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Genotype by environment interaction in response to cold stress in a composite beef cattle breed

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*Extreme weather conditions such as cold stress influence the productivity and survivability of beef cattle raised on pasture. The objective of this study was to identify and evaluate the extent of the impact of genotype by environment interaction due to cold stress on birth weight (**BW**) and weaning weight (**WW**) in a composite beef cattle population. The effect of cold stress was modelled as the accumulation of total cold load (**TCL**) calculated using the Comprehensive Climate Index units, considering three TCL classes defined based on temperature: less than −5°C (**TCL5**), −15°C (**TCL15**) and −25°C (**TCL25**). A total of 4221 and 4217 records for BW and WW, respectively, were used from a composite beef cattle population (50% Red Angus, 25% Charolais and 25% Tarentaise) between 2002 and 2015. For both BW and WW, a univariate model (ignoring cold stress) and a reaction norm model were implemented. As cold load increased, the direct heritability slightly increased in both BW and WW for TCL5 class; however, this heritability remained consistent across the cold load of TCL25 class. In contrast, the maternal heritability of BW was constant with cold load increase in all TCL classes, although a slight increase of maternal heritability was observed for TCL5 and TCL15. The direct and maternal genetic correlation for BW and maternal genetic correlation for WW across different cold loads between all TCL classes were high ($r > 0.99$), whereas the lowest direct genetic correlations observed for WW were 0.88 for TCL5 and 0.85 for TCL15. The Spearman rank correlation between the estimated breeding value of top bulls ($n = 79$) using univariate and reaction norm models across TCL classes showed some re-ranking in direct and maternal effects for both BW and WW particularly for TCL5 and TCL15. In general, cold stress did not have a big impact on direct and maternal genetic effects of BW and WW.*

Keywords: bovine, reaction norm, cold load, birth weight, weaning weight

Implications

Cold stress negatively impacts the productivity of beef cattle production. The effect of cold stress on the genetic merit of beef cattle has not been explored. The results of this study showed evidence of the existence of genotype by environment interaction due to cold stress on birth weight and weaning weight in a composite beef cattle population.

Introduction

Cold stress has been reported to negatively impact the productivity and the survivability of beef cattle, especially in the Northern Great Plains region (Hoelscher, 2001; Mader, 2003). Phenotypes are the product of the joint effects of the animal genetic makeup, the environment and their potential interactions. Thus, beef cattle genetic evaluation programmes should account for genotype by environment interaction (**G × E**). Ignoring G × E can alter estimates of the model parameters (Mattar *et al.*, 2011; Pfeiffer *et al.*, 2016) and could lead to biased estimated breeding values (**EBVs**) and re-ranking of animals with negative effects in selection response (Streit *et al.*, 2012).

A common approach to evaluate G × E is using reaction norm models (Haile-Mariam *et al.*, 2008; Hayes *et al.*, 2009; Lillehammer *et al.*, 2009; Hammami *et al.*, 2015). These models postulate random regression functions to express quantities of interest (e.g. additive genetic effect). The slope of the reaction norm model provides a measure of the phenotypic plasticity differences among animals, which allows the

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ranking of animals from more (plastic genotype) to less (robust genotype) sensitive (De Jong, 1990; Falconer, 1990).

Most studies in the literature on cold tolerance or adaptation are in the field of evolutionary biology using model organisms (Karan and David, 2000; Ayrinhac *et al.*, 2004; Klepsatel *et al.*, 2013). Contrary to the extensive literature in the study of heat stress and its effects on livestock species (Bohmanova *et al.*, 2008; Haile-Mariam *et al.*, 2008; Zumbach *et al.*, 2008; Brügemann *et al.*, 2011; Menéndez-Buxadera *et al.*, 2012, 2014; Hammami *et al.*, 2015; Fragomeni *et al.*, 2016), no study, to the best of our knowledge, has investigated the genetic basis of cold stress and its effects on growth traits in beef cattle. The objective of this study was to evaluate the existence and extent of genotype by environment interaction effects due to cold stress on growth traits in a composite beef cattle population using reaction norm models.

Material and methods

Phenotypic data

Data used in this study were collected from a composite beef cattle herd referred to as composite gene combination (50% Red Angus, 25% Charolais and 25% Tarentaise) between 2002 and 2015 at USDA-ARS, Fort Keogh Livestock and Range Research Laboratory (**LARRL**), Miles City, MT situated at 46° 22′ N latitude and 105° 52′ W longitude. The purpose of this composite beef cattle population was to produce animals with better adaptation and productivity under the harsh climatic conditions of the region. Detailed information about the establishment and management of this population can be found in Newman *et al.* (1993a) and Roberts *et al.* (2016). The growth-related traits analysed in this study were birth weight (**BW**) and weaning weight (**WW**). The pedigree consisted of 6620 offspring (2732 males and 3888 females) of 174 bulls and 1908 dams born between 1990 and 2017. The average number of paternal sibship was 32.78 (range: 1 to 121) and maternal sibship was 3.26 (range: 1 to 10). The average pedigree depth, measured by the sum of known ancestors over traced generations (equivalent complete generations), was 2.41 generations with a maximum of five and a half generations. A summary description of the data and population structure is presented in Table 1.

Climate data

In order to evaluate the effect of cold stress on growth traits, historical weather data were downloaded from the National Solar Radiation Database (Sengupta *et al.*, 2018). All the required weather variables including temperature (**T**, °C), relative humidity (**RH**, %), wind speed (**WS**, m/s) and solar radiation (**SR**, W/m^2) were collected for every half hour from the weather station located near the Miles City Municipal Airport, situated at 46°41′ N latitude and 105°90′ W longitude. This weather station is less than 15 km away from LARRL where the phenotypic data were collected. Different indices such as Temperature Humidity Index (Thom, 1959), Black Globe-Humidity Index (Buffington *et al.*, 1981), Equivalent Temperature Index (Baeta *et al.*, 1987), Heat Load Index (Gaughan *et al.*, 2008) and Index of Thermal Stress for Cows (Da Silva *et al.*, 2015) have been developed to assess the risk of thermal stress on livestock. The Comprehensive Climate Index (**CCI**) proposed by Mader *et al.* (2010) was selected for this study, since this index assesses thermal stress due to hot (45°C) and cold (−30°C) conditions. In addition, Mader *et al.* (2010) indicated that the CCI thresholds for cold stress depend on the susceptibility of the animal and reflect the stress level based on environmental conditions, management and physiological status.

The following equation proposed by Mader *et al.* (2010) was used to calculate the CCI:

$$\mathrm{CCI} = T + \mathrm{RH}_c + \mathrm{WS}_c + \mathrm{SR}_c \tag{1}$$

where RH_c, WS_c and SR_c are the correction factors to RH, WS and SR, respectively, and are given by the following equations:

$$\begin{aligned}\mathrm{RH}_c = {} & e^{\left(0.00182\times\mathrm{RH}+1.8\times10^{-5}\times T\times\mathrm{RH}\right)} \\ & \times\left(0.000054\times T^2+0.00192\times T-0.0246\right) \\ & \times\left(\mathrm{RH}-30\right)\end{aligned} \tag{2}$$

$$\begin{aligned}\mathrm{WS}_c = {} & \left[\frac{-6.56}{e^{\left(\frac{1}{(2.26\times\mathrm{WS}+0.23)^{0.45\times\left(2.9+1.14\times10^{-6}\times\mathrm{WS}^{2.5}-\log_{0.3}(2.26\times\mathrm{WS}+0.33)^{-2}\right)}}\right)}}\right] \\ & -0.00566\times\mathrm{WS}^2+3.33\end{aligned} \tag{3}$$

$$\begin{aligned}\mathrm{SR}_c = {} & 0.0076\times\mathrm{SR}-0.00002\times\mathrm{SR}\times T+0.00005\times T^2 \\ & \times\sqrt{\mathrm{SR}}+0.1\times T-2\end{aligned} \tag{4}$$

Once the CCI was computed for every half hour from the weather data, a daily cold load score (**CL**) was calculated as:

$$\mathrm{CL} = \sum_{i=1}^{48}\max\left(0, \mathrm{CCI}_T-\mathrm{CCI}_i\right) \tag{5}$$

in which CCI_i is the cold load score for the half hour i, CCI_T is the CCI threshold for the onset of cold stress and CL is the daily cold stress load. The CL score measures the daily sum of cold stress exposure (CCI below the threshold) of an animal. Based on the arbitrary definition of CCI thresholds for the onset of cold stress defined by Mader *et al.* (2010), a set of thresholds derived for beef cattle acclimated to outdoor environment were chosen for animals with lower susceptibility. Specifically, three CCI thresholds for the onset of cold stress ($\mathrm{CCI}_T = -5°\mathrm{C} \rightarrow$ mild cold stress (**TCL5**); $\mathrm{CCI}_T = -15°\mathrm{C} \rightarrow$ moderate cold stress (**TCL15**) and $\mathrm{CCI}_T = -25°\mathrm{C} \rightarrow$ severe cold stress (**TCL25**)) were used

Table 1 *Summary statistics of pedigree, data and different cold load classes (TCL5, TCL15 and TCL25)[1] used in the analysis of genotype by environment interaction in growth traits of a composite beef cattle population*

	Growth traits	
Item	Birth weight	Weaning weight
Pedigree structure		
Animals (*n*)	6620	
Bulls (*n*)	174	
Dams (*n*)	1908	
Founders (*n*)	397	
Animals with records (*n*)	4221	4217
Bulls with progeny records (*n*)	147	147
Dams with progeny records (*n*)	1461	1460
Data structure		
Contemporary groups (CGs; *n*)	386	
Average records per CG	10.93	
Range of records per CG (*n*)	5 to 34	
Mean (SD) of trait (kg)	35.19 (5.63)	209.83 (32.37)
Range of trait (kg)	17.27 to 63.50	110.22 to 318.42
Cold load structure		
Mean (SD) of TCL5	754.10 (162.30)	
Range of TCL5	514.99 to 1090.89	
Mean (SD) of TCL5 exposure (days)	161.78 (12.30)	
Range of TCL5 exposure (days)	126 to 204	
Mean (SD) of TCL15	151.96 (67.51)	
Range of TCL15	59.51 to 296.23	
Mean (SD) of TCL15 exposure (days)	53.17 (14.62)	
Range of TCL15 exposure (days)	28 to 79	
Mean (SD) of TCL25	8.60 (6.98)	
Range of TCL25	0.42 to 24.79	
Mean (SD) of TCL25 exposure (days)	7.69 (4.25)	
Range of TCL25 exposure (days)	2 to 17	

TCL = total cold load.

[1] TCL5: mild cold stress (onset of cold stress when climate index is less than −5°C), TCL15: moderate cold stress (onset of cold stress when climate index is less than −15°C) and TCL25: severe cold stress (onset of cold stress when climate index is less than −25°C).

in this study. The total cold stress load during a year (TCL) was defined as the summation of CL between the first of September and the birth date of the animal (March through April). The TCL score is specific to each animal due to variation in the onset of cold stress across years, date of conception and gestation length. However, animals with the same birth date will have the same TCL score. A summary description of different TCL classes is presented in Table 1.

Statistical models

Univariate animal model

For comparison purposes, a classical univariate mixed animal model that ignores cold stress was used to estimate direct and maternal EBV for BW and WW data:

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Zu} + \boldsymbol{Wm} + \boldsymbol{e} \qquad (6)$$

where $\boldsymbol{y}$ is the vector of BW or WW phenotypes, $\boldsymbol{\beta}$ is the vector of fixed effects including the contemporary groups (**CGs**), and BW and age at weaning weight (**AW**) as covariates (only for WW), $\boldsymbol{u}$ is the vector of direct genetic effects, $\boldsymbol{m}$ is the vector of maternal genetic effects and $\boldsymbol{e}$ is the vector of random residuals. $\boldsymbol{X}$, $\boldsymbol{Z}$ and $\boldsymbol{W}$ are known incidence matrices that link the records to fixed, direct genetic and maternal genetic effects, respectively. Additionally, it was assumed that $\boldsymbol{u} \sim \boldsymbol{N}(\boldsymbol{0}, \boldsymbol{A}\sigma_u^2)$ and $\boldsymbol{m} \sim \boldsymbol{N}(\boldsymbol{0}, \boldsymbol{A}\sigma_m^2)$, where $\boldsymbol{A}$ is the average additive relationship matrix, σ_u^2 is the direct genetic variance and σ_m^2 is the maternal genetic variance. The maternal permanent environment effect was not included for both BW and WW models due to the small number of progenies per dam. The CGs for BW and WW were constructed based on year of birth (14 levels), sex (2 levels), age of dam subclass (2 years = 1; 3 years = 2; 4 years = 3 and greater than 5 years = 4), animal's diet treatment (5 levels) and dam's diet treatment (5 levels). Calves were weaned at an average (SD) age of 185.49 (17.18) days and weaning was from September to October. A total of 386 CGs with at least 5 animals were kept for the analysis of 4221 and 4217 phenotypes for BW and WW, respectively.

Reaction norm model

To model the response of each genotype for growth-related traits to the change in the environment due to cold stress, a random regression model was implemented using each onset threshold value for calculating total cold stress load (TCL5, TCL15 and TCL25) and to provide the environmental gradient (**EG**) with respect to each onset threshold. This model is described as follows:

$$y_{ijkl} = \mathrm{CG}_i + b_1\mathrm{BW}_l + b_2\mathrm{AW}_l + \sum_{j=0}^{1} f_j\mathrm{EG}_{jl} + \sum_{j=0}^{1} d_{jl}\mathrm{EG}_{jl} + \sum_{j=0}^{1} m_{jk}\mathrm{EG}_{jl} + e_{ijkl}$$

where y_{ijkl} is the growth-related phenotype of animal l within CG_i, f_j is the fixed regression coefficient j $(j = 0, 1)$ of the trait on cold stress load for animal l, EG_{jl} $(\mathrm{EG}_{0l} = 1$ and $\mathrm{EG}_{1l} = \mathrm{TCL}_l)$; d_{jl} and m_{jk} $(j = 0, 1)$ are the random genetic intercept and slope for the l^{th} animal direct and k^{th} maternal effects, respectively and e_{ijkl} is the random residual effect assuming homogeneous variances. b_1 and b_2 are fixed regressions on BW and AW used only for the analysis of WW. The following covariance structure was assumed for the different random effects in the reaction norm model for trait $(t = \mathrm{BW}, \mathrm{WW})$:

$$\mathrm{var}\begin{bmatrix}\boldsymbol{d}\\ \boldsymbol{m}\\ \boldsymbol{e}\end{bmatrix} = \begin{bmatrix}\boldsymbol{G}_{\boldsymbol{d},\boldsymbol{t}}\otimes A & 0 & 0\\ 0 & \boldsymbol{G}_{\boldsymbol{m},\boldsymbol{t}}\otimes A & 0\\ 0 & 0 & \boldsymbol{R}_{\boldsymbol{t}}\end{bmatrix}$$

with

$$\boldsymbol{G}_{\boldsymbol{d},\boldsymbol{t}} = \begin{bmatrix}\sigma^2_{intd} & \sigma_{intd.Sd}\\ \sigma_{intd.Sd} & \sigma^2_{Sd}\end{bmatrix} \text{ and } \qquad \boldsymbol{G}_{\boldsymbol{m},\boldsymbol{t}} = \begin{bmatrix}\sigma^2_{intm} & \sigma_{intm.Sm}\\ \sigma_{intm.Sm} & \sigma^2_{Sm}\end{bmatrix} \tag{7}$$

where $\boldsymbol{G}_{\boldsymbol{d},\boldsymbol{t}}$ and $\boldsymbol{G}_{\boldsymbol{m},\boldsymbol{t}}$ are 2×2 matrices of genetic covariances between the intercept (int) and slope (S) for the direct and maternal effects for trait $\boldsymbol{t}$, respectively. Thus, σ^2_{intd} and σ^2_{intm} are the direct and maternal variances for the intercept. Similarly, σ^2_{Sd} and σ^2_{Sm} are the genetic variances for the slope. The off-diagonal elements of $\boldsymbol{G}_{\boldsymbol{d},\boldsymbol{t}}$ and $\boldsymbol{G}_{\boldsymbol{m},\boldsymbol{t}}$ are the corresponding covariances between the intercept and slope terms for the direct $(\sigma_{intd.Sd})$ and maternal $(\sigma_{intm.Sm})$ effects for trait $\boldsymbol{t}$. $\boldsymbol{A}$ is the average relationship matrix, and $\boldsymbol{R}_{\boldsymbol{t}} = \boldsymbol{I}\boldsymbol{\sigma}^2_{\boldsymbol{e},\boldsymbol{t}}$ is the residual covariance matrix for trait $\boldsymbol{t}$. The covariances between direct and maternal genetic effects were assumed equal to zero. The average-information REML algorithm as implemented in BLUPf90 family programme was used for the univariate analysis of standard and reaction norm models (Misztal *et al.*, 2016).

Genetic parameters and phenotypic plasticity via reaction norm

The direct and maternal genetic variances for trait $\boldsymbol{t}$ $(t = \mathrm{BW}, \mathrm{WW})$ at a specific cold load score (EG) can be estimated as:

$$\boldsymbol{\sigma}^2_{\boldsymbol{d},\boldsymbol{t}}|\mathbf{EG} = \boldsymbol{x}'_{\boldsymbol{EG}}\hat{\boldsymbol{G}}_{\boldsymbol{d},\boldsymbol{t}}\boldsymbol{x}_{\mathbf{EG}}$$

$$\boldsymbol{\sigma}^2_{\boldsymbol{m},\boldsymbol{t}}|\mathbf{EG} = \boldsymbol{x}'_{\boldsymbol{EG}}\hat{\boldsymbol{G}}_{\boldsymbol{m},\boldsymbol{t}}\boldsymbol{x}_{\mathbf{EG}}$$

where EG is a specific cold stress load score, $\boldsymbol{x}_{\mathrm{EG}} = [1\ \mathrm{EG}]'$ and $\hat{\boldsymbol{G}}_{\boldsymbol{d},\boldsymbol{t}}$ and $\hat{\boldsymbol{G}}_{\boldsymbol{m},\boldsymbol{t}}$ are estimates of matrices presented in equation (7).

The direct $(\boldsymbol{h}^2_{\boldsymbol{d},\boldsymbol{t}})$ and maternal $\left(\boldsymbol{h}^2_{\boldsymbol{m},\boldsymbol{t}}\right)$ heritabilities at a specific cold stress load for trait $\boldsymbol{t}$ can be obtained as:

$$\boldsymbol{h}^2_{\boldsymbol{d},\boldsymbol{t}} = \boldsymbol{\sigma}^2_{\boldsymbol{d},\boldsymbol{t}}/(\boldsymbol{\sigma}^2_{\boldsymbol{d},\boldsymbol{t}} + \boldsymbol{\sigma}^2_{\boldsymbol{m},\boldsymbol{t}} + \boldsymbol{\sigma}^2_{\boldsymbol{e},\boldsymbol{t}})$$

$$\boldsymbol{h}^2_{\boldsymbol{m},\boldsymbol{t}} = \boldsymbol{\sigma}^2_{\boldsymbol{m},\boldsymbol{t}}/(\boldsymbol{\sigma}^2_{\boldsymbol{d},\boldsymbol{t}} + \boldsymbol{\sigma}^2_{\boldsymbol{m},\boldsymbol{t}} + \boldsymbol{\sigma}^2_{\boldsymbol{e},\boldsymbol{t}})$$

Similarly, direct and maternal genetic covariances for trait $\boldsymbol{t}$ at two specific cold loads (EG1 andEG2) can be obtained as:

$$\boldsymbol{\sigma}_{\boldsymbol{d},\boldsymbol{t}}|\mathrm{EG1},\ \mathrm{EG2} = \boldsymbol{x}'_{\mathbf{EG1}}\hat{\boldsymbol{G}}_{\boldsymbol{d},\boldsymbol{t}}\boldsymbol{x}_{\mathbf{EG2}}$$

$$\boldsymbol{\sigma}_{\boldsymbol{m},\boldsymbol{t}}|\mathrm{EG1},\ \mathrm{EG2} = \boldsymbol{x}'_{\mathbf{EG1}}\hat{\boldsymbol{G}}_{\boldsymbol{m},\boldsymbol{t}}\boldsymbol{x}_{\mathbf{EG2}}$$

where $\boldsymbol{\sigma}_{\boldsymbol{d},\boldsymbol{t}}$ and $\boldsymbol{\sigma}_{\boldsymbol{m},\boldsymbol{t}}$ are the direct and maternal genetic covariances for growth trait $\boldsymbol{t}$ at specific cold stress loads EG1 and EG2, $\boldsymbol{x}_{\boldsymbol{EG1}} = [1\ \mathrm{EG1}]'$ and $\boldsymbol{x}_{\boldsymbol{EG2}} = [1\ \mathrm{EG2}]'$. The direct and maternal correlations could be easily obtained by dividing the covariances by the square root of the product of the corresponding genetic variances at cold stress loads EG1 and EG2.

The estimated direct $(\boldsymbol{u}_{\boldsymbol{i},\boldsymbol{t}})$ and maternal $(\boldsymbol{m}_{\boldsymbol{i},\boldsymbol{t}})$ genetic effects for animal $\boldsymbol{i}$ and trait $\boldsymbol{t}$ at a specific cold load (EG) are also easy to obtain using the following equations:

$$\boldsymbol{u}_{\boldsymbol{i},\boldsymbol{t}}|\mathrm{EG} = \hat{d}_{0i} + \left(\hat{d}_{1i} \times \mathrm{EG}\right)$$

$$\boldsymbol{m}_{\boldsymbol{i},\boldsymbol{t}}|\mathrm{EG} = \hat{m}_{0i} + (\hat{m}_{1i} \times \mathrm{EG})$$

where $\hat{d}_{0i}$, $\hat{d}_{1i}$, $\hat{m}_{0i}$, $\hat{m}_{1i}$ are the estimated intercept and slope for the direct and maternal effects, respectively, for animal $\boldsymbol{i}$ and trait $\boldsymbol{t}$. After computation of breeding values using the reaction norm model, bulls with at least 20 offspring were selected to compare the ranking between models using Spearman rank correlations.

One of the features of reaction norm models suggested by Falconer (1990) is the ability to assess the environmental sensitivity or phenotypic plasticity using the estimates of the slope. Following Mattar *et al.* (2011), animal sensitivity to cold stress could be classified into three classes, robust genotype $(|S_i| < \sigma_S)$, plastic genotype $(\sigma_S \leq |S_i| < 2\sigma_S)$ and extremely plastic genotypes ($|S_i| \geq 2\sigma_S$), where S_i is the slope estimate for animal ***i*** and σ_S is the SD of slopes.

Results and discussion

Estimates of direct and maternal heritabilities (SE) using standard univariate model were 0.46 (0.04) and 0.06 (0.02) for BW and 0.12 (0.03) and 0.34 (0.02) for WW, respectively. Estimate of direct heritability for BW was in line with the results reported by Mujibi and Crews Jr (2009), MacNeil (2003) and Cortés-Lacruz *et al.* (2017). The maternal heritability was, in general, slightly lower than estimates (0.08 to 0.14) reported in the literature (MacNeil, 2003; Eriksson *et al.*, 2004; Mujibi and Crews Jr, 2009) but was higher than the 0.005 obtained by Cortés-Lacruz *et al.* (2017). The results of direct and maternal heritabilities for WW were not in concordance with the reported estimates in the literature (MacNeil, 2005; Costa *et al.*, 2011). Our heritability estimates for WW showed larger maternal heritability compared to direct heritability which are similar to those reported by Koch *et al.* (1994) and Splan *et al.* (2002).

Figures 1 and 2 show the estimates of direct and maternal heritabilities as a function of cold stress using reaction norm models for the BW and WW, respectively. When the onset of cold stress was set at −25°C (TCL25), there was little to no variation in the estimated heritability of BW as a function of cold stress load (Figure 1c), and it was very similar to the estimate (0.46) obtained using the classical univariate model. This is likely due to the limited variation in cold stress load (0 to 20) between animals using TCL25. However, using −5°C as a threshold for the onset of cold stress for TCL5 class, the estimates of direct heritability increased with the increase in cold stress load (range of top 75th percentile: 0.48 to 0.52)

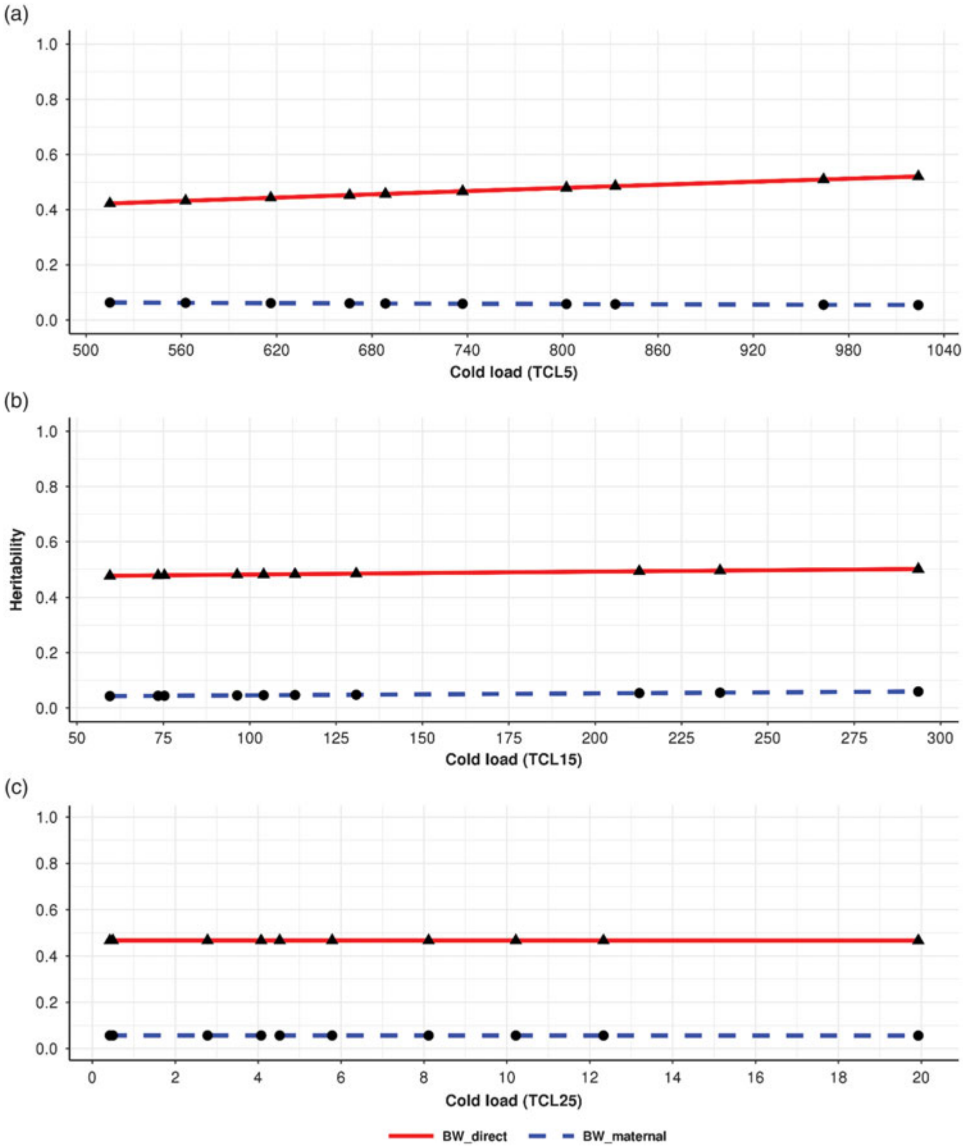

Figure 1 Estimates of direct (red solid line) and maternal (blue dashed line) heritabilities for birth weight (BW) using reaction norm model across different classes of the total cold load with thresholds of less than −5°C (TCL5) (a), −15°C (TCL15) (b) and −25°C (TCL25) (c) in a composite beef cattle population.

as indicated in Figure 1a. A similar trend was observed using TCL15 (cold stress onset at −15°C), although with smaller variation (Figure 1b) compared to the TCL5 class (range of top 50th percentile: 0.48 to 0.50). Maternal heritability for BW using reaction norm model was similar to the estimate obtained using the classical univariate model, except for the TCL15 class. For the latter, estimated maternal heritability was slightly lower than the univariate model estimate (Figure 1). Under both models, direct genetic variance was higher than the maternal counterpart, implying that BW is controlled more by calf genetics than its dam's genetics (Trus and Wilton, 1988). Several studies have shown the influence of uterine environment on the embryo and provided evidence for the existence of developmental programming in prenatal environment where the placenta plays a central role in regulating foetal growth and development (Reynolds et al., 2010; Fowden et al., 2011). However, these changes could be of epigenetic nature and may not be quantified by simple quantitative genetic models.

Estimates of direct heritability of WW were similar for the classical univariate model and the reaction norm approach under the TCL25 class (0.12). However, the reaction norm direct heritability for WW using TCL5 (range of top 25th percentile: 0.13 to 0.18) and TCL15 (range of top 5th percentile: 0.13 to 0.17) was slightly larger than using the classical univariate model (0.12) as indicated in Figure 2. Similar trend was observed for the maternal heritability of WW and the reaction norm estimates under the TCL5 (range of top 60th percentile: 0.33 to 0.37) and TCL15 (range of top 75th percentile: 0.33 to 0.40) classes were larger than their counterpart using the classical univariate model (0.33) as shown in Figure 2. In contrast to BW, surprisingly the

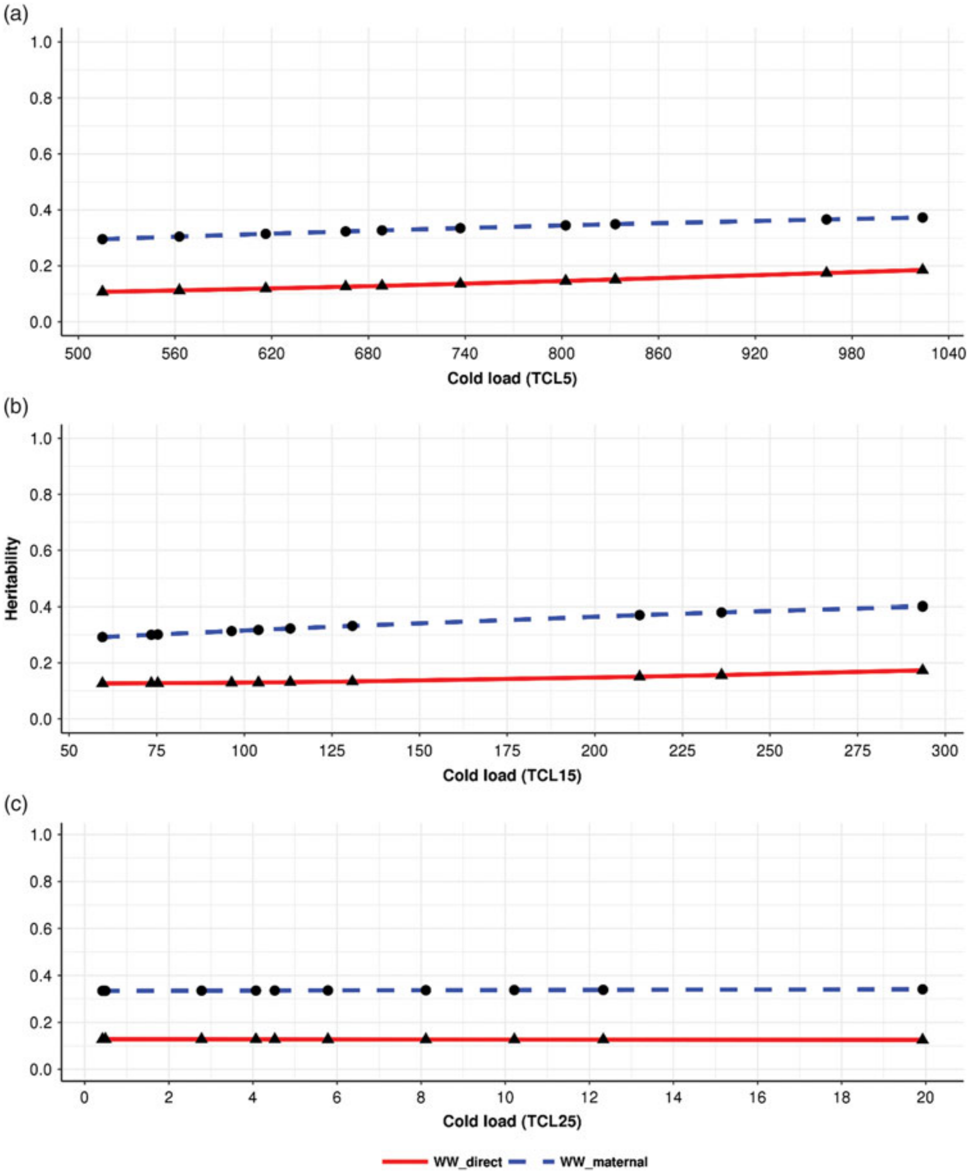

Figure 2 Estimates of direct (red solid line) and maternal (blue dashed line) heritabilities for weaning weight (WW) using reaction norm model across different classes of the total cold load with thresholds of less than −5°C (TCL5) (a), −15°C (TCL15) (b) and −25°C (TCL25) (c) in a composite beef cattle population.

estimates of maternal heritability using either the classical univariate or reaction norm models for WW were larger than the direct heritability indicating the importance of maternal genetic effect in WW of calves. This effect for WW is involved in the milking ability of the dam and its capability to provide a suitable environment for its newborn offspring until weaning (Drewry *et al.*, 1959; Baker, 1980). In other words, the maternal genetic effect of WW is related to gestational cold stress affecting the dam's ability to raise a calf.

Differences in EG of total cold stress load calculated under each of the three threshold values reflected the differences in total time animals experienced cold below the threshold. As would be expected, calculated total cold stress load increased as threshold for classification was relaxed (higher temperature). The number of records and average BW and WW as a function of cold stress load using three cutoff thresholds for the onset of cold stress (TCL5, TCL15 and TCL25) are shown in Supplementary Material Figures S1 and S2. There is no clear phenotypic trend on averages of BW and WW as a function of the cold stress load across the three TCL classes. However, there seems to be a slight upward trajectory for WW as a function of cold stress load (Supplementary Material Figure S2).

Figures 3 and 4 represent the heat maps for direct (upper diagonal) and maternal (lower diagonal) genetic correlations, at different cold stress onset thresholds, using reaction norm models for BW and WW, respectively. The direct and maternal genetic correlations for BW were high (0.99) across the three TCL classes. This high correlation was expected given the lack of significant cold stress impact on BW direct and maternal effects. On the other hand, the direct genetic correlation for WW ranged between 0.88 (35th percentile) and 0.97 (75th percentile) for TCL5 class (Figure 4a). For the TCL15 class, the direct genetic correlation was equal to 0.84 and 0.97 for the 65th and 75th percentile (Figure 4b). However, the maternal genetic correlations between different cold loads across the three TCL classes were high (>0.99) indicating no significant change in maternal genetic effects due to cold stress. Similarly, Bradford *et al.* (2016) reported strong maternal genetic correlations (>0.85) for WW across heat loads in Angus in the Upper South regions. Contrarily, Santana *et al.* (2016) reported weaker direct and maternal genetic correlations in extreme heat stress conditions for WW in Nelore, Brangus and Tropical Composite populations. Furthermore, the latter study reported strong direct and maternal genetic correlations (>0.80) in intermediate heat stress conditions for WW in Nelore and Brangus populations.

Spearman rank correlations between direct and maternal EBV for top bulls with at least 20 offspring obtained using the classical univariate and reaction norm models for BW and WW are presented in Table 2. In general, high rank correlations for direct (0.97 to 0.99 for BW; 0.96 to 0.99 for WW) and maternal (0.94 to 0.99 for BW; 0.98 to 0.99 for WW) effects were observed. However, limited re-ranking of bulls is likely between the classical univariate and reaction norm models

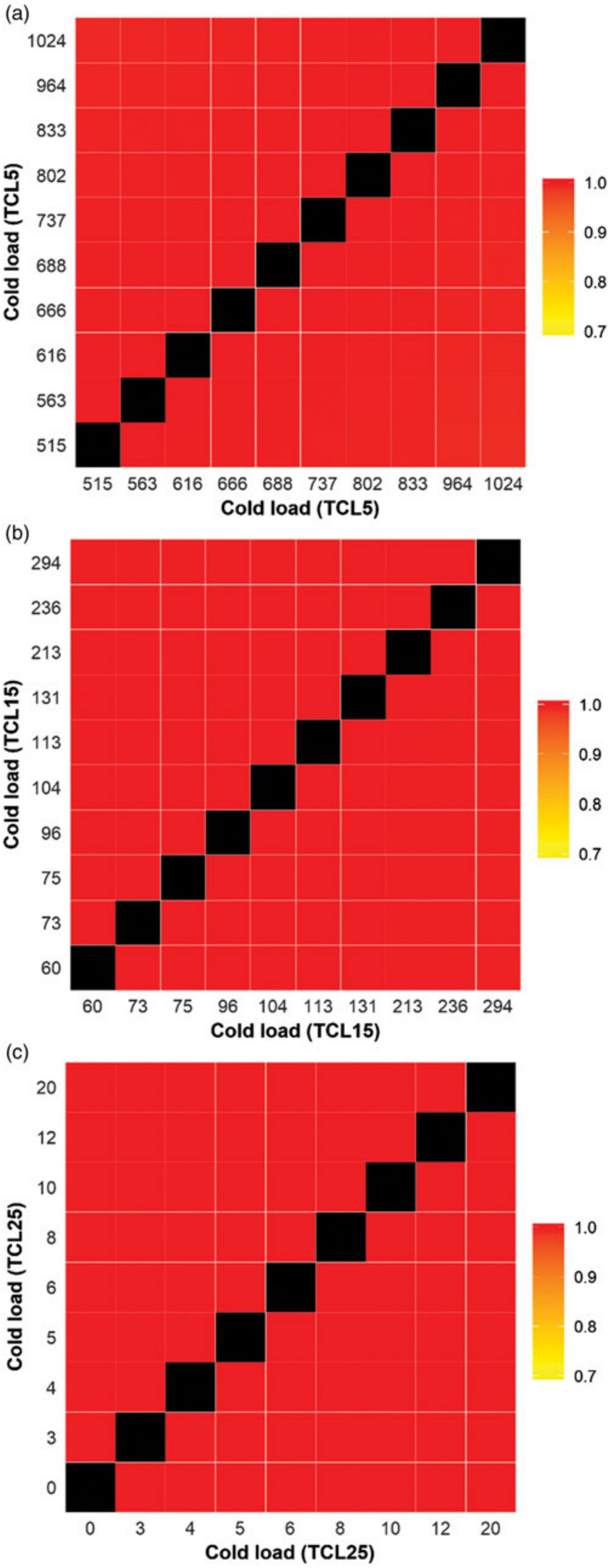

Figure 3 Heat map of direct (above diagonal) and maternal (below diagonal) genetic correlations for birth weight using reaction norm model for different classes of the total cold load with thresholds of less than −5°C (TCL5) (a), less than −15°C (TCL15) (b) and less than −25°C (TCL25) (c) in a composite beef cattle population.

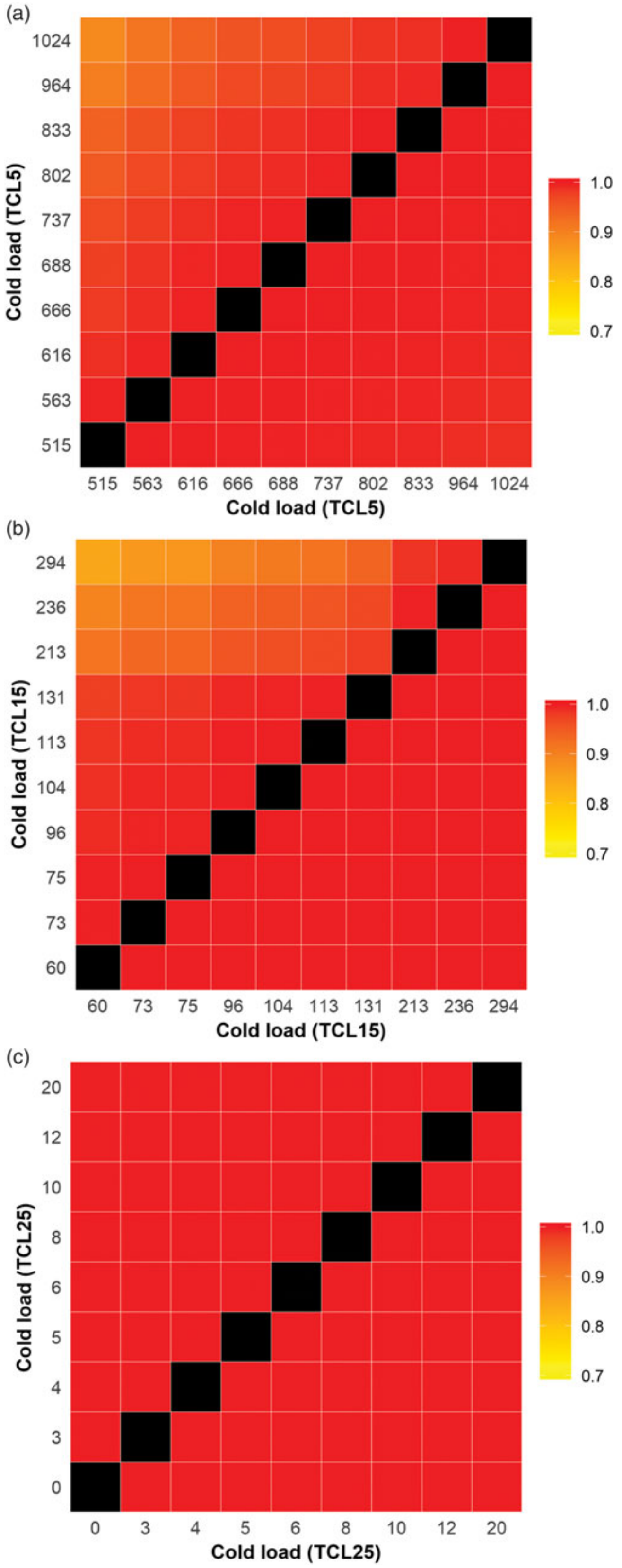

Figure 4 Heat map of direct (above diagonal) and maternal (below diagonal) genetic correlations for weaning weight using reaction norm model under different classes of the total cold load with thresholds of less than −5°C (TCL5) (a), less than −15°C (TCL15) (b) and less than −25°C (TCL25) (c) in a composite beef cattle population.

under TCL5 and TCL15 classes. Bradford *et al.* (2016) reported strong rank correlations between univariate and reaction norm models for heat stress for WW direct and maternal EBV for Angus cattle in the Upper South region of the USA. However, they reported some re-ranking for direct EBV of WW in proven sires under extreme heat load. Results from the present study indicate that the classical univariate model could be adequate to identify the best bulls for growth traits across different cold stress classes. However, the composite population used in this study has been closed to external exchange of genetic material and may be adapted for cold stress tolerance/resistance through indirect selection. Furthermore, the development of this composite population aimed to optimize the specific attribute of each of three breeds: Red Angus for maternal characteristic and carcass quality; Charolais for its growth rate and milk production; and Tarentaise for its toughness of production in less ideal environments. The formation of this population is expected to have a maximum percentage of retained heterosis equal to 63%. Therefore, the composite breed offers the opportunity to use the different genetic attributes among breeds to sustain or improve a variety of economically important traits including climatic adaptability, growth rate, milk production and fertility in a wide range of production environments (Newman *et al.*, 1993a and 1993b).

The distribution of phenotypic plasticity for BW and WW across the three TCL classes using the direct and maternal slope of EBV obtained using reaction norm model is presented in Supplementary Material Figure S3. No extremely plastic genotypes were found using either the direct or maternal slopes for BW and WW. For the direct effects, there were 14.62% (0.95%) and 14.4% (0.07%) of plastic genotypes for BW (WW) under TCL5 and TCL15 scenarios, respectively (Supplementary Material Figure S3a). For maternal effects, there were only 1.02% plastic genotypes for BW under TCL15 class (Supplementary Material Figure S3b). However, there were 3.91%, 6.26% and 3.46% plastic genotypes for WW under TCL5, TCL15 and TCL25 classes, respectively. These results indicate that cold stress is affecting the direct and maternal genetic effects of BW, and maternal genetic effects of WW for some animals especially under the TCL5 and TCL15 classes. In this study, genotype by environment interaction due to cold stress is not as high as expected and there is no need to account for it in our breeding programme.

Figure 5 presents the EBVs of five bulls as a function of cold stress load (bulls selected based on EBVs obtained from the distribution between 25th and 75th percentile using the classical univariate model) for the direct and maternal effects for BW. Figure 6 presents the EBVs as a function of cold stress load of the top five bulls (based on EBVs obtained using the classical univariate model) for the direct and maternal effects for WW. The figures show the direct (solid line) and maternal (dashed line) EBV changes along the EG using different classes of TCL. For BW, there is no indication of G × E interaction across the different TCL classes for the direct and maternal effects (Fig. 5). In fact, EBV lines are almost perfectly parallel

Table 2 *Spearman rank correlations of direct (above diagonal) and maternal (below diagonal) estimated breeding values for bulls with at least 20 offspring for growth traits from a composite beef cattle population using univariate and reaction norm models*

		Models			
		AM	RN		
Growth traits	Models	UNI	TCL5[1]	TCL15[1]	TCL25[1]
Birth weight (*n* = 79)	UNI		0.97	0.98	0.99
	TCL5	0.94		0.98	0.98
	TCL15	0.97	0.96		0.99
	TCL25	0.99	0.95	0.98	
Weaning weight (*n* = 79)	UNI		0.96	0.97	0.99
	TCL5	0.98		0.97	0.96
	TCL15	0.98	0.98		0.98
	TCL25	0.99	0.98	0.99	

AM = univariate (UNI) animal models; RN = reaction norm models; TCL = total cold load.

[1] TCL5: mild cold stress (onset of cold stress when climate index is less than −5°C), TCL15: moderate cold stress (onset of cold stress when climate index is less than −15°C) and TCL25: severe cold stress (onset of cold stress when climate index is less than −25°C).

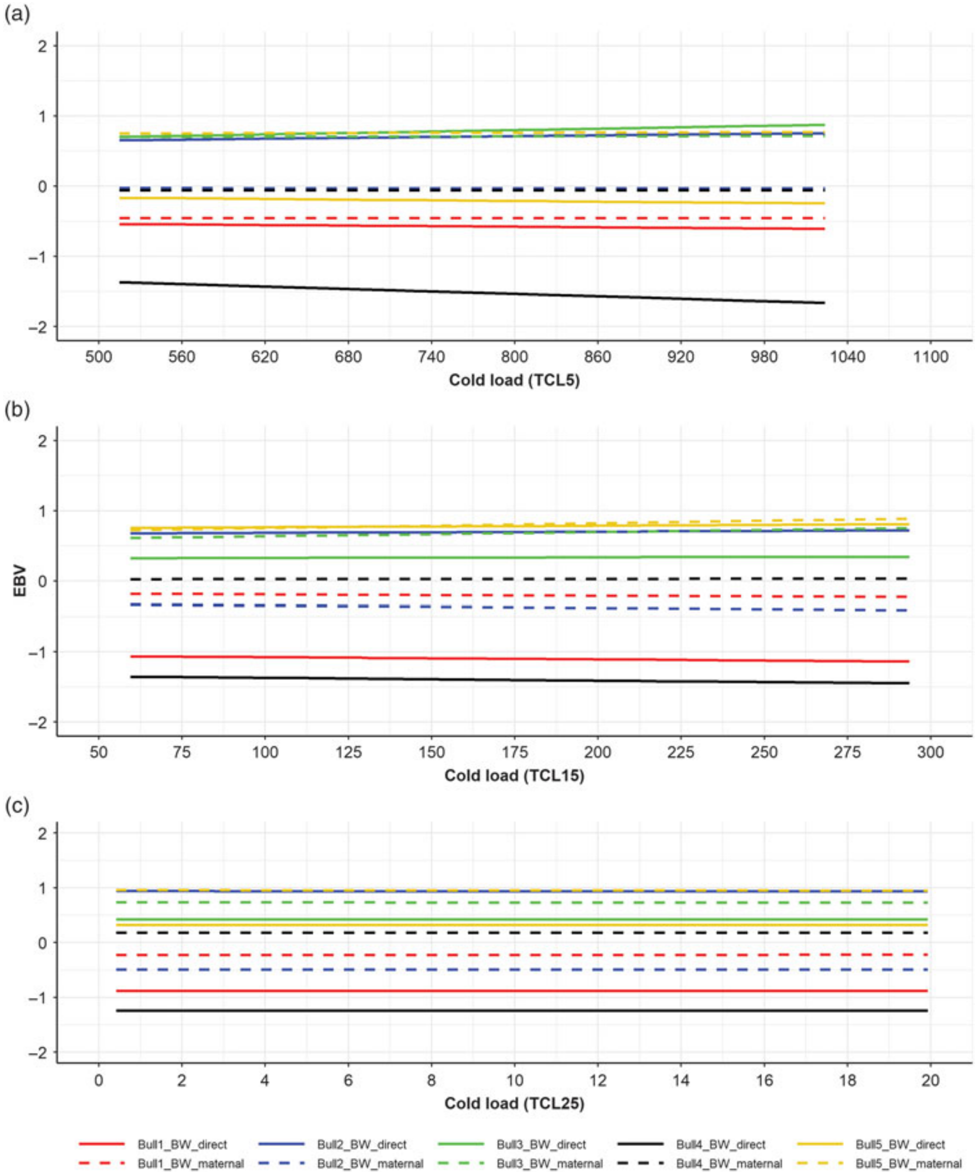

Figure 5 Estimates of direct (solid line) and maternal (dashed line) breeding values in kg for birth weight (BW) using reaction norm model for 5 bulls (with at least 20 offspring records) with estimated breeding values (EBV) between 25th and 75th percentiles from the univariate analysis. Pairs of coloured solid and dashed lines represent the direct and maternal effects of a specific bull for a specific year within each cold load class with thresholds of less than −5°C (TCL5) (a), less than −15°C (TCL15) (b) and less than −25°C (TCL25) (c).

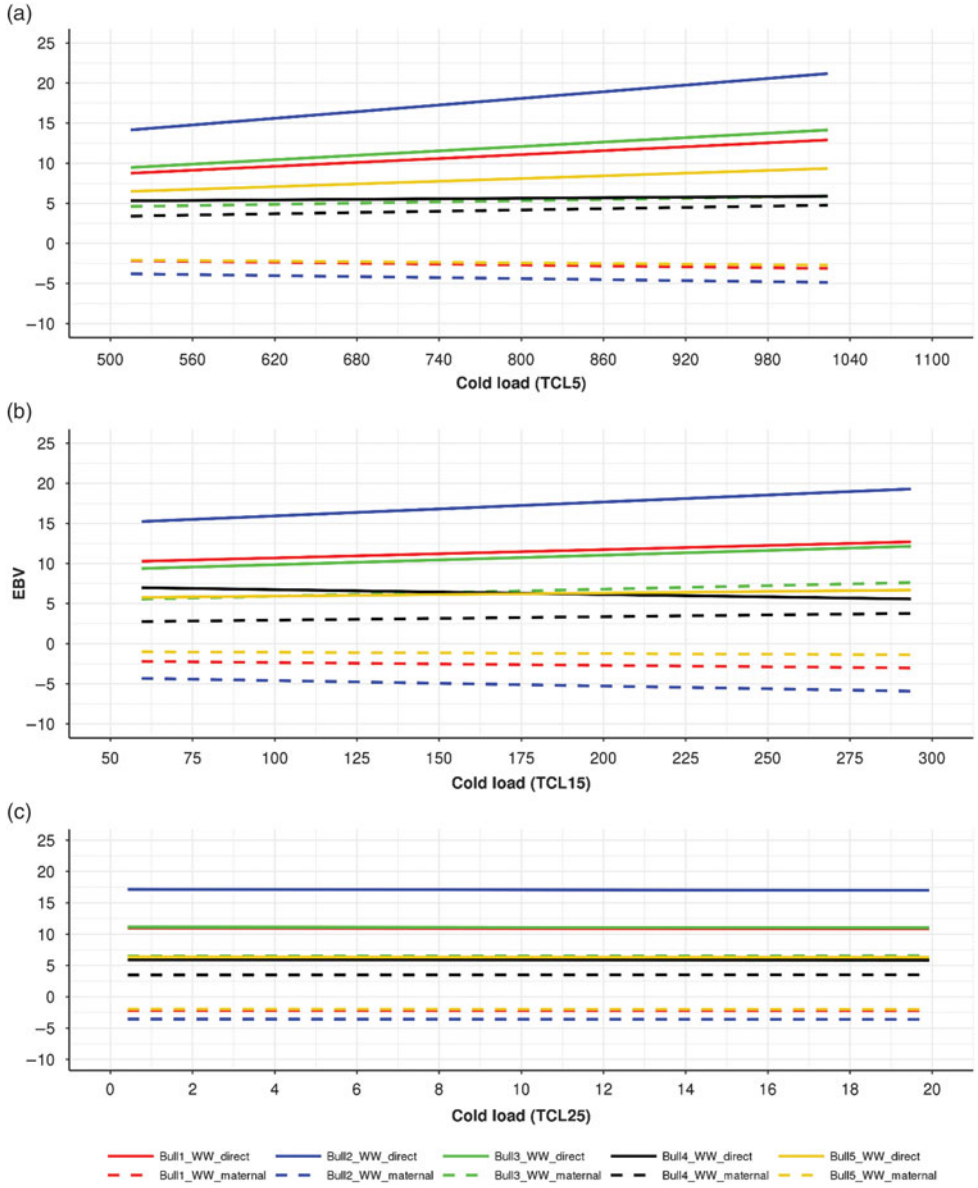

Figure 6 Estimates of direct (solid line) and maternal (dashed line) breeding values in kg for weaning weight (WW) using reaction norm model for the top 5 bulls (with at least 20 offspring record) from the univariate analysis. Pairs of coloured solid and dashed lines represent the direct and maternal effects of a specific bull for a specific year within each cold load class with thresholds of less than −5°C (TCL5) (a), less than −15°C (TCL15) (b) and less than −25°C (TCL25) (c). EBV = estimated breeding values.

across TCL classes with no re-ranking. However, for WW there are changes in the trend and the ranking of EBVs (black and gold colour in Fig. 6b) between TCL5 and TCL15 classes, especially for the direct genetic effects.

Conclusions

The present study explores the extent and impact of genotype by environment interaction due to cold stress on growth traits in a composite beef cattle population. In general, some evidence of phenotypic plasticity was observed for BW direct genetic effect and WW maternal genetic effect. In addition, the direct and maternal EBV for both growth traits of superior bulls did not show large changes in magnitude or re-ranking. Overall, the impact of G × E interaction due to cold stress on BW and WW was minimal which could be due to the potential adaptation of this cattle population to the cold weather conditions.

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Declaration of interest

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Ethics statement

Ethics committee approval was not required because the data used in this study were provided by USDA-ARS Fort Keogh Livestock and Range Research Laboratory.

Software and data repository resources

None of the data were deposited in an official repository.

Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.1017/S1751731120000531

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