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Herd of origin effect on weight gain of station-tested beef bulls

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Abstract

The effect of herd of origin on genetic evaluation of weight gain of beef bulls in central test stations was examined by univariate and bivariate analyses, which included bull's estimated weight gain on test (BEG) and pre-weaning gain (WG) of bulls and their contemporaries in the herd of origin. Bulls were weighed every 28 days on 112 or 140-day station test. BEG was estimated fitting fixed linear regressions to the weights on test of each bull. The bivariate model included random direct additive genetic and dam effects and fixed breed effects for both traits, fixed management group and sex of calf by age of cow effects for WG and fixed test group and random herd of origin by year (HY) effects for BEG. Variance components and EBV were estimated applying models with or without HY effect, which were compared using likelihood ratio test and two information criteria. The effect of HY was significant on BEG, contributing around 8% to total phenotypic variation. Inclusion of HY effect caused EBV to re-rank among top bulls (rank correlation of 0.85 and 0.75 among 5% and 1% best bulls, respectively). Interaction of HY by sire was shown not to be of concern.

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1. Introduction

Central testing of beef bulls has developed into an important component of genetic improvement programs for beef cattle (Scholtz et al., 1998; Archer et al., 1999).

The main aim of a central performance test is to compare beef bulls fairly under uniform management and environmental conditions. Testing of bulls in central stations involves beef bulls from different herds, which may have different environmental con-

ditions and management practices. A potential problem for evaluation of bulls is the influence of pre-environmental factors related to herd of origin of a bull. Studies have shown important effects of the herd of origin on the performance of bulls on test despite adjustment periods (e.g. Collins-Lusweti and Curran, 1985; Tong et al., 1986; Amal and Crow, 1987; Mantovani et al., 1999; Liu and Makarechian, 1993; Schenkel et al., 2002) and the existence of negative environmental correlations between pretest and test weight gain, indicating compensatory gain on test (e.g. Tong, 1982; Tong et al., 1986; De Rose et al., 1988a).

Studies on the effect of herd of origin have mostly used a sire model in univariate analyses and, therefore, did not account for possible different genetic levels of cows among herds and for the pre-selection of bulls at

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weaning, which could partially explain the herd of origin effect found. Meanwhile, Schenkel et al. (2002), using an individual animal model in univariate analysis, found that herd of origin by year effect still explained around 8% of the total variance of the bulls' weight gain on test over the entire test period.

De Rose et al. (1988b) argued that the use of a two-trait model, incorporating performance to weaning and performance in test station, would account for the pretest environmental carry-over effect on the performance on test. Including information from correlated performance to weaning would also account for the selection of bulls entering test stations (Pollak and Quaas, 1981).

The use of a two-trait individual animal model with maternal effects, incorporating pretest performance in the herd of origin, would address the within-herd-year aspect of the environmental carry-over, which encompasses those influences that vary within a herd-year, such as maternal effects (De Rose et al., 1988a). However, the across-herd-year component of the environmental carry-over, which constitutes those effects that generally are consistent within herd-year, but that may vary among herd-years, such as nutritional plan, health, management factors, etc. (De Rose et al., 1988a), may not be addressed unless a herd-year effect is included in the model for performance in station.

Therefore, the use of a two-trait individual animal model with maternal effects, incorporating pretest performance in the herd of origin, would be of interest for evaluating the impact of across herd of origin by year environmental carry-over on growth performance of bulls in central evaluation stations.

The objectives of this research were to determine the significance of herd of origin effect on genetic evaluation of weight gain of station-tested beef bulls and the influence of herd of origin effect on phenotypic variance of this trait and rank of bulls based on the resulting estimated breeding values.

2. Materials and methods

2.1. Data

Data were collected from central stations in Ontario, Canada, between 1988 and 2000. Stations operated

year round, with the majority of groups on test from late fall until early spring. Identified bulls were delivered to central stations soon after weaning. Age at delivery averaged 212 days with S.D. of 23 days across all tested bulls. Bulls composing a test group (TG) were restricted, by policy, to a 90-day age range and a maximum age at delivery of 280 days. Program policy also required a minimum of 20 bulls prior to 1995 (inclusive) and 12 bulls afterwards from at least four sires in any TG. A minimum weight of 181 kg was recommended. Following a 28-day adjustment period, bulls were tested for 140 days prior to 1995 (inclusive) and for 112 days afterwards. Bulls had access ad libitum to feed, usually consisting of pelleted diet of minimum 60% total digestible nutrients. Bulls were delivered to test centers from multiple herds, including multiple breeds and crossbreeds at any individual center.

The dataset used to estimate the bulls' gain on test consisted of 146,150 weight records on 25,315 bulls. Bulls had five or six weight measures with 20,008 bulls having six weight records.

The dataset used for investigating herd of origin effect consisted of estimated gain on test of bulls with available weaning weight and management group information, and the weaning weight of all contemporary calves (herdmates) of those tested bulls. Only bulls coming from weaning management groups with more than four calves were considered. Animals born from multiple births, such as twins, born from embryo transfer, or raised by foster dams were excluded from the analyses. The edited dataset had 10,927 bulls with estimated gain on test and weaning weight and 20,620 contemporary calves with weaning weight only. There was an average of 10.6 and 1.7 calves with weaning records per sire and dam, respectively, and 5.0 and 1.4 tested bulls per sire and dam, respectively. The average number of known ancestors in the pedigree file was 3.3. A summary of the data is given in Table 1.

A total of 14 breeds were represented in the data. Some bulls had part of the breed composition (usually a small fraction) from an undefined breed (XX). The 14 breeds were: Charolais (CH), Limousin (LM), Red Angus (AR), Simmental (SM), Polled Hereford (HP), Blonde d-Aquitaine (BD), Horned Hereford (HH), Maine-Anjou (MA), Gelbvieh (GV), Shorthorn (SS), Aberdeen Angus (AA), Shaver Beef Blend (SV), Salers (SA), and XX. The distribution of purebred calves and bulls per breed is given in Table 2.

Table 1
Summary of the data used to assess herd of origin effect on BEG^a

Number of:	
Calves with WG ^a	31,547 (80%) ^b
Bulls with BEG	10,927 (88%) ^b
Dams of calves	18,284
Sires of calves	2976
Animals in the pedigree	61,888
Breeds	14
Management groups at weaning	1136
Sex of calf by age of dam classes	48
Test groups	532
Herd of origin by year groups	993
Average of:	
BEG (kg)	237 (38) ^c
WG (kg)	210 (41) ^c

^a WG, pre-weaning weight gain (adjusted to 200 days of age); BEG, bull's estimated weight gain on station test (140-day test).

^b Percentage of purebred animals (fraction of one breed higher than 30/32).

^c Standard deviation.

Weight gains from birth to weaning were linearly adjusted to 200 days of age at weaning. Weight gains were linearly pre-adjusted for heterosis on the basis of the individual bull's heterozygosity for breed composition (Robison et al., 1981). An ad hoc heterosis of 5% for individual and maternal heterosis

on weight gain from birth to weaning and 3% for individual heterosis on weight gain on test were assumed for an individual with heterozygosity of 100%, regardless of the breeds involved (Sullivan et al., 1999).

2.2. Estimation of weight gain on test

The test weight gain of bulls was obtained through a fixed univariate linear regression of the weights (w_{ij}) (taken on about every 28 days (j) after starting test) on the actual days on test (d_{ij}) for each bull i , using the model:

$$w_{ij} = a_i + b_i d_{ij} + e_{ij} \quad (1)$$

where a_i is the intercept of the i th bull; b_i is the linear regression coefficient of the i th bull; e_{ij} is the random residual effect.

The bull's estimated weight gain on test (BEG) was calculated by multiplying the linear regression coefficient estimated from (1) by the number of days on test (140 days). Subsequently, BEG was used as an observation in the genetic evaluation model for assessing the herd of origin by year effect.

Table 2
Number of sex by age classes (S×A), management groups (MG), test groups (TG), herd of origin by year classes (HY), sires, calves, and bulls by breed^a of the calf/bull and trait^b

Breed ^c	WG				BEG			
	S×A	MG	Sires	Calves	TG	HY	Sires	Bulls
CH	46	275	480	5297	207	257	388	2151
LM	45	298	553	6392	240	216	410	2425
AR	40	78	146	1483	90	68	123	606
SM	45	179	498	3463	164	163	335	1211
HP	41	173	400	4269	152	148	292	1364
BD	37	63	181	864	80	48	135	387
HH	30	33	52	681	30	22	40	277
MA	23	13	28	167	17	13	20	51
GV	16	16	34	125	16	13	21	49
SS	31	30	69	596	26	24	53	265
AN	42	72	192	879	70	63	139	357
SV	30	12	85	813	17	11	57	303
SA	33	19	36	316	17	14	26	117
XX	3	2	1	12	0	0	0	0
Crossbred	48	636	912	6190	307	330	450	1364

^a Purebred calves/bulls=fraction of one breed higher than 30/32.

^b WG, pre-weaning weight gain; BEG, bull's estimated weight gain on station test.

^c Breed: see breed definitions in Section 2.1.

2.3. Evaluation of weight gain on test

Bivariate and univariate analyses were carried out to examine the herd of origin by year (HY) effect on BEG. The most complete bivariate model (B1) used was:

$$\begin{aligned} \text{WG}_{ijkl} = & \sum_{n=1}^{14} \beta_{1n} \text{B}_{1in} + \sum_{n=1}^{14} \beta_{2n} \text{B}_{2jn} + C_k + S \\ & \times A_l + G_i + D_j + E_{ijkl} \end{aligned} \quad (2)$$

and

$$\begin{aligned} \text{BEG}_{ijkl} = & \sum_{n=1}^{14} \beta_{1n} \text{B}_{1in} + \sum_{n=1}^{14} \beta_{2n} \text{B}_{2jn} + T_k \\ & + \text{HY}_l + G_i + D_j + E_{ijkl} \end{aligned} \quad (3)$$

where in (2) WG_{ijkl} is the pre-weaning weight gain (adjusted to 200 days of age); β_{1n} and β_{2n} are the linear regression coefficients of the n th breed; B_{1in} is the breed composition of the i th calf or bull for the n th breed; B_{2jn} is the breed composition of the j th dam for the n th breed; C_k is the fixed effect of the k th weaning management group (herd + weaning weight group + management code); $S \times A_l$ is the fixed effect of the l th class of sex of calf (three levels) by age of dam (16 levels); G_i is a random direct additive genetic effect of the i th bull; D_j is the random dam effect of the j th dam; E_{ijkl} is the random residual effect, and in (3) BEG_{ijkl} is the bull's estimated weight gain on test; β_{1n} , β_{2n} , B_{1in} , B_{2jn} are as in (2); T_k is the fixed effect of the k th test group (test center + center weigh group + test year); HY_l is the random effect of l th herd of origin by year group; G_i , D_j , and E_{ijkl} are as in (2).

Random effects HY, G, D, and E, were assumed uncorrelated with each other within traits. Covariance matrices of the effects were equal to $I\sigma_{\text{hy}}^2$, $A\sigma_{\text{g}}^2$, $I\sigma_{\text{d}}^2$, and $I\sigma_{\text{e}}^2$, respectively, where **A** is the additive numerator relationship matrix among animals augmented by phantom genetic groups and **I** is an identity matrix. There were 61,888 animals in **A**. Genetic groups were formed on the basis of birth year of the animal with unknown parent and sex of the unknown parent to account for possible different genetic trend over years for the missing sires and dams. The additive genetic direct, dam, and residual effects were assumed correlated between traits.

A random dam effect was fitted in place of maternal additive genetic and permanent environment effects to create a more sparse system of equations, which reduced the virtual computer memory required, enabling the bivariate analyses.

The HY effect on BEG was fitted as random to allow estimation of its variance. The data structure with a large number of small HY groups (42% with six or less bulls) also favored treating HY as random. With respect to practical application, genetic evaluation of BEG would likely involve an even higher percentage of small HY groups, which would make fitting HY as a fixed effect unfeasible.

The models assumed for WG and BEG (excluding HY and D effects on BEG) were essentially the same as those used for these two traits in the genetic evaluations performed in Ontario (Sullivan et al., 1999).

Table 2 shows the distribution of number of sex by age classes, management groups, test groups, herd of origin by year classes, sires, calves, and bulls by breed and trait. All test groups had more than one breed represented in them and all test groups were genetically connected to another test group by, at least, one sire.

Univariate analysis of BEG, fitting both maternal genetic and permanent environmental effects separately, was also performed using the following model:

$$\begin{aligned} \text{BEG}_{ijkl} = & \sum_{n=1}^{14} \beta_{1n} \text{B}_{1in} + \sum_{n=1}^{14} \beta_{2n} \text{B}_{2jn} + T_k \\ & + \text{HY}_l + G_i + M_j + P_j + E_{ijkl} \end{aligned} \quad (4)$$

where β_{1n} , β_{2n} , B_{1in} , B_{2jn} , T_k , HY_l , G_i , and E_{ijkl} are as in (3); M_j is the random maternal additive effect of the j th dam; P_j is the random permanent environmental effect of the j th dam.

Random effects HY, G, M, P, and E, were assumed uncorrelated with each other, except for G and M. Covariance matrices of the effects were equal to $I\sigma_{\text{hy}}^2$, $A\sigma_{\text{g}}^2$, $A\sigma_{\text{m}}^2$, $I\sigma_{\text{p}}^2$, and $I\sigma_{\text{e}}^2$, respectively.

The univariate linear regressions used to estimate BEG (Eq. (1)) were fitted using PEST (Groeneveld, 1990). Variance component and breeding value estimates for WG and BEG were obtained using ASREML (Gilmour et al., 2000).

2.4. Alternative bivariate models

Two alternative bivariate models were also analyzed. Bivariate model two (B2) did not include effect of D in Eq. (3) of model B1 for BEG. Bivariate model three (B3) did not include effect of HY in Eq. (3) of model B1 for BEG. In both cases, the Eq. (2) for WG was not modified.

2.5. Model comparison and assessment of herd of origin by year effect

The alternative bivariate models were compared using comparison methods based on restricted likelihood function. They included likelihood ratio test (LRT) and two information criteria: Akaike's information criterion (AIC) and Bayesian information criterion (BIC) (Bozdogan, 2000; Myung, 2000). The criteria were calculated by:

$$\text{LRT} = -2 \log (\text{ML}_k / \text{ML}_f)$$

$$\text{AIC}_k = -2 \log (\text{ML}_k) + 2p_k$$

$$\text{BIC}_k = -2 \log (\text{ML}_k) + p_k \log (n - q)$$

where $\log (\text{ML}_k)$ is the natural logarithm of the restricted maximum likelihood function of model k , p_k is the number of unknown (co)variance parameters in the model k , q is the rank of incidence matrix for fixed effects (the same for all models), and n is the number of observations that contributes to the likelihood. ML_f is the restricted maximum likelihood of the full model B1.

Comparisons using likelihood ratio test tend to favor more complex models, while the information criteria try to adjust for the number of (co)variance components estimated, penalizing models with higher number of (co)variance components. BIC was designed to find the most probable model given the data, while AIC was designed to find a model that produces estimates of the density which is close, on average, to the true density function of the data (Wasserman, 2000). For $n - q$ greater than 8, BIC penalizes more the likelihood of models with higher number of unknown (co)variance components than does AIC.

2.6. Comparison of breeding values

Predicted breeding values for BEG from bivariate models with or without HY effect (B1 vs. B3) were compared using Spearman's rank correlations considering different proportions of selected animals, namely, all, the first and the last 20%, and the top 5% and 1% bulls, sires (sires of bulls + sires from pedigree), or sires of bulls. The selected proportion of animals was based on EBV from model B1. The coincidence of bulls and sires that would be selected by using B1 or B3 was also calculated for the best 1% best bulls and sires. Coincidence was obtained by listing the 1% best bulls/sires based on EBV from B1 and based on EBV from B3. The number of coincident bulls/sires in both lists was then counted.

3. Results

3.1. Maternal and herd of origin by year effects

Results of comparison among alternative bivariate models are given in Table 3. The importance of D effect on BEG was evaluated by comparing models B1 and B2. Model B1 was superior to B2 based on AIC, but inferior to B2 based on BIC. BIC penalizes the likelihood of models with a higher number of unknown (co)variance components more than AIC. The LRT for comparing B1 and B2 did not show strong evidence that B1 would be superior to B2

Table 3

Model comparison criteria and alternative bivariate models to analyze WG^a and BEG

Model ^b	Criterion ^c			P^d
	AIC	BIC	LRT	
B1	378,275	378,361	–	–
B2	378,283	378,252	5.93 ^e	5.20%
B3	378,358	378,418	44.34 ^f	0.00%

^a WG, pre-weaning weight gain; BEG, bull's estimated weight gain on station test.

^b B1, full model; B2, model without dam effect; B3, model without herd of origin by year effect.

^c AIC, Akaike's information criterion; BIC, Bayesian information criterion; LRT, likelihood ratio test.

^d Level of significance of the LRT.

^e LRT for B2 vs. B1.

^f LRT for B3 vs. B1.

($P=0.052$), despite the fact that LRT favors more complex models. Estimate of variance component ratio with respect to phenotypic variance for D effect, given by model B1, was small and not significantly different from zero (0.02 ; $P>0.05$). Therefore, the evidence indicates that the dam effect was not relevant for BEG.

All criteria indicated that the model including HY effects (B1 vs. B3) was superior. The likelihood ratio test comparing model B1 vs. B3 was highly significant ($P<0.001$), indicating an important improvement of model B1 over B3 after the inclusion of HY effect. Mantovani et al. (1999), analyzing 940 bulls for ADG in a central test station in Italy, also reported important effect of the herd of origin on all three breeds investigated (Chianina, Marchigiana, and Romagnola).

Estimates of variance ratios with respect to phenotypic variance and correlations given by bivariate models are presented in Table 4. Heritabilities of WG and BEG were 0.36 and 0.34, 0.36 and 0.35, and 0.36 and 0.41 for models B1, B2, and B3, respectively ($P<0.01$ for all). Heritability of BEG was higher for model B3 than B1, indicating that part of the HY effect was attributed to direct genetic effects in model B3.

The dam effect variance ratios for BEG, given by models B1 and B3, were 0.02 and 0.01 ($P>0.05$), respectively. The dam effect variance ratio for WG was 0.34 ($P<0.01$) for all models.

The contribution of HY effect to the total variance was 8% with models B1 and B2. Collins-Lusweti and Curran (1985), Tong et al. (1986), and Liu and Makarechian (1993) reported similar variation due to herd of origin on average daily gain (ADG) of bulls on test. Dinkel and Busch (1973) reported a similar contribution of herd of origin (ranch) to ADG of 679 centrally tested Hereford steers. Collins-Lusweti and Curran (1985) used a model without any genetic effect, while Tong et al. (1986) and Liu and Makarechian (1993) used a sire model to analyze the data. Tong et al. (1986) credited the herd by year variation mostly to breed of cow effect, but the average genetic effects of cows and real environmental differences (e.g. feed and management practices) were also discussed as possible reasons for herd by year effects. In the present study, breed and genetic direct effect of the cows were taken into account. The maternal genetic and permanent environment effects of the dams were accounted for through the D effect, although not optimally. Therefore, HY variation found in this study is more likely associated with real pre-weaning environmental effects than other sources of variation, such as genetic.

Schenkel et al. (2002), using random regression univariate analyses for BEG, found variation associated to HY around 8% from the beginning to the end of the test, demonstrating a permanent nature of this effect on BEG over the entire period.

Table 4

Estimated variance ratios with respect to phenotypic variance for additive direct (G), dam (genetic+permanent environment; D), weaning herd-year (HY), and residual (R) effects with corresponding S.E. (in brackets), using alternative bivariate models B1, B2, and B3^a for WG^b and BEG

Effect	Models					
	B1		B2		B3	
	WG	BEG	WG	BEG	WG	BEG
G	0.36 (0.02)	0.44 ^c (0.05) 0.34 (0.03)	0.36 (0.02)	0.45 (0.05) 0.35 (0.03)	0.36 (0.02)	0.44 (0.05) 0.41 (0.03)
D	0.34 (0.00)	0.12 (0.05) 0.02 (0.02)	0.34 (0.00)	– –	0.34 (0.00)	0.20 (0.20) 0.01 (0.02)
HY		0.08 (0.01)		0.08 (0.01)		–
R	0.30 (0.01)	0.03 (0.03) 0.56 (0.03)	0.30 (0.01)	0.03 (0.03) 0.56 (0.03)	0.30 (0.01)	0.02 (0.03) 0.58 (0.03)
σ_p^{2d}	945	744	945	745	945	713

^a B1, full model; B2, model without dam effect; B3, model without herd of origin by year effect.

^b WG, pre-weaning weight gain; BEG, bull's estimated weight gain on station test.

^c For G, D, and R, ratios are on the diagonal and correlation between traits are off diagonal.

^d Estimated phenotypic variance (kg^2).

The number of studies on herd of origin effect on ADG or weight gain on test is not abundant as it is for weights during the test, which are known to be much more affected by herd of origin effects than ADG or gain (e.g. Amal and Crow, 1987). There are several reports in the literature showing important proportion of the phenotypic variance (around 20–30%) due to herd of origin for end of test weights and yearling weights of bulls (e.g. Wilson et al., 1972; Collins-Lusweti and Curran, 1985; Amal and Crow, 1987).

Possible maternal additive genetic differences among HY groups were not accounted for in the bivariate model B1, because a joint genetic + permanent environmental dam effect was estimated (not making use of the additive genetic relationship among dams). To investigate if maternal genetic effects were confounded with HY effects, a univariate model for BEG was analyzed, fitting maternal genetic and permanent environmental effects separately (Eq. (4)). The variance components estimated, however, were very similar to those from B1 and B2 with HY still explaining 8% of the variation in BEG (Table 5). The maternal additive heritability was close to zero and permanent environmental variance ratio was low (2%) and not significantly different from zero ($P>0.05$). This was in agreement with the variance ratio found for the dam effect from the bivariate analyses (B1 and B3), indicating again that maternal effects are not of concern for evaluation of BEG.

This single trait analysis fitting additive maternal genetic and permanent environmental effects was not feasible for a full bivariate analysis. However, reasonable evidence is presented here, that the HY effect is environmental in nature and not due to detectable

maternal genetic and permanent environmental effects.

Estimates of heritability for weight gain on test obtained in this study from models with HY effect (from 0.34 to 0.35) are within the range reported in the literature for ADG of Canadian beef bulls tested in central evaluation stations (e.g. Tong, 1982; Tong et al., 1986; Amal and Crow, 1987; De Rose et al., 1988a; Liu and Makarechian, 1993), but less than that proposed as standard (0.43) for genetic improvement of Canadian beef cattle (AAFC, 1993). The estimate of 0.41 from model B3 was close to the proposed standard, but the inclusion of the HY effect reduced the estimate to 0.34 (Table 4).

Analyzing a larger data set (weight gains from 25,315 bulls, described in Section 2.1 of the present study), Schenkel et al. (2002) reported a higher heritability (0.38) for weight gain on test, using a univariate animal model including HY effect. However, this estimate was still lower than that proposed as standard for Canadian beef cattle, indicating that inclusion of HY effect in the evaluation model for BEG will require modification of the assumed heritability for BEG. Analyzing bulls for ADG in a central test station in Italy, Mantovani et al. (1999) also found diminution in the estimated heritability for two out of three breeds considered when herd of origin effect was included in the model.

Heritability of WG given by all analyses (0.36) was higher than those previously estimated by De Rose et al. (1988a) (0.25) and proposed as standard (0.30) for genetic improvement of Canadian beef cattle (AAFC, 1993). Nevertheless, the WG records used in the present study were only a fraction of the available WG records, which was of relevance for the investigation of HY effect on BEG.

Residual covariances between WG and BEG estimated by models B1, B2, and B3 (Table 4) were very small and not significantly different from zero ($P>0.05$). This suggests that there was no important compensatory gain during the station test, after the adjustment period of 28 days, for those bull calves that did not perform well to weaning on account of poor within-herd-year environmental conditions.

There was some evidence of pre-selection of bulls entering test stations. The average WG of tested bull calves was 19 kg higher than that of non-tested bull calves (227 ± 38 vs. 208 ± 44 kg), which corresponds

Table 5

Estimated ratios of variance components with respect to phenotypic variance for additive direct (G) and maternal (M), permanent environmental (P), weaning herd-year (HY), and residual (R) effects with corresponding S.E. (in brackets), using univariate model for BEG^a

Effects				
G	M	P	HY	R
0.35 (0.03)	0.00 (0.01)	0.02 (0.02)	0.08 (0.01)	0.54 (0.03)
-0.20 ^b (0.61)				

^a BEG, bull's estimated weight gain on station test.

^b Genetic correlation between direct and maternal effects.

to a differential of only 0.46 observed phenotypic S.D. This relatively weak pre-selection did not appear to contribute to the HY effect, because this effect accounted for 8% of the phenotypic variation of BEG in both the bivariate analyses (B1 and B2) and the univariate analysis (Eq. (4)).

3.2. Breeding values

Breeding values estimated by bivariate models B1 and B3 (including or not the HY effect) were compared on the basis of Spearman's rank correlations. Rank correlations between EBV for weight gain on test, given by models B1 and B3, were calculated for different selected groups of bulls and sires across test groups (Table 6). Considering all bulls with BEG, all sires (sires of bulls + sires from pedigree), and sires of bulls only, the overall rank correlation was very high (0.99, 0.98, and 1.00, respectively). However, when, for instance, the best 5% and 1% under model B1 were considered, rank correlations were much lower: 0.85 and 0.75 for bulls, 0.83 and 0.83 for all sires, and 0.83 and 0.81 for sires of bulls, respectively. These results indicate a re-ranking, especially among top bulls and sires. Among the 1% best bulls, 20% of selected bulls based on model with HY effect (B1) would not be selected based on model not accounting for HY (B3). Likewise for all sires and for sires of bulls, 11% and 14%, respectively, would not be selected. Evaluating performance of bulls in a central test station in Italy, Mantovani et al. (1999) found large changes in rank of bulls for ADG when models with or without herd of origin effect were compared (rank correlation of 0.49 on average for the three breeds analyzed). Contrarily to the current study, Mantovani et al. (1999) assumed herd of origin as a fixed effect in their analyses.

Results for WG (data not shown) indicated high rank correlation between EBV estimated by models B1 and B3, even among the top 1% bulls and sires ($r > 0.98$). Rank correlation of EBV for BEG between models B1 and B2 were very high, even among the top 1% bulls and sires ($r > 0.97$, data not shown), supporting that maternal effects are not of concern for genetic evaluation of bulls and sires for weight gain in station.

3.3. Herd of origin by sire interaction

Accuracy of breeding value estimation could be reduced by a common environmental covariance among sibs of the same sire. This could happen if, within herds, sibs of the same sire are preferentially treated or with seasonal use of sires, which is common when AI sires are used followed by natural mating. This common environmental covariance among sibs of the same sire would, in most respects, be equivalent to a sire by herd of origin interaction (Dimov et al., 1996).

As analyses of the weight gain on test presented here have shown, variation due to herd of origin by year is significant. It is therefore important to quantify the contribution of HY by sire interaction to the variation of BEG and determine if it is important to account for this interaction in evaluation models.

In the attempt to assess the existence of HY by sire interaction (HY×S), univariate analyses of BEG using Eq. (3) including a term for HY×S were performed with subsets from the data described in Table 1. The analyses performed, datasets used, as well as the results obtained are presented in Table 7. The three subsets varied regarding the minimum number of bulls in a HY×S group (half-sib family size), minimum

Table 6

Spearman's rank correlations between EBV of bulls and of sires for BEG^a, given by bivariate models with (B1) and without (B3) herd of origin by year effect

Animals (number)	Rank correlation					C ^b
	Overall	20% best	20% worst	5% best	1% best	
Bulls (10,927)	0.99	0.93	0.92	0.85	0.75	80%
All sires (6576)	0.98	0.91	0.84	0.83	0.83	89%
Sires of bulls (2191)	1.00	0.91	0.88	0.83	0.81	86%

^a BEG, bull's estimated weight gain on station test.

^b C, coincidence of bulls (or sires) among 1% best bulls (or sires) for BEG EBV given by models B1 and B3.

Table 7

Estimates of variance ratios with respect to phenotypic variance for herd–year (HY), herd–year by sire (HY×S), and additive genetic direct (G) effects on BEG^a and estimated genetic correlation (r_g) between average performance of half sibs of a sire coming from two different HY groups

Subset	Data structure ^b			# Obs. ^c	Variance ratio			r_g
	# Bulls	# Sires	# Hy		HY	HY×S	G	
Subset 1	≥2	≥2	≥2	7170	0.079	0.012	0.334	0.87
Subset 2	≥3	≥2	≥2	4627	0.137	0.017	0.292	0.81
Subset 3	≥4	≥1	≥2	5387	0.100	0.007	0.345	0.93

^a BEG, bull's estimated weight gain on station test.

^b Data structure: # bulls, minimum number of bulls in a HY×S group (half-sib family size); # sires, minimum number of sires in a HY group; # hy, minimum number of HY groups where a sire had progeny; # obs., number of bulls with BEG.

^c All three conditions were met for an observation to be included in the data subset.

number of sires in a HY group, and minimum number of HY groups where the sires had progeny. In the subsets, animals with breed composition from MA and GV were excluded due to small number of bulls tested.

Results show that HY×S interaction variance component amounted, on average, to only 15% of the variance that would be attributable to sire variance component. The estimated proportion of the total variance explained by HY×S interaction was, on average, 1.2% (Table 7). The expected genetic correlation (r_g) between average performance of half sibs of a sire coming from two different HY groups could be calculated by the intraclass correlation (t) given by:

$$r_g = t = \frac{1/4\sigma_a^2}{1/4\sigma_a^2 + \sigma_e} = \frac{h^2}{h^2 + 4c^2},$$

where $c^2 = \sigma_{\text{HY}\times\text{S}}^2 / \sigma_{\text{phen}}^2$.

σ_a^2 is the additive genetic variance and σ_e is the environmental covariance among paternal half sibs within HY groups, which would cause an observed HY×S interaction. Therefore c^2 values reflect the environmental covariance among paternal half sibs within HY groups as a proportion of the phenotypic variance (σ_{phen}^2).

Thus, for subset 1, for example, r_g was 0.334/(0.334 + 4(0.012)) = 0.87. Therefore, for the three subsets, the expected genetic correlation was on average 0.87. Genetic correlations smaller than 0.80 between performances in different environments are considered as evidence of possible important genotype by environment interaction (Robertson, 1959).

Therefore, results indicate that the interaction HY by sire is not a problem for the current genetic

evaluation of bulls tested in the central evaluation stations examined in this study, provided that HY is included in the genetic evaluation model.

4. Discussion

Central station tests are an aid to young sire selection. However, individual bull performance in central test stations seems to depend upon pre-weaning besides post-weaning genetic and environmental factors, which should be accounted for accordingly. The HY effect had substantial impact on the variation of the weight gain of bulls on test despite the 28 day-adjustment period. Other studies also indicated that herd of origin could contribute considerably to growth performance over the entire test (Tong et al., 1986; Amal and Crow, 1987; Liu and Makarechian, 1993; Schenkel et al., 2002).

For the particular data analyzed in the current investigation, enlargement of the adjustment period apparently would not reduce the HY effect. Schenkel et al. (2002), using a larger data set described in Section 2.1 of the present study, found that the contribution of HY effect on weight gain on test was quite constant (around 8%) over the entire period of test. They also found that the weight gain on the last 112 days of test and the gain on the entire 140-day test were similarly affected by HY effects.

The estimated residual correlation between WG and BEG was close to zero and not significant for models with and without HY effect. Several authors (e.g. Tong, 1982; Tong et al., 1986; De Rose et al., 1988a) have found moderate negative environmental correlations between pretest ADG and station-test

ADG (from -0.09 to -0.41). These negative environmental correlations previously reported suggested that bulls that did not perform well during the pre-weaning period within their herds of origin due to management-related limitations, compensate by gaining more during station test, especially at the beginning of the test, and that the adjustment period was not completely removing this source of variation. If real, this negative environmental correlation between these two growth phases would result in problems in the evaluation, ranking and selection of bulls from different herd backgrounds on the basis of performance in central stations. However, this does not seem to be the case with the dataset analyzed, possibly indicating that the adjustment period was effective in removing the variation resulting from compensatory gain. Another possibility is that the individual animal model used in the present study fit the data better and eliminated the estimated negative environmental correlation between pretest ADG and station-test ADG, which was found by previous investigations (for instance, [Tong et al. \(1986\)](#) and [De Rose et al. \(1988a\)](#) used a sire model and [Tong \(1982\)](#) used a model without genetic effects).

[De Rose et al. \(1988b\)](#) argued that the use of a two-trait evaluation model, incorporating the two correlated traits, ADG during pre-weaning period in herd of origin and ADG during station-test period, would account for pretest environmental carry-over and pretest selection of bull calves. Bivariate and univariate analyses of BEG in the present study, however, yielded similar estimates of the contribution of HY to the phenotypic variance, indicating that, if existent, preselection did not contribute to the HY effect found.

The inclusion of HY in models for evaluating growth of station-tested bulls would account for the across-herd–year aspect of pretest environmental influences and minimize the possible interaction between HY and sire. With HY effect in the evaluation models, the interaction HY by sire was small and not of concern.

5. Conclusions

Herd of origin by year effect accounts for a substantial amount of the variation of the gain of station-tested beef bulls in Ontario, despite the 28-day adjustment period observed. Bivariate analysis, in-

cluding weaning weight gain, does not remove the herd of origin carry-over effect on the gain of bulls in station. Genetic evaluation of gain of station-tested beef bulls should account for herd of origin by year effect in bivariate analysis with growth to weaning. This more complete model will control this environmental source of variation, which can cause re-ranking of bulls and sires.

Further investigations on herd of origin effect on bull performance in central evaluation stations are warranted.

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