Re-ranking in International Beef Cattle Evaluations due to ignoring Direct-Maternal Genetic Correlations Between Countries

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Abstract

Many traits of economical relevance in beef cattle are influenced in their phenotypic expression by the dam. Genetic evaluations of maternally affected traits require to model direct, maternal and direct-maternal genetic (co)variances next to non-genetic effects. In Interbeef beef cattle international evaluations, direct-maternal genetic correlations (r_{dm}) may be different both within countries (r_{dm_WC}) and between countries (r_{dm_BC}). r_{dm_WC} for growth traits up to weaning are often reported to be negative and significantly different from zero. As r_{dm_BC} are difficult to estimate, these are currently assumed to be equal to zero in Interbeef evaluations. The objective of this study was to evaluate the impact of using estimated values for r_{dm_BC} instead of assuming them to be zero, on international estimated breeding values (IEBV). We implemented two scenarios that differed only in the modelling of r_{dm_BC}: A) the current Interbeef evaluation with assumes r_{dm_BC} to be 0 and fits estimated r_{dm_WC}, and B) an Interbeef evaluation in which both estimated r_{dm_WC} and r_{dm_BC} were fitted. Weaning weight phenotypes and pedigree information were available for more than 3 million Limousin beef cattle males and females, born between 1972 and 2017, and distributed across ten European countries. We evaluated the impact of ignoring r_{dm_BC} on different groups of animals by comparing animals' direct and maternal IEBV between scenarios A and B. Ignoring r_{dm_BC} resulted in no re-ranking for direct IEBV, and limited re-ranking for maternal IEBV. Less re-ranking in maternal IEBV was observed with increasing reliability. Moreover, ignoring r_{dm_BC} resulted in no re-ranking for publishable sires, i.e. of sires with IEBV that can be exchanged across countries. Our study suggests that the current practice of ignoring r_{dm_BC} has limited impact on Interbeef evaluations when r_{dm_BC} are close to 0 on average (ranging from +0.14 to -0.14) as is the case for weaning weight.

Key words: beef cattle, direct-maternal genetic correlation, international estimated breeding values, maternal effects, weaning weight.

Introduction

Developments in reproduction technologies allowed breeders to access elite sires from other countries, leading to both importers and exporters of genetic material to seek a fair comparison of the genetic merit of foreign and domestic sires. International evaluations (Palucci et al., 2018) allow comparing the genetic merit of sires across countries by computing an individual international estimated breeding value (IEBV). These IEBV are computed taking into account existing genetic connections between populations and data from relatives recorded in other countries.

In beef cattle, many traits of economic relevance are affected in their phenotypic expression by maternal effects, defined as the effect of the mother on the phenotype of the offspring (Willham, 1980). Such maternal effects start from uterine development and

continue up to weaning and can be divided into a genetic component (maternal genetic effect) and an environmental effect (maternal permanent environmental effect) (Willham, 1963). Breeders account for the presence of maternal effects when making selection decisions (Van Vleck et al., 1977) using genetic evaluations which model direct, maternal and direct-maternal genetic (co)variances next to non-genetic effects (Bijma, 2006). The magnitude of the genetic correlation between direct and maternal genetic effects (r_{dm}) has been studied for a long time and it has often been reported to be difficult to estimate accurately, as a proper data structure is required, e.g. large datasets and good connections between management units (Meyer, 1992; Clément et al., 2001; Bijma, 2006). When this data structure is lacking, some authors suggested setting r_{dm} to 0 in genetic evaluations (David et al., 2015; Schaeffer, 2019).

To date, beef cattle international routine evaluations led by Interbeef (Interbeef, 2020) involves up to 14 countries, 5 breeds (Limousin, Charolais, Hereford, Angus, Beef Simmental) and 3 traits (weaning weight, calving ease, and birth weight). In Interbeef evaluations for maternally affected traits, r_{dm} can be different both within-country (r_{dm_WC}) and between-country (r_{dm_BC}). Estimates of r_{dm_WC} are often reported to be negative and significantly different from zero (Robinson, 1996; Meyer, 1997; Pabiou et al., 2014). r_{dm_BC} however are difficult to estimate and currently are assumed to be equal to zero (Venot et al., 2007; Bonifazi et al., 2020b). The objective of this study was to evaluate the impact on beef cattle international estimated breeding values (IEBV) of using estimated values for r_{dm_BC} instead of assuming them to be zero.

Materials and Methods

A total of 3,155,598 Limousin male and females phenotypes for age-adjusted weaning weight (AWW) were available from the 2018 routine Interbeef evaluation, recorded from 1972 up to 2018 and distributed across 19,330 herds. AWW were recorded in ten different countries for a total of eight populations: Czech Republic (CZE), Denmark, Finland and Sweden (considered as one single population; DFS), Spain (ESP), Great Britain (GBR), Ireland (IRL), France (FRA), Germany (DEU), and Switzerland (CHE). Hereafter, for simplicity, we will refer to populations as countries. Pedigree included a total of 3,431,742 animals. Table 1 reports a summary of AWW available in each country.

Table 1. Age-adjusted weaning weights (AWW) per country and associated country code (COU) [1].

Country	COU	AWW
Czech Republic	CZE	10,500
Denmark, Finland, Sweden	DFS	90,456
Spain	ESP	33,152
Great Britain	GBR	127,840
Ireland	IRL	20,609
France	FRA	2,714,368
Germany	DEU	88,628
Switzerland	CHE	30,045
Total		3,115,598

Breeding values were estimated using the current Interbeef multi-trait animal model with maternal effects in which countries are modelled as different correlated traits (Phocas et al., 2005):

$$\mathbf{y = Xb + Cr + Zu + Wm + Ppe + e}$$

where $\mathbf{y}$ is the vector of AWW, $\mathbf{b}$ and $\mathbf{r}$ are the vector of fixed and random environmental effects, respectively; $\mathbf{u}$ is the vector of random direct additive genetic effects; $\mathbf{m}$ is the vector of random maternal additive genetic effects; $\mathbf{pe}$ is the vector of random maternal permanent environmental effects; $\mathbf{e}$ is the vector of random residual effects. $\mathbf{X}$ and $\mathbf{C}$ are incidence matrices linking records to fixed, and random environmental effects, respectively. $\mathbf{Z}$, $\mathbf{W}$, and $\mathbf{P}$ are incidence matrices linking records to the animal, maternal genetic and maternal

permanent environmental effects, respectively. The list of environmental effects fitted in each national model is reported in Bonifazi et al. (2020a, Additional file 1, Table S1). All random effects are assumed to be independent of each other, except for the direct and maternal genetic effects. Genetic and environmental variances were the same as those estimated at the national level. Random direct and maternal genetic covariances between countries were estimated in a previous study (Bonifazi et al., 2020a) and are reported in
Table 2.

IEBV were estimated in two scenarios which differed only in the modelling of r_{dm_BC}:

- **Scenario A** represents the current Interbeef evaluations where r_{dm_BC} are assumed to be 0 and only r_{dm_WC} are fitted (
- Table 2). An unweighted bending procedure was applied to ensure that the genetic co-variance matrix was positive definitive using the R package *mbend* (Nilforooshan, 2020) (method "hj unweighted" and threshold of 10^{-3}).
- **Scenario B** in which both estimated r_{dm_WC} and r_{dm_BC} were fitted.

Both direct and maternal IEBV and their approximated reliabilities (REL) were obtained using MiX99 (MiX99 Development Team, 2017). REL were computed for scenario B using Tier and Meyer (2004) method. The convergence criteria for the preconditioned conjugate gradient (PCG) algorithm was defined as the square root of the relative difference between solutions of the last two PCG iterations rounds and was set at 10^{-7}.

We evaluated the impact of ignoring r_{dm_BC} on the re-ranking of IEBV by computing the Spearman rank correlation (ρ) between IEBV of scenario A and B for different groups of animals:

- **ALL**: All 3,431,742 animals included in the international evaluations.
- **REL groups**: Animals grouped by their associated REL of the direct and maternal IEBV. Animals were grouped in three classes: REL ≤ 0.3, 0.3 < REL ≤ 0.6 and 0.6 < REL.
- **Publishable sires**: all sires with a direct and maternal IEBV publishable in other countries. According to Interbeef rules, sires' direct IEBV are publishable if its associated REL is ≥ 0.5 in at least one country scale, and sires have at least 25 recorded progeny across all countries. Sire's maternal IEBV are publishable if: i) its associated REL is ≥ 0.3 in at least one country scale;

Table 2. Direct and maternal within-country genetic variances (diagonal) and within-country and across-country genetic correlations (below diagonal).

		Direct genetic effect								Maternal genetic effect							
		CZE	DFS	ESP	GBR	IRL	FRA	DEU	CHE	CZE	DFS	ESP	GBR	IRL	FRA	DEU	CHE
Direct genetic effect	CZE	310															
	DFS	0.87	269														
	ESP	0.74	0.77	136													
	GBR	0.71	0.82	0.94	268												
	IRL	0.83	0.76	0.87	0.91	450											
	FRA	0.76	0.89	0.77	0.82	0.76	242										
	DEU	0.76	0.94	0.76	0.77	0.62	0.81	383									
	CHE	0.85	0.81	0.76	0.71	0.70	0.70	0.70	130								
Maternal genetic effect	CZE	-0.12	0.04	0.07	0.12	-0.01	-0.10	0.08	0.01	197							
	DFS	-0.05	-0.14	0.02	-0.01	-0.02	-0.11	-0.07	-0.01	0.68	120						
	ESP	0.03	0.09	-0.22	-0.08	-0.09	-0.05	0.05	0.02	0.67	0.68	68					
	GBR	0.14	0.06	-0.03	-0.10	-0.03	-0.14	0.07	0.08	0.79	0.69	0.70	55				
	IRL	-0.03	0.07	-0.06	-0.05	-0.19	-0.12	0.12	0.11	0.69	0.68	0.81	0.72	194			
	FRA	-0.02	-0.05	-0.03	-0.06	-0.09	-0.33	-0.01	0.08	0.85	0.69	0.71	0.87	0.82	62		
	DEU	-0.02	-0.09	-0.03	-0.01	0.06	-0.10	-0.24	0.09	0.68	0.68	0.67	0.69	0.68	0.69	326	
	CHE	0.12	0.11	0.07	0.08	0.03	-0.05	0.06	0.40	0.73	0.68	0.67	0.66	0.65	0.77	0.66	54

ii) sires have at least 15 daughters with recorded progeny; iii) sires have at least 25 recorded grand-progeny from daughters across all countries; iv) sires' direct IEBV is publishable.

We considered that large, small and no re-ranking of IEBV was present when $\rho < 0.980$, $0.980 \leq \rho < 0.990$, and $0.990 \leq \rho$, respectively.

Results & Discussion

Table 3 reports the IEBV rank correlations for all animals included in the international evaluation. For direct IEBV, rank correlations were always higher than 0.990 in all country scales suggesting that ignoring r_{dm_BC} led to no re-ranking of animals compared to fitting them in the model. For maternal IEBV, rank correlations were between 0.980 and 0.990 for most countries except for ESP, FRA and CHE for which rank correlations were higher than 0.990, suggesting that ignoring r_{dm_BC}, instead of fitting them, would lead to small re-ranking of animals in some countries.

To further investigate the observed re-ranking for maternal IEBV, animals were grouped by classes of individual REL. Table 3 confirms that for direct IEBV ignoring r_{dm_BC} led to no re-ranking in any class of REL and any country scale ($\rho > 0.990$). For maternal IEBV, small re-ranking ($0.980 \leq \rho < 0.990$) was present for animals with REL ≤ 0.30 in all

countries except for ESP and CHE. With higher maternal REL, (almost) no re-ranking was observed in all country scales. When REL was higher than 0.6, no re-ranking was present for maternal IEBV in any country scale.

The total amount of sires with publishable IEBV in other country scales was 32,208 and 13,016 for direct and maternal IEBV, respectively. Table 3 reports the direct and maternal IEBV rank correlations for publishable sires in all country scales. For publishable sires, there was no re-ranking when ignoring r_{dm_BC}, for both direct and maternal IEBV. To further evaluate the impact of ignoring r_{dm_BC} on publishable sires, we quantified the mean change in position of the top 100 publishable sires selected under scenario B when ranked under scenario A. The average absolute mean change in position was 1.9 and 4.9 on average across countries for direct and maternal IEBV, respectively (results not shown).

Overall, results suggest that ignoring r_{dm_BC}, instead of fitting them, would lead to no re-ranking for direct IEBV and limited re-ranking for maternal IEBV, particularly if the maternal IEBV is based on few performances records (REL ≤ 0.3, Table 3). In this study, r_{dm_BC} were low in magnitude and on average close to 0 (ranging from +0.14 to -0.14).

Table 3. Rank correlations of direct (dir) and maternal (mat) IEBV in each country [1] for all animals included in the international evaluation (All), for animals grouped by class of reliability of direct and maternal IEBV (REL), and publishable sires.

	All		REL $\leq$ 0.3		0.3 < REL $\leq$ 0.6		0.6 < REL		Publishable sires	
COU [1]	Dir	Mat	Dir	Mat	Dir	Mat	Dir	Mat	Dir	Mat
CZE	0.998	0.986	0.997	0.985	0.998	0.990	0.996	0.990	0.997	0.990
DFS	0.998	0.980	0.996	0.980	0.998	0.987	0.997	0.998	0.997	0.990
ESP	0.999	0.994	0.999	0.994	0.999	0.995	0.999	0.997	0.999	0.997
GBR	0.999	0.984	0.999	0.983	0.999	0.990	0.999	0.993	0.999	0.992
IRL	0.999	0.988	0.999	0.988	0.999	0.992	0.999	0.992	0.999	0.994
FRA	1.000	0.992	0.999	0.989	1.000	0.995	1.000	0.998	1.000	0.997
DEU	0.997	0.982	0.997	0.982	0.997	0.985	0.996	0.999	0.996	0.991
CHE	0.997	0.995	0.997	0.995	0.997	0.997	0.995	0.996	0.995	0.997

[1] COU: Country, see Table 1 for country codes.

These values close to 0 could explain the small impact of ignoring r_{dm_BC} in Interbeef evaluations. David et al. (2015) observed a similar pattern with r_{dm} having a higher impact on maternal EBV compared to direct EBV in national evaluations of other livestock species. David et al. (2015) suggested that r_{dm} may impact more on maternal EBV compared to direct EBV as the former is mainly derived from records on the offspring while the latter is mainly derived from records on the animal itself. This possible explanation was supported by the results observed in Table 3 where the higher the REL the smaller the re-ranking for maternal IEBV. This relationship suggests that when more information becomes available at the animal level for the estimation of maternal IEBV, r_{dm_BC} have less impact on maternal IEBV. On the other hand, direct IEBV are already estimated with good accuracy by having records on the animal themself, leading to a negligible impact of ignoring r_{dm_BC}.

Publishable sires are the main "output" of Interbeef routine evaluations (Venot et al., 2014; Bonifazi et al., 2020a) and ignoring r_{dm_BC} did not impact their re-ranking in any country scale. The Interbeef publication rules currently in place may have mitigated the impact of ignoring r_{dm_BC} on publishable sires by requiring them to have progeny recorded across two or three generations. A larger re-ranking from ignoring r_{dm_BC} could be expected for foreign young bulls with none or few domestic progenies, no domestic grand progeny and, at the same time, recorded progeny in the foreign country. For such animals, the domestic maternal IEBV is influenced by its foreign direct IEBV via the r_{dm_BC}. As soon as domestic progeny accumulates and the domestic direct IEBV is computed with reasonable accuracy, the r_{dm_BC} is expected to have less impact on the domestic maternal IEBV.

Conclusions

Results of this study support the current procedure of ignoring r_{dm_BC} in Interbeef evaluations and shows a limited impact on Interbeef evaluations when r_{dm_BC} are close to 0 on average.

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