixed and random effects (see below in the text). The model contained maternal genetic effect and maternal permanent environmental effect as random effects and age at weaning as covariant. General formula of the BLUP animal models was used as follows (Henderson 1975):

$$y = \mathbf{X}_b + \mathbf{Z}_u + \mathbf{W}_m + \mathbf{S}_{pe} + e \qquad (2)$$

where:

y – the observation vector (trait);
$\mathbf{X}$ – incidence matrix of fixed effects;
b – vector of fixed effect(s);
$\mathbf{Z}$ – incidence matrix of random effects;
u – vector of random effect (animal);
$\mathbf{W}$ – incidence matrix of maternal genetic effect;
m – vector of maternal genetic effect;
$\mathbf{S}$ – incidence matrix of maternal permanent environmental effect;
pe – vector of maternal permanent environmental effect;
e – error vector.

Two different BLUP animal models were used for BV estimation (Table 2). Model number 1 was used for the evaluation of the purebred dataset (database 1) only according to Keeton et al. (1996) and Dodenhoff et al. (1999). Herd, parity of the cows, year and season at birth, and sex of the calves were considered as fixed effects (Gregory et al. 1995; Lee at al. 1997). Model number 2 was used for the evaluation of the data of crossbred progeny (database 2) according to the method of BV estimation across breeds as suggested by Van Vleck et al. (1992), Lo et al. (1997), Roso et al. (2005) and Brandt et al. (2010). In model number 2 the genotype of calves was considered as fixed effect according to the study of Splan et al. (2002).

Estimation of breeding values

Direct and maternal BV of sires and total herd were estimated both in purebred and crossbred population. The rank of the sires according to their different breeding values was compared; moreover, the rank correlation analysis was done according to Nunez-Dominguez et al. (1995).

Breeding values are shown only for 25 sires with the highest number of offspring due to size reasons.

Table 2. Used BLUP animal models

Type of models	BLUP animal model	
	model 1	model 2
Database used	database 1 (purebred)	database 2 (crossbred)
Method	BVE	across breed BVE
Genotype of calves in database	LIM	HUS × LIM (F_1; R_1)
Random effects		
Animal (calf)	+	+
Maternal genetic effect (dam)	+	+
Maternal permanent environment effect (dam)	+	+
Fixed effects		
Genotype of calf	–	+
Herd	+	+
Parity of dam	+	+
Birth year of calf	+	+
Birth season of calf	+	+
Sex of calf	+	+
Pedigree matrix		
Animal, full sibs, half sibs, sires, dams, grandparents	+	+
Trait studied		
Weaning weight	+	+
Covariant		
Age at weaning	+	+

+ = the model includes this effect; – = the model does not include this effect; BVE = breeding value estimation; HUS = Hungarian Simmental; LIM = Limousin

Calculation of genetic trends

The genetic trend of the above-mentioned trait was evaluated using weighted linear regression. BV of sires as well as BV of each animal in the total population obtained were weighted-averaged annually. The annual mean values were dependent values, the appropriate year was an independent value, the number of animals was the weight in the used regression method.

Used software

Variance, co-variance, correlation, heritability and breeding values according to the above-mentioned two models were estimated as it can be seen in the studies of Willham (1972), Henderson (1975), Trus and Wilton (1988), Meyer et al. (1993), Lee et al. (1997) and Vanderick et al. (2017).

DFREML (Meyer 1998) and MTDFREML (Boldman et al. 1993) software was used for the estimation.

RESULTS

The population genetic parameters such as variance, covariance, correlation and heritability values can be seen in Table 3. As it is shown in the table, there are no differences in variance components and other population genetic parameters between purebred (model 1) and crossbred (model 2) population. The maternal heritability (h_m^2 ± SE = 0.29 ± 0.03; 0.32 ± 0.10) is approximately half of the direct heritability (h_d^2 ± SE = 0.63 ± 0.05; 0.68 ± 0.12). The direct maternal covariance is negative, the direct maternal genetic correlation coefficients (r_{dm} ± SE = –0.80 ± 0.03 and –0.96 ± 0.07) are high and negative.

Results of direct and maternal BV estimation are summarized in Table 4. In this table only 25 sires with the highest number of progeny out of the total 240 evaluated sires are listed. Each sire in the table had the creditable number of both purebred and crossbred progeny. Data of Table 4 show large differences between direct and maternal BV of the same sires both in purebred and crossbred population obtained on WW. Differences appear not only in the extent of breeding values but also, in many cases, in their negative/positive sign. In the total 25 progeny groups there were 20 groups in purebred population in which the signs of BV were different (negative and positive), while in crossbred population the difference was observed in 24 cases. The mentioned changes in the sign of BV indicate also a negative relationship between direct and maternal genetic effects.

The above-mentioned differences also resulted in differences in the rank of sires in question (Table 5). As it is shown in the table, a medium

Table 3. Estimated population genetic parameters of weaning weight of Limousin calves

Population genetic parameters	Weaning weight	
	model 1 (purebred)	model 2 (crossbred)
Additive direct genetic variance (σ_d^2)	651.39	580.06
Maternal genetic variance (σ_m^2)	305.78	270.60
Direct-maternal genetic covariance (σ_{dm})	–359.21	–382.30
Maternal permanent environmental variance (σ_{pe}^2)	88.30	104.83
Residual variance (σ_e^2)	355.13	278.09
Phenotypic variance (σ_p^2)	1 041.39	851.27
Direct heritability (h_d^2)	0.63 ± 0.05	0.68 ± 0.12
Maternal heritability (h_m^2)	0.29 ± 0.03	0.32 ± 0.10
Direct-maternal genetic correlation (r_{dm})	–0.80 ± 0.03	–0.96 ± 0.07
Ratio of the permanent environmental variance to the phenotypic variance (c^2)	0.09 ± 0.01	0.12 ± 0.05
Ratio of the residual variance to the phenotypic variance (e^2)	0.34 ± 0.04	0.33 ± 0.09
Sum of the maternal heritability and permanent environmental variance ($h_m^2 + c^2$)	0.38	0.44
Total heritability (h_T^2)	0.25	0.17

Table 4. Direct and maternal breeding value of Limousin sires in different populations based on the weaning weight of their calves

Registration number of sire	Weaning weight (kg)					
	purebred calves			crossbred calves		
	n	breeding value		*n*	breeding value	
		direct	maternal		direct	maternal
9034	61	+2.82	+0.88	394	−5.16	+0.27
12015	608	−7.17	−12.30	257	−18.30	+14.10
12470	43	+7.75	−6.18	50	−4.41	+2.28
12481	88	+1.06	−5.65	66	−14.63	+7.78
12482	54	+11.37	−1.29	54	−16.61	+11.74
12483	79	+7.88	−8.94	56	−20.60	+12.97
12484	72	−1.22	+6.74	59	−10.48	+7.64
12485	49	+9.15	−0.28	60	−13.26	+8.64
13098	1 019	−3.17	+3.88	516	+0.13	+0.93
13869	259	−10.88	−4.31	31	+6.38	−5.41
14284	177	−16.77	+4.99	48	+0.08	−0.05
14473	185	−10.27	+2.66	55	+13.07	−10.15
14474	216	−6.51	+4.73	77	−7.31	+4.46
14475	109	−6.39	+2.62	32	+10.09	−6.65
14476	207	−8.09	+4.65	51	−6.58	+4.34
14602	52	−4.13	−1.36	198	−22.89	+13.12
14684	792	−21.92	−3.18	107	−5.73	+3.81
14709	66	−18.34	+10.11	80	+29.46	−19.42
14714	37	−1.43	+0.79	119	+12.85	−8,47
15250	619	−35.39	+22.97	165	−60.03	+39.56
16444	485	−9.74	+4.97	62	+12.80	−8.44
16851	80	−10.85	+23.90	36	+7.09	−4.68
16854	202	+1.63	−1.66	45	+33.78	−23.41
17562	153	+3.11	+0.53	52	+23.80	−16.48
21207	86	−8.63	−4.66	31	+21.38	−14.59
Overall mean (± SE)	225.7 ± 3.8			221.5 ± 1.23		

and negative ($r_{rank} = -0.33$; $P < 0.01$) correlation coefficient was found between the ranks of evaluated sires based on maternal and direct BV in purebred population, while a strong negative correlation ($r_{rank} = -0.99$; $P < 0.01$) was revealed in crossbred population.

Genetic trends of WW are illustrated in Figure 1 and 2. Both figures show no increasing tendency during the last 28-year period. The graphs of the above figures indicate also a negative relationship between direct and maternal BV. Both in the BV of sires (Figure 1) and BV of each animal in the total

Table 5. The Spearman rank correlation matrix between direct and maternal breeding values of the evaluated sires

Spearman rank correlation coefficients (r_{rank})	Maternal breeding value in purebred population	Direct breeding value in crossbred population	Maternal breeding value in crossbred population
Direct breeding value in purebred population	−0.33*	−0.11	+0.11
Maternal breeding value in purebred population	–	+0.19	−0.18
Maternal breeding value in crossbred population	–	–	−0.99*

*$P < 0.01$

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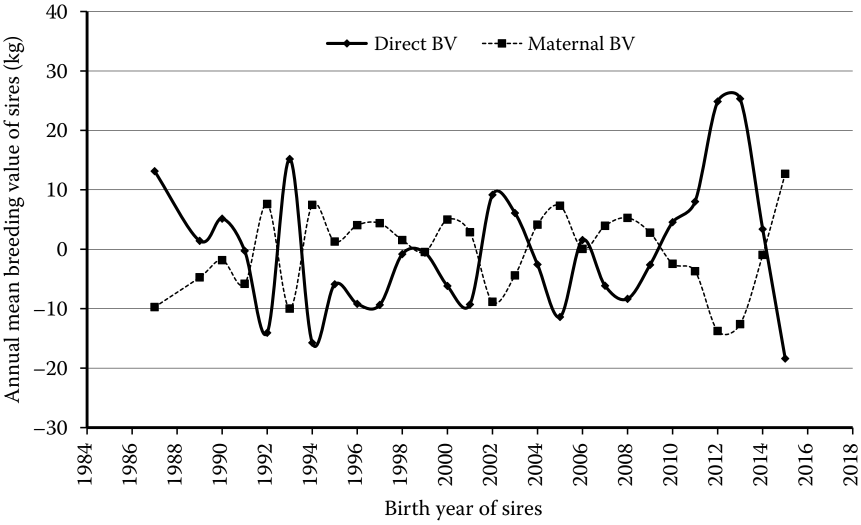

Figure 1. Genetic trend of weaning weight of Limousin calves based on direct and maternal breeding value (BV) of sires

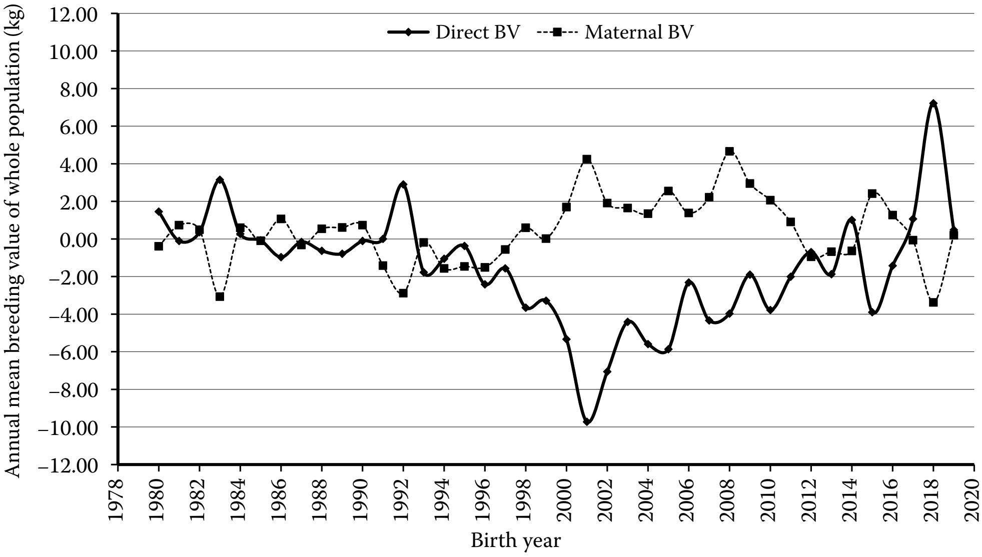

Figure 2. Genetic trend of weaning weight of Limousin calves based on direct and maternal breeding value (BV) of the total population

evaluated population (Figure 2) an adverse annual change occurs. Namely, when the direct BV goes up, the maternal BV goes down, or vice versa.

Parameters of the linear regression function are summarized in Table 6. As it is seen in the table, the slope coefficient (*b*) is close to zero, that means no genetic progress was achieved in weaning weight of Limousin calves in the studied population.

DISCUSSION

Heritability values of weaning weight of Limousin calves for both purebred and crossbred population in this study are similar to the results reported by Koury Filho et al. (2010) and Chud et al. (2014), they are low and moderate. Obtained results are similar or somewhat lower than those obtained by Keeton et al. (1996), Dodenhoff et al. (1999), Crews and Kemp (1999), Splan et al. (1998) and Lukaszewicz et al. (2015). However, heritability values are somewhat higher than those published by Albuquerque and Meyer (2001), Tilki et al. (2008), Martinez et al. (2016) and Boligon et al. (2018). According to several previous findings this result confirms that the environmental effect on weaning weight of beef calves is higher than the genetic effect.

Table 6. Genetic trend in the weaning weight of Limousin calves

Annual mean of breeding values (*Y*)	Slope coefficient		*Y*-intercept coefficient		Coefficient of determination
	b	SE	*a*	SE	
Purebred population, breeding value of sires					
DBV	+0.19	0.23	–377.17	468.40	0.03
MBV	+0.04	0.15	–84.44	298.29	0.00
Crossbred population, breeding value of sires					
DBV	+0.02	0.26	–37.61	512.63	0.00
MBV	+0.01	0.17	–14.90	340.64	0.00
Purebred population, breeding value of whole population					
DBV	–0.05	0.03	+97.65	64.15	0.06
MBV	+0.03	0.02	–69.17	47.71	0.05
Crossbred population, breeding value of whole population					
DBV	–0.03	0.04	+57.77	79.55	0.01
MBV	+0.02	0.03	–33.22	51.44	0.01

DBV = direct breeding value; MBV = maternal breeding value

The maternal heritability values estimated both in purebred and crossbred population were higher in the studied Limousin population than those published in the literature (Keeton et al. 1996; Lee et al. 1997; Kaps et al. 2000).

In the present study the estimated negative direct maternal genetic covariance is similar to our previous findings (Lengyel et al. 2004; Bene et al. 2010; Szabo et al. 2012; 2013). The strong negative correlation coefficients between direct and maternal genetic effect in crossbred population and in purebred population in this study are higher than the findings of Cubas et al. (1991), Tilki et al. (2008), Penasa et al. (2012) and Martinez et al. (2016).

Obviously, the negative direct maternal covariance and direct maternal genetic correlation coefficients indicate a negative relationship between direct and maternal genetic effect.

Likewise, a negative relationship between direct and maternal genetic effect was indicated by the rank of evaluated sires. Namely, different rank of Limousin sires was found in this study depending on that direct or maternal BV was the basis of ranking. This result of the medium negative rank correlation in purebred population and strong negative rank correlation in crossbred population corresponds to some previously published findings.

The negative relationship between direct and maternal genetic effect also appears in the genetic trend obtained by direct and maternal BV of sires and of each animal in the total population. Practically, no genetic progress in the WW in the studied period occurred; however, there is a large annual variation in BV when the direct BV shows an increasing tendency and the maternal BV is decreasing at the same time.

CONCLUSION

The negative relationship between direct and maternal genetic effect calls attention to the importance of maternal breeding value. When the breeders do not take into consideration the maternal BV and practically select sires on their direct BV, the weaning performance of grand-offspring will decrease and no genetic progress can be forecasted in the WW of beef calves.

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Conflict of interest

The authors declare no conflict of interest.

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