

Estimation of genetic parameters and trends for growth traits in Hays Converter cattle using multiple-trait and random regression models

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ABSTRACT

Hays Converter (HC), the first registered Canadian beef breed, was developed by Harry Hays in the 1950's as a composite with contributions from Holstein, Hereford, Brown Swiss and with a later introgression of Angus. The breed is well adapted to the Western Canadian climate. Calves reach market weight early, convert feed to gain efficiently, and have excellent carcass quality and yield. The edited data consisted of 21,612 weight records taken at ages 1 to 474 days, from 8,850 animals born at Red Bow Ranching Ltd., Calgary, Alberta between 1970 and 2016. This study aimed to evaluate the genetic parameters and trends in birth, weaning and yearling weights of HC through comparison of different multiple trait models (MTM) with a random regression model (RRM). In MTM scenarios, both adjusted and unadjusted data were examined besides considering contemporary groups (CG) as fixed or random. Estimates of variance components, heritability and genetic correlations from the two approaches were not substantially different and showed similar changes along the growth trajectory. Although there was a considerable reduction in genetic trends from 2004 to 2008, due to weak sire selection, trends generally increased through 2016. Overall, both models performed similarly and fixed CG were preferred.

1. Introduction

Hays Converter (HC), was developed by Harry Hays in the 1950's, and was the first beef breed of Canadian origin to be registered under the Canadian Livestock Pedigree Act in 1975 (Fleming et al., 2016). HC combined Holstein, Hereford and Brown Swiss breeds (Fleming et al., 2016). It is known for rapid growth with excellent carcass grading under Canadian standards and adapts to the climatic conditions of Western Canada (Fleming 2013). Since its formation, the breeding objective for HC was to create a beef breed that excelled in growth and efficiently converted feed to gain so that the cattle reached market weight at earlier ages than other competing breeds. Sire selection always used the phenotypic records of weaning and yearling weights and a subjective evaluation of growth potential. There was no selection based on EBV or an index until 2014. However, visual inspection and use of individual phenotypes of animals that are candidates for

selection may not maximize response to selection. Use of estimated breeding values (EBV) as the basis for selection is expected to produce more rapid genetic improvement (Mofakkarul Islam et al., 2013). Preliminary work with single-trait and bivariate models and fixed contemporary groups has produced estimates of genetic parameters and genetic trends for growth traits of HC (Fleming 2013).

Currently, most genetic evaluation programs predict EBV for growth traits in beef cattle using multiple trait models (MTM: Farquharson et al., 2003; Meyer 2004; Delgadillo et al., 2017). In this approach, weight records are collected within defined windows of time within which growth is assumed to be linear along the growth curve and standardized to 205 and 365 days of age for weaning weight and yearling weight, respectively (Beef Improvement Federation 2018). Other weights recorded outside of these windows are not used in the evaluations. This approach may lead to EBV with lower accuracies than if all available data were used (Meyer 2004; Mota et al., 2013).

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Random regression models (RRM) facilitate use of all available weights that are recorded over time for each animal (Schaeffer 2004). Although pre-adjustment to standard ages is not necessary, fitting RRM models is similar to MTM in computational complexity. However, RRM are sensitive to sparse data, as may occur at extremes of age-weight trajectories (Meyer 1999).

Contemporary groups (CG) allow for elimination of bias caused by different environmental factors. Including CG in the genetic evaluation leads to a more accurate EBV and thus the potential for increased genetic improvement (Van Vleck 1987; Ramirez-Valverde et al., 2008). When they are considered as fixed effects, the bias due to non-random relationship between sires and CG is reduced. If they are considered random, then the prediction error variance is reduced because more information is used to predict the EBV (Visscher and Goddard, 1993). Application of the predicted breeding values to predict the merit of progeny in currently unobservable future contemporary groups would argue for considering CG as random effects.

Therefore, the goal of this study was to evaluate alternatives for prediction of EBV in HC. Specific objectives were to assess RRM versus MTM and the use of random versus fixed CG and to estimate genetic parameters and genetic trends of birth, weaning and yearling weights.

2. Materials and methods

The data used for this study was collected and provided by a commercial enterprise (Red Bow Ranching Ltd, Calgary, AB) using industry standard production practices which were generally consistent with the guidelines of the Canadian Council on Animal Care (Olfert et al., 1993)

Raw data consisted of weights recorded at birth (BW), weaning (WW from 100 to 315 days of age), and yearling (YW from 245 to 544 days of age) (Table 1), from animals born between 1970 and 2016. In order to edit data for further analysis, all weaning and yearling weight records obtained at ages that deviated from the respective mean ages by more than three standard deviations were excluded from the data.

CGs were defined by concatenation of herd, year, season of birth (Jan-Mar, Apr-June, July-Sept, and Oct-Dec) and sex (male or female). CGs of less than three animals were excluded from the respective analyses where they were considered as fixed. Age of dam at calving was categorized into five classes (2 years old, 3 years old, 4 years old, 5-7 years old, and ≥ 8 years old). Records from calves produced through embryo transfer and also those with unidentified dams were excluded. Finally, and in contrast to Fleming (2013), all conjectural birth weights were eliminated from the data. The number of sires and dams in the pedigree were equal to 137 and 1701 in which 63% and 17% of dams were daughters of sires or dams that were used as dams, respectively (Table 1). Animals with unknown parents were assigned to generation zero. For animals with recorded parents, generation numbers were calculated following the approach of Brinks et al. (1961) wherein generation numbers for descendants of animals in generation 0 were calculated as the average generation number of their parents plus one. The average generation interval was estimated as the linear regression

Table 1

Descriptive statistics detailing distributions of ages at the recording of weaning and yearling weights, and the weight traits along with number of sires, dams and their daughters as dams. Statistics from the data set after editing are shown parenthetically.

	N	Mean	SD	Min	Max
Weaning age (days)	8748 (7776)	188.7	22.0	100 (123)	315 (254)
Yearling age (days)	6474 (5936)	375.9	32.8	245 (280)	544 (474)
Birth weight (kg)	7119 (6519)	39.7	5.7	13.6 (22.7)	74.8 (56.7)
Weaning weight (kg)	8585 (7776)	247.3	40.5	61.7 (126.1)	412.8 (365.1)
Yearling weight (kg)	6396 (5936)	444.0	79.3	138.8 (217.7)	739.4 (679.9)
Sires	137				
Dams	1701				
Daughters of sires as dams	1069				
Daughters of dams as dams	291				

of birth year on generation number.

After this initial editing, datasets were prepared for different MTM scenarios and RRM analysis. For the RRM analysis, all weights between 1 and 474 (the maximum yearling age after $\pm 3SD$ edit) days of age were used along with 1381 records that were recorded during the period when feed intake was measured. This dataset contained 21,612 records from 8,850 animals with minimum and maximum numbers of 1 to 9 records per animal (Fig. 1, Table 2). For MTM analyses, two sets of data were extracted. Dataset 1 was based on the windows of age recommended by the Beef Improvement Federation (2018) for weaning and yearling weights (i.e., ranges of ± 45 days from the average ages at which weaning (188 d) and yearling (365 d) weights were recorded in HC) and included all available records of BW. These weights were linearly adjusted for age as follows:

$$W_{188} = BW + \frac{(WW - BW)}{\text{Weaning age}} \times 188$$

$$W_{365} = W_{188} + \frac{(YW - WW)}{(\text{Yearling age} - \text{Weaning age})} \times 177$$

where: W_{188} and W_{365} represent age-adjusted weaning and yearling weights, respectively ($N = 15,107$ records including BW). Dataset 2 had wider windows in order to incorporate additional data making it more similar to the dataset analyzed with RRM. In the second dataset the windows for acceptable weights were expanded to ± 65 days and age effects were estimated simultaneously in MTM models. In total, approximately 30% and 26% more records were available for the RRM analysis than in the first and second datasets used in the MTM analyses. The growth trajectory from 123 to 474 days of age is shown in Fig. 1. Note that, except for BW with an average 40 kg, the weights recorded at ages less than 123 days were not used in either analysis due to their low frequency.

3. Models

3.1. Different MTM scenarios

First, for the analysis of age-adjusted weights, the MTM was defined as follows:

$$y_{ijlmt} = CG_i + \sum_{n=0}^2 b_n (aod_j)^n + a_{it} + d_{mt} + e_{ijlmt}$$

where y_{ijlmt} is the t^{th} weight record for BW, W_{188} and Y_{365} of the animal l in the i^{th} CG and the j^{th} class of age of dam at calving (aod); b_n is a fixed regression adjusted to linear and quadratic effects for the aod as a covariate; a_{it} is the random direct additive genetic effect of the animal l for weight t ; d_{mt} is the random maternal additive genetic effect of the dam m for weight t and e_{ijlmt} is the random residual effect. To avoid the failure that occurred in the approximation of standard errors for maternal permanent environmental parameters due to small sample size and/or over-parameterization (Meyer 2018), these effects were



Fig. 1. Numbers of records at each age and trajectory of average weight (kg) in the data.

Table 2

Structure of data for analysis with RRM with reference to the number of records per animal.

	No. of animals	Percentage
with records	8850	100.00%
1 record	1425	16.10%
2 records	3388	38.30%
3 records	3801	42.90%
7-9 records	236	2.70%
Records in total	21612	

removed from the MTMs.

This model can be described in matrix notation as follows:

$$y = X\beta + Z_1d + Z_2m + \varepsilon$$

where y is the vector of weight records; β is the vector of fixed effects (CG classes and aod regressions); d is the vector of random direct additive genetic effects; m is the vector of random maternal additive genetic effects and ε is the vector of residual effects; X , Z_1 and Z_2 are the incidence matrices for the corresponding effects. The assumptions for this analysis were as follows:

$$E \begin{bmatrix} y \\ d \\ m \\ \varepsilon \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad V \begin{bmatrix} d \\ m \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_d \otimes A & 0 & 0 & 0 \\ 0 & G_m \otimes A & 0 & 0 \\ 0 & 0 & R \otimes I_n & 0 \end{bmatrix}$$

where G_d and G_m are (co)variance matrices of random effects for direct additive genetic and maternal additive genetic effects, respectively; A is the numerator relationship matrix; I_n is the identity matrix whose order is equal to the number of records; R is a (co)variance matrix of random residual effects and \otimes is the kronecker product operator. A parallel analysis to that just described was conducted using the weight records which had not been pre-adjusted for age and including linear covariates in the model to account for the age effects.

To evaluate consideration of CG effects as being either fixed or random, both of the datasets were analyzed similarly, but only using the data which was not pre-adjusted for age. For convenience these analyses are referred to as MTM-data1-CG-fixed, MTM-data1-CG-random, MTM-data2-CG-fixed and MTM-data2-CG-random. No maternal genetic effect was considered for YW (due to numerical errors). To test the non-linearity of age effects on WW and YW, the second dataset was also analyzed with two additional 3-traits models, i.e. MTM-data2-CG-fixed-age quadratic and MTM-data2-CG-random-age quadratic, respectively. In each of the six models above, when considering CG as a random effect, the assumptions were as follows;

$$E \begin{bmatrix} y \\ d \\ m \\ cg \\ \varepsilon \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \quad V \begin{bmatrix} d \\ m \\ cg \\ \varepsilon \end{bmatrix} = \begin{bmatrix} G_d \otimes A & 0 & 0 & 0 \\ 0 & G_m \otimes A & 0 & 0 \\ 0 & 0 & G_{cg} \otimes I_g & 0 \\ 0 & 0 & 0 & R \otimes I_n \end{bmatrix}$$

where G_{cg} is the (co)variance matrix of random effects for contemporary groups and I_g is the identity matrix whose order is equal to the number of contemporary groups.

In order to estimate direct (h_a^2) or maternal (h_m^2) heritability when considering CG as fixed or random, the respective phenotypic variances ($\text{Var}(p)$) were calculated as follows;

$$\text{Var}(p)_{CG\text{-fixed}} = \text{Var}(a) + \text{Var}(m) + \text{Var}(e)$$

$$\text{Var}(p)_{CG\text{-random}} = \text{Var}(a) + \text{Var}(m) + \text{Var}(CG) + \text{Var}(e)$$

where $\text{Var}(a)$, $\text{Var}(m)$, $\text{Var}(CG)$ and $\text{Var}(e)$ are additive genetic, maternal genetic, contemporary group and residual variances, respectively. Therefore,

$$h_{a/m}^2 = \text{Var}(a/m)_{CG\text{-fixed}} / \text{Var}(p)_{CG\text{-fixed}}$$

$$h_{a/m}^2 = \text{Var}(a/m)_{CG\text{-random}} / \text{Var}(p)_{CG\text{-random}}$$

4. RRM analysis

In implementing the RRM analysis, quadratic Legendre polynomials were selected for the fixed regression coefficients to define changes in the population mean trend. Random regressions of different orders (k) of Legendre polynomials were modeled to describe variation in direct additive genetic (a), direct permanent environmental (p), maternal additive genetic (m) and maternal permanent environmental (c) effects, respectively. Initially, models with quadratic, cubic and quartic degrees of Legendre polynomials for the direct additive genetic and permanent environmental effects were evaluated (i.e., $k_a = k_p = 3, 4$ and 5 , respectively). For the maternal additive genetic and permanent environmental effects, linear, quadratic and cubic degrees of polynomials were initially considered (i.e., $k_m = k_c = 2, 3$ and 4 , respectively). Assuming heterogeneity of residual variances across the growth curve, they were categorized into four age classes as follows: 1 to 60, 61 to 205, 206 to 365 and 366 to 474 days of age, respectively. Therefore, the RRM was defined as:

$$y_{ijlmt} = CG_i + \sum_{n=0}^2 b_n(aod_j)^n + \sum_{n=0}^2 \beta_n \phi_n(\text{age}_t) + \sum_{n=0}^{k_a-1} \alpha_{ln} \phi_n(\text{age}_t) + \sum_{n=0}^{k_m-1} \gamma_{mn} \phi_n(\text{age}_t) + \sum_{n=0}^{k_p-1} \delta_{ln} \phi_n(\text{age}_t) + \sum_{n=0}^{k_c-1} \rho_{mn} \phi_n(\text{age}_t) + \varepsilon_{ijlmt}$$

where y_{ijlmt} is each of the weight records taken at age t for the animal l

with the dam m , in the i^{th} CG and the j^{th} class of aod; b_n are fixed regressions relative to aod; β_n are fixed regression coefficients that model the average growth trajectory of the population; $\Phi_n(\text{age}_t)$ is the n^{th} Legendre polynomial according to age t ; α_{in} , γ_{mn} , δ_{in} and ρ_{mn} are the n^{th} random regression coefficients of direct additive genetic, maternal additive genetic, direct permanent environmental and maternal permanent environmental effects, respectively and ε_{ijlmt} is the random residual error associated with the age t of the l^{th} animal.

In matrix notation, the model was represented as follows:

$$y = X\beta + Z_1\alpha + Z_2\gamma + W_1\delta + W_2\rho + \varepsilon$$

where y is the vector of observations; β is the vector of fixed effects; α , γ , δ and ρ are the vectors of random regression coefficients for direct additive genetic, maternal additive genetic, direct permanent environmental and maternal permanent environmental effects, respectively; X , Z_1 , Z_2 , W_1 and W_2 are the incidence matrices for corresponding effects and ε is the vector of residual effects. The following assumptions were considered for the RRM:

$$E \begin{bmatrix} y \\ \alpha \\ \gamma \\ \delta \\ \rho \\ \varepsilon \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} V \begin{bmatrix} \alpha \\ \gamma \\ \delta \\ \rho \\ \varepsilon \end{bmatrix} = \begin{bmatrix} K_a \otimes A & 0 & 0 & 0 & 0 \\ 0 & K_m \otimes A & 0 & 0 & 0 \\ 0 & 0 & K_p \otimes I_{N_a} & 0 & 0 \\ 0 & 0 & 0 & K_c \otimes I_{N_m} & 0 \\ 0 & 0 & 0 & 0 & R \end{bmatrix}$$

where K_a , K_m , K_p and K_c are (co)variance matrices between random regression coefficients for direct additive genetic, maternal additive genetic, direct permanent environmental and maternal permanent environmental effects, respectively; A is the numerator relationship matrix; I is an identity matrix; N_a is the total number of individuals with records; N_m is the number of dams; R is a diagonal matrix of residual variances and \otimes is the kronecker product operator. The covariance between direct and maternal additive genetic effects was assumed to be zero for both MTM and RRM. To find an appropriate RRM, preliminary analyses with different orders of fit for Legendre polynomials were examined from 1111 to 5343 (higher orders produced numerical errors) where 1111 indicates the four random effect regressions being modeled as linear effects and 5343 indicated the random effects being modeled with quadratic, cubic, quartic, and cubic polynomials, respectively. These analyses were initially compared using the likelihood statistics, Akaike information criterion (AIC), and Bayesian information criterion (BIC) (Table 3). According to these criteria, the model 5343 initially indicated improved description of variation in the data, although BIC imposed a greater penalty than AIC for the number of parameters estimated (Olori et al., 1999; Meyer 2001; Boligon et al., 2010). However, to avoid very large estimates at the boundaries of growth trajectory (Albuquerque and Meyer, 2001; Nobre et al., 2003; Meyer 2005a), RRM models producing parameter estimates more similar to those from MTM with age-adjusted weights were compared through LRT (log-likelihood ratio test). This statistic was calculated as twice the difference in log L between complete and reduced models:

$$LRT_{ij} = 2(\log L_i - \log L_j)$$

where $\log L_i$ and $\log L_j$ were the maximum of log L for the complete model i and reduced (nested) model j , respectively. If the LRT with degrees of freedom equal to the difference between the number of parameters estimated in complete and reduced models and the significance level of $P < 0.05$, was higher than a tabulated chi-square (χ^2), the complete model provided a better description of the variation (Mota et al., 2013). This led to selection of RRM-4333. However, in

Table 3
Different orders of Legendre polynomials in RRM along with statistical criteria of log L, AIC and BIC.

Model	Order of polynomials					Statistical criteria		
	K_a^a	K_m^b	K_p^c	K_c^d	np^e	log L	AIC	BIC
3232	3	2	3	2	22	-73862.0	147768.0	147943.2
3233	3	2	3	3	25	-73845.2	147740.3	147939.5
3332	3	3	3	2	25	-73833.3	147716.5	147915.7
3333	3	3	3	3	28	-73826.5	147709.0	147932.1
3433	3	4	3	3	32	-73768.4	147600.8	147855.8
3343	3	3	4	3	32	-73724.2	147512.4	147767.3
3353	3	3	5	3	37	-73603.3	147280.5	147575.3
4332	4	3	3	2	29	-73723.5	147505.1	147736.1
4333	4	3	3	3	32	-73709.8	147483.6	147738.6
4432	4	4	3	2	33	-73713.1	147492.3	147755.2
4342	4	3	4	2	33	-73698.9	147463.8	147726.8
4343	4	3	4	3	36	-73691.4	147454.7	147741.6
4344	4	3	4	4	40	-73689.4	147458.9	147777.6
4443	4	4	4	3	40	-73687.9	147455.9	147774.6
5332	5	3	3	2	34	-73561.8	147191.6	147462.5
5333	5	3	3	3	37	-73554.7	147183.5	147478.3
5432	5	4	3	2	38	-73559.1	147194.2	147497
5342	5	3	4	2	38	-73529.5	147135.0	147437.8
5343	5	3	4	3	41	-73520.9	147123.8	147450.4

^a order of fit for direct additive genetic
^b maternal additive genetic
^c direct permanent environmental and ^dmaternal permanent environmental effects ^enumber of parameters

order to do an appropriate comparison with MTM-adjusted weights, an equivalent RRM without maternal permanent environmental effects, i.e. RRM-433, which was not significantly different from RRM-4333 through LRT, was used for estimating parameters.

As a residual effect in MTM is equivalent to the sum of direct permanent environmental and residual effects in RRM, when comparing both models, residual variances in RRM must be considered as a composed variance of direct permanent environmental and residual effects (Nobre et al., 2003; Legarra et al., 2004). In RRM, the EBV of the l^{th} animal at age t was calculated as follows:

$$EBV_{lt} = \sum_{n=0}^{k_a-1} \alpha_{in} \phi_n(\text{age}_t)$$

Coefficients of the Legendre polynomials and the resulting statistics log L, AIC, BIC, (co)variance components, genetic parameters, EBVs in MTM analysis, and random regression coefficients in RRM were calculated using the WOMBAT software implementation of restricted maximum likelihood method (REML) (Meyer 2007). Genetic trends were obtained from the EBVs by linear regression on birth year.

5. Results

The fixed regression curve by RRM-433 that described the changes in weight over time was nearly linear and approximately parallel to the trend in the observed weights indicating attainment of 500 kg by 463 days of age (Fig. 2).

Estimates of variance components and genetic parameters from the MTM scenarios and RRM-433 for growth traits of BW, WW and YW were presented in Table 4. For BW, estimates of the variance components and genetic parameters were unaffected by the analytical procedure when considering CG as fixed. For random CG, despite an increase in the Var (p) and as a result a decrease in h_a^2 and h_m^2 , no changes were observed in variance components. For both WW and YW, the Var (p) estimated with the RRM was greater than the corresponding estimate from the MTMs with fixed CG due primarily to the difference in the estimates of Var (e). This resulted in the estimated (h_a^2) for WW from the RRM being marginally less than that from the MTM using pre-adjusted weights and considerably less than the estimates from MTM with that

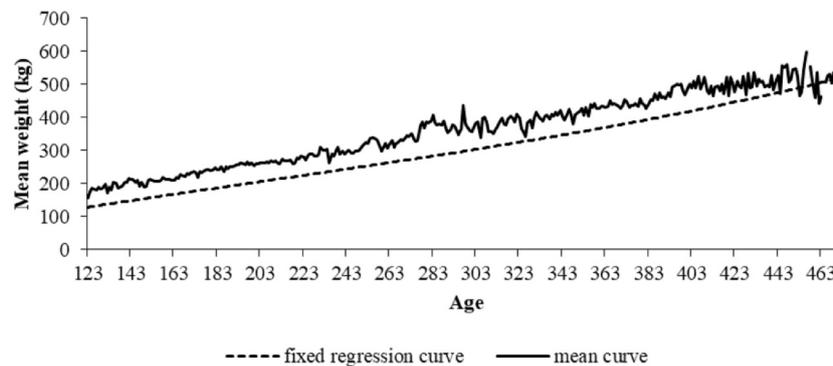


Fig. 2. Plots of the fixed regression curve of weight on age from the random regression analysis and average weight across the growth trajectory of Hays Converter cattle.

incorporated simultaneous adjustment for age due to larger estimates of additive genetic variance (Var (a)). Similarly, for YW, although the Var (a) was greater for the RRM than the MTM with pre-adjusted weights, both methods produced similar estimates of h_a^2 . The MTM in which age was accounted for simultaneously and CG were considered fixed produced a larger h_a^2 due to a lower Var (p) and a higher Var (a) than the corresponding values from RRM and MTM with pre-adjusted weights, respectively. Considering CG random, h_a^2 for WW was smaller than the respective values for MTM with fixed CG due to a larger Var (p). However, it was still slightly higher than RRM and MTM with pre-adjusted weights. However, in terms of YW when CG was random, the resulting h_a^2 was lower than the other models due to having the largest Var (p). For all three traits the estimates of direct additive genetic variance were not detectably different whether CG were considered random or fixed.

The estimates of maternal additive genetic variance (Var (m)) were small fractions of the corresponding Var (p) and except for WW in

MTM-adjusted weights, the estimates of maternal heritability (h_m^2) were near or essentially zero.

Over the span of ages between 123 d and 474 d, estimates of variance components estimated using RRM fluctuated most markedly in intervals where the data were relatively sparse. This was particularly true after 365 d for all variances (Figs. 3 and 4). However, both h_a^2 and h_m^2 reduced after yearling and weaning ages in RRM, respectively (Fig. 5).

Estimates of the direct additive genetic correlations ($r(a)$) of BW and subsequent weights were similar and greater when estimated with different MTMs than with RRM, and likewise between WW and YW (Table 5). Estimates of maternal additive genetic correlations ($r(m)$) in RRM were greater between BW and WW or YW, and less between WW and YW. There were no differences in $r(m)$ between BW and WW for all MTM scenarios. Moreover, the $r(m)$ between BW and YW or WW and YW in MTM-adjusted weights showed the least and greatest magnitudes, respectively. Although slightly greater, the estimates of direct

Table 4

Estimates of variance components and genetic parameters for birth weight (BW), weaning weight (WW) and yearling weight (YW) from different MTM scenarios and RRM-433 analyses.

Trait	Model	Variance components ^a					Genetic parameters ^b	
		Var (a)	Var (m)	Var (CG)	Var (e) ^c	Var (p)	h_a^2	h_m^2
BW	RRM	1.75 ± 0.48	0.21 ± 0.19	-	16.49	18.45 ± 0.34	0.10 ± 0.03	0.01 ± 0.01
	MTM-adjusted weights	1.86 ± 0.48	0.19 ± 0.19	-	16.2 ± 0.46	18.23 ± 0.33	0.10 ± 0.03	0.01 ± 0.01
	MTM-data1-CG fixed	1.85 ± 0.47	0.19 ± 0.18	-	16.19 ± 0.46	19.07 ± 0.33	0.10 ± 0.02	0.01 ± 0.01
	MTM-data1-CG random	2.02 ± 0.48	0.19 ± 0.18	11.43 ± 1.50	16.01 ± 0.46	30.59 ± 1.53	0.07 ± 0.02	0.006 ± 0.006
	MTM-data2-CG fixed	1.82 ± 0.47	0.20 ± 0.18	-	16.21 ± 0.46	18.91 ± 0.33	0.10 ± 0.02	0.01 ± 0.01
	MTM-data2-CG random	1.99 ± 0.47	0.20 ± 0.18	11.32 ± 1.5	16.03 ± 0.46	30.42 ± 1.52	0.07 ± 0.02	0.006 ± 0.006
	MTM-data2-CG fixed-age quadratic	1.81 ± 0.47	0.19 ± 0.18	-	16.21 ± 0.46	18.87 ± 0.33	0.10 ± 0.02	0.01 ± 0.01
	MTM-data2-CG random-age quadratic	1.99 ± 0.47	0.19 ± 0.18	11.30 ± 1.49	16.03 ± 0.46	30.38 ± 1.52	0.07 ± 0.02	0.006 ± 0.006
WW	RRM	140.35 ± 24.71	76.51 ± 14.83	-	892.97	1109.84 ± 18.94	0.13 ± 0.02	0.07 ± 0.01
	MTM-adjusted weights	150.9 ± 34.17	115.5 ± 19.8	-	629.52 ± 26.45	895.94 ± 19.91	0.17 ± 0.04	0.13 ± 0.02
	MTM-data1-CG fixed	236.82 ± 34.45	48.68 ± 10.41	-	599.81 ± 27.19	885.31 ± 19.48	0.27 ± 0.04	0.05 ± 0.01
	MTM-data1-CG random	229.75 ± 33.26	47.58 ± 10.07	332.24 ± 49.01	604.56 ± 26.63	1214.1 ± 52.17	0.19 ± 0.03	0.04 ± 0.008
	MTM-data2-CG fixed	238.09 ± 33.52	44.59 ± 10.12	-	594.04 ± 26.31	876.73 ± 18.9	0.27 ± 0.03	0.05 ± 0.01
	MTM-data2-CG random	229.31 ± 32.25	43.99 ± 9.8	326.27 ± 47.43	599.05 ± 25.72	1198.6 ± 50.52	0.19 ± 0.03	0.04 ± 0.008
	MTM-data2-CG fixed-age quadratic	234.94 ± 33.47	45.05 ± 10.23	-	595.9 ± 26.29	875.9 ± 18.86	0.27 ± 0.03	0.05 ± 0.01
	MTM-data2-CG random-age quadratic	226 ± 32.14	44.52 ± 9.9	323.04 ± 47.02	601.21 ± 25.68	1194.8 ± 50.12	0.19 ± 0.03	0.04 ± 0.008
YW	RRM	960.8 ± 118.58	139.82 ± 50.23	-	3259.44	4360.06 ± 88.93	0.22 ± 0.03	0.03 ± 0.01
	MTM-adjusted weights	387.93 ± 84.37	100.97 ± 35.97	-	1215.15 ± 62.88	1704.05 ± 44.08	0.23 ± 0.05	0.06 ± 0.02
	MTM-data1-CG fixed	574.5 ± 80.31	-	-	1112.8 ± 65.9	1687.3 ± 46.33	0.34 ± 0.04	-
	MTM-data1-CG random	570.08 ± 78.89	-	3234.3 ± 419.14	1118.4 ± 65.06	4922.8 ± 420.85	0.12 ± 0.02	-
	MTM-data2-CG fixed	622.73 ± 79.84	-	-	1148.1 ± 64.19	1770.8 ± 45.7	0.35 ± 0.04	-
	MTM-data2-CG random	610.3 ± 78	-	3189.6 ± 402.48	1157.7 ± 63.20	4957.6 ± 404.35	0.12 ± 0.02	-
	MTM-data2-CG fixed-age quadratic	614.15 ± 78.42	-	-	1126.9 ± 63.04	1741.1 ± 45.04	0.35 ± 0.04	-
	MTM-data2-CG random-age quadratic	601.74 ± 76.58	-	3220.6 ± 405.52	1136.3 ± 62.04	4958.6 ± 407.3	0.12 ± 0.02	-

^a Var (a) = direct additive genetic variance, Var (m) = maternal additive genetic variance, Var (CG) = contemporary group variance, Var (e) = residual variance, Var (p) = phenotypic variance

^b h_a^2 = direct heritability, h_m^2 = maternal heritability

^c For the RRM = sum of estimates of variance for permanent environmental effects due to animals and residual

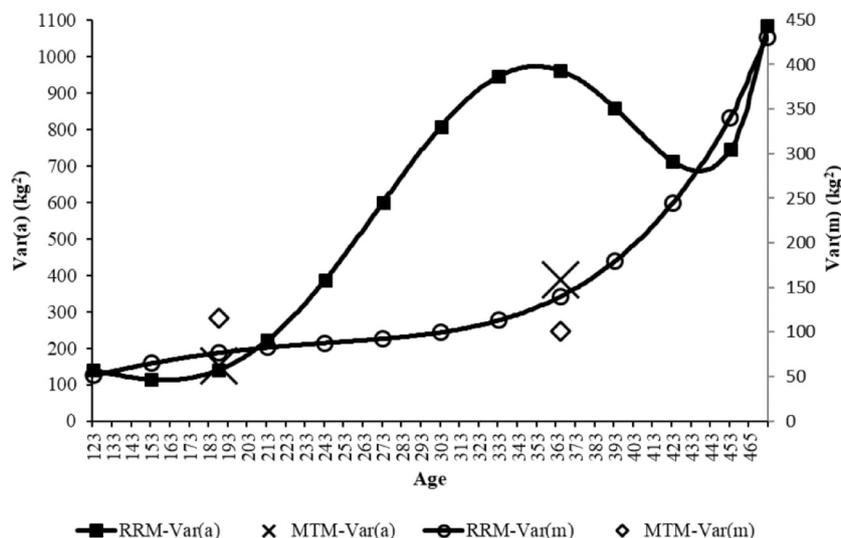


Fig. 3. Estimates of Var (a) and Var (m) in RRM-433 together with MTM-adjusted weights along the growth trajectory.

permanent environmental correlations from RRM were similar to those for residual correlations in all MTM scenarios. When using CG as a random effect in MTM, estimates of CG correlations ($r(CG)$) between BW and WW or YW was less than WW with YW. Estimates of phenotypic correlations in both models were similar and slightly less in RRM.

Based on the EBVs estimated by RRM, the genetic trends for direct effects on BW, WW, and YW were -3.6 ± 0.7 , 116 ± 8 , and 280 ± 21 g/yr, respectively (Table 6). The corresponding estimates of genetic trend based on MTM-adjusted weights were -7.1 ± 1 , 63.3 ± 9.6 , and -73 ± 16 g/yr, respectively. Although using CG as a random effect in MTMs resulted in substantially lower genetic trends for all weight traits than using fixed effects, all the six MTMs were in accordance with MTM-adjusted weights results. In total, estimates of the genetic trends from MTM were clearly less than those from RRM. Generation numbers in the recorded Hays Converter pedigree ranged from a minimum 0 for animals with unknown parents to a maximum of 5.16 over the period 1970 to 2016. The average generation interval was 5.35 ± 0.07 yr. In order to realize how sire selection over the past years has affected the genetic trends, the selection differential (SD) of HC sires were compared to the best males available that were not chosen as sires (Fig. 6). Irrespective of how the data were analyzed, there was a consistent loss of

selection pressure on the individual traits relative to the opportunities that existed in the population.

6. Discussion

Different orders of Legendre polynomials were evaluated with various statistical criteria to find the RRM that was used to describe the variation in body weights over time for the HC population. Baldi et al. (2010) suggested taking precision into account when adding random effects (including direct additive genetic, maternal additive genetic, animal permanent environmental and maternal permanent environmental effects) to a model due to the potential for over-parameterization. Moreover, convergence problems and susceptibility to numerical errors may be avoided by excluding non-essential parameters from the model (Arango et al., 2004; Legarra et al., 2004). Although in utilizing RRM to evaluate milk test day records, Jamrozik and Schaeffer (2002) indicated that models may be assessed differently when using different statistical criteria, and which model would be the most suitable may be unclear. Similar issues were observed in this study.

The main goal of creating HC was to develop an animal that would

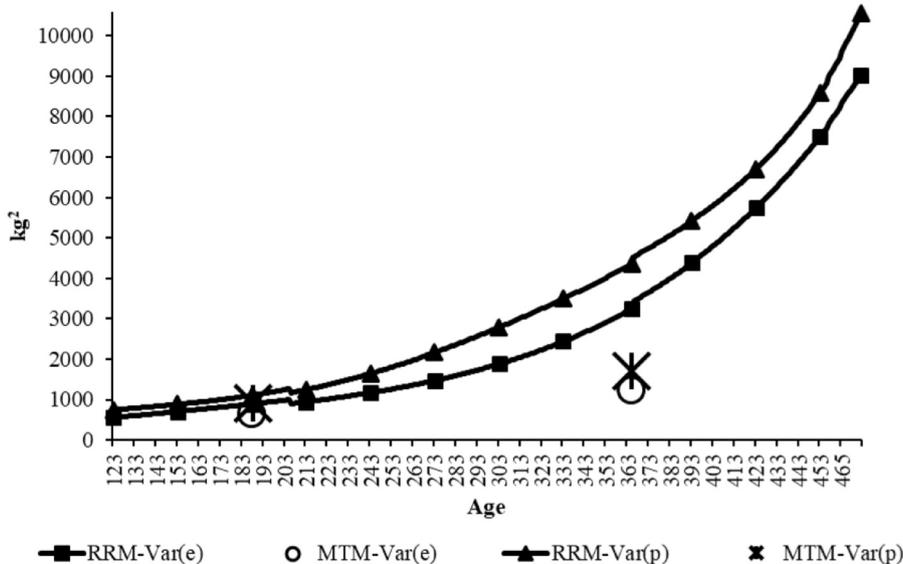


Fig. 4. Estimates of Var (e) and Var (p) by RRM-433 and MTM-adjusted weights along the growth trajectory.

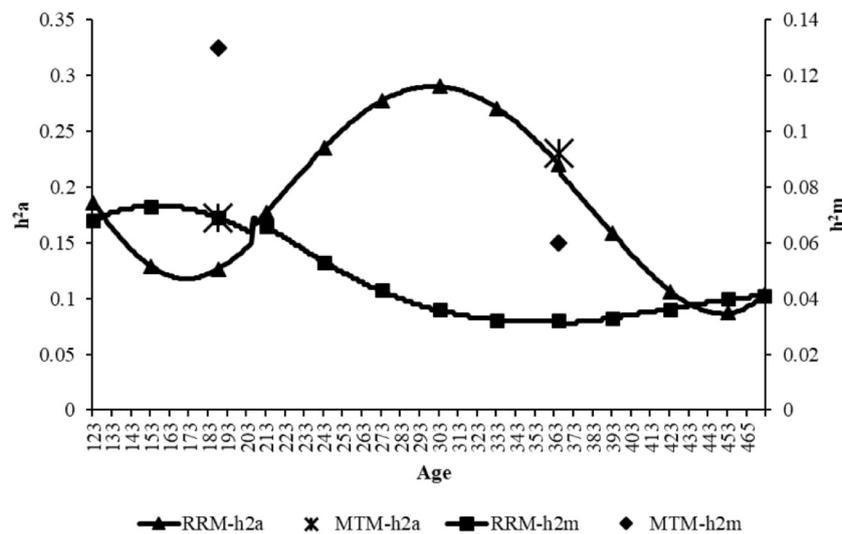


Fig. 5. Estimates of direct and maternal heritabilities in RRM-433 and MTM-adjusted weights along the growth trajectory.

efficiently convert feed to gain and reach the desirable market weight of 500 kg at the earliest age possible (Fleming et al., 2016). Considering the fixed regression curve in Fig. 2, the attainment of 500 kg by 463 days of age was deemed consistent with the breeding goal of reaching desirable market weight at a young age. However, it only addresses that component of efficient conversion of feed to gain that results from avoiding the additional feed consumed in satisfying maintenance requirements over a longer time on feed (Nielsen et al., 2013).

To date, RRRMs have most frequently used orthogonal (Legendre) polynomials because they flexibly model changes in variance and covariance along a continuous scale, especially at higher orders (Meyer 2005b). However, observations at the extremes are over-emphasized and this may be problematic for models that are parameterized in this way. In fact, as ‘Runge’s phenomenon’ describes, implausible errors in variance component estimates may be observed at the ends of the growth trajectory due to small numbers of extreme

Table 6

Estimates of genetic trends (g/yr) for RRM-433 and different MTM scenarios.

Models	BW	WW	YW
RRM	-3.6 ± 0.7	116 ± 8	280 ± 21
MTM-adjusted weights	-7.1 ± 1	63.3 ± 9.6	-73 ± 16
MTM-data1-CG fixed	-5.1 ± 1	117.7 ± 13.5	-14 ± 20.1
MTM-data1-CG random	-17 ± 1	76.2 ± 13.2	-59.45 ± 20.5
MTM-data2-CG fixed	-6.2 ± 1	82 ± 13.8	-147.9 ± 22.03
MTM-data2-CG random	-19.4 ± 1	37.6 ± 13.5	-194.4 ± 21.7
MTM-data2-CG fixed-age quadratic	-6.7 ± 1	78.9 ± 13.7	-172.5 ± 22
MTM-data2-CG random-age quadratic	-20.07 ± 1	34.7 ± 13.3	-212.8 ± 21.7

Table 5

Estimates of direct and maternal additive genetic, contemporary group, residual (permanent environmental in RRM) and phenotypic correlations by RRM-433 and different MTM scenarios.

Traits	Models	WW r(a) ^a	YW	WW r(m) ^b	YW	WW r(CG) ^c	YW	WW r(e) ^d	YW	WW r(p) ^e	YW
BW	RRM	0.21 ± 0.15	0.47 ± 0.12	0.43 ± 0.31	0.56 ± 0.40	-	-	0.17 ± 0.11	0.10 ± 0.07	0.16 ± 0.02	0.15 ± 0.02
	MTM-adjusted weights	0.67 ± 0.13	0.77 ± 0.12	0.28 ± 0.31	-0.11 ± 0.47	-	-	0.14 ± 0.02	0.11 ± 0.03	0.21 ± 0.01	0.20 ± 0.02
	MTM-data1-CG fixed	0.60 ± 0.12	0.65 ± 0.11	0.27 ± 0.33	-	-	-	0.14 ± 0.02	0.12 ± 0.03	0.21 ± 0.01	0.21 ± 0.02
	MTM-data1-CG random	0.53 ± 0.12	0.62 ± 0.11	0.31 ± 0.34	-	0.28 ± 0.09	0.29 ± 0.09	0.15 ± 0.02	0.12 ± 0.03	0.23 ± 0.03	0.24 ± 0.04
	MTM-data2-CG fixed	0.59 ± 0.12	0.60 ± 0.11	0.23 ± 0.33	-	-	-	0.14 ± 0.02	0.12 ± 0.03	0.20 ± 0.01	0.20 ± 0.01
	MTM-data2-CG random	0.52 ± 0.12	0.61 ± 0.11	0.3 ± 0.33	-	0.26 ± 0.10	0.20 ± 0.09	0.15 ± 0.02	0.12 ± 0.03	0.22 ± 0.03	0.19 ± 0.04
	MTM-data2-CG fixed-age quadratic	0.59 ± 0.12	0.60 ± 0.11	0.22 ± 0.33	-	-	-	0.14 ± 0.02	0.12 ± 0.03	0.20 ± 0.01	0.20 ± 0.01
	MTM-data2-CG random-age quadratic	0.52 ± 0.12	0.62 ± 0.11	0.29 ± 0.34	-	0.26 ± 0.10	0.21 ± 0.09	0.15 ± 0.02	0.11 ± 0.03	0.22 ± 0.03	0.20 ± 0.04
WW	RRM	-	0.54 ± 0.07	-	0.55 ± 0.13	-	-	-	0.71 ± 0.02	-	0.61 ± 0.01
	MTM-adjusted weights	-	0.90 ± 0.05	-	0.92 ± 0.07	-	-	-	0.65 ± 0.02	-	0.72 ± 0.01
	MTM-data1-CG fixed	-	0.91 ± 0.03	-	-	-	-	-	0.64 ± 0.02	-	0.70 ± 0.01
	MTM-data1-CG random	-	0.92 ± 0.03	-	-	-	0.50 ± 0.08	-	0.64 ± 0.02	-	0.56 ± 0.03
	MTM-data2-CG fixed	-	0.89 ± 0.04	-	-	-	-	-	0.56 ± 0.02	-	0.65 ± 0.01
	MTM-data2-CG random	-	0.90 ± 0.04	-	-	-	0.45 ± 0.08	-	0.56 ± 0.02	-	0.52 ± 0.03
	MTM-data2-CG fixed-age quadratic	-	0.88 ± 0.04	-	-	-	-	-	0.56 ± 0.02	-	0.64 ± 0.01
	MTM-data2-CG random-age quadratic	-	0.90 ± 0.04	-	-	-	0.46 ± 0.08	-	0.56 ± 0.02	-	0.52 ± 0.03

^a direct additive genetic correlation

^b maternal additive genetic correlation

^c contemporary group correlation

^d residual correlation in MTM and direct permanent environmental correlation in RRM

^e phenotypic correlation

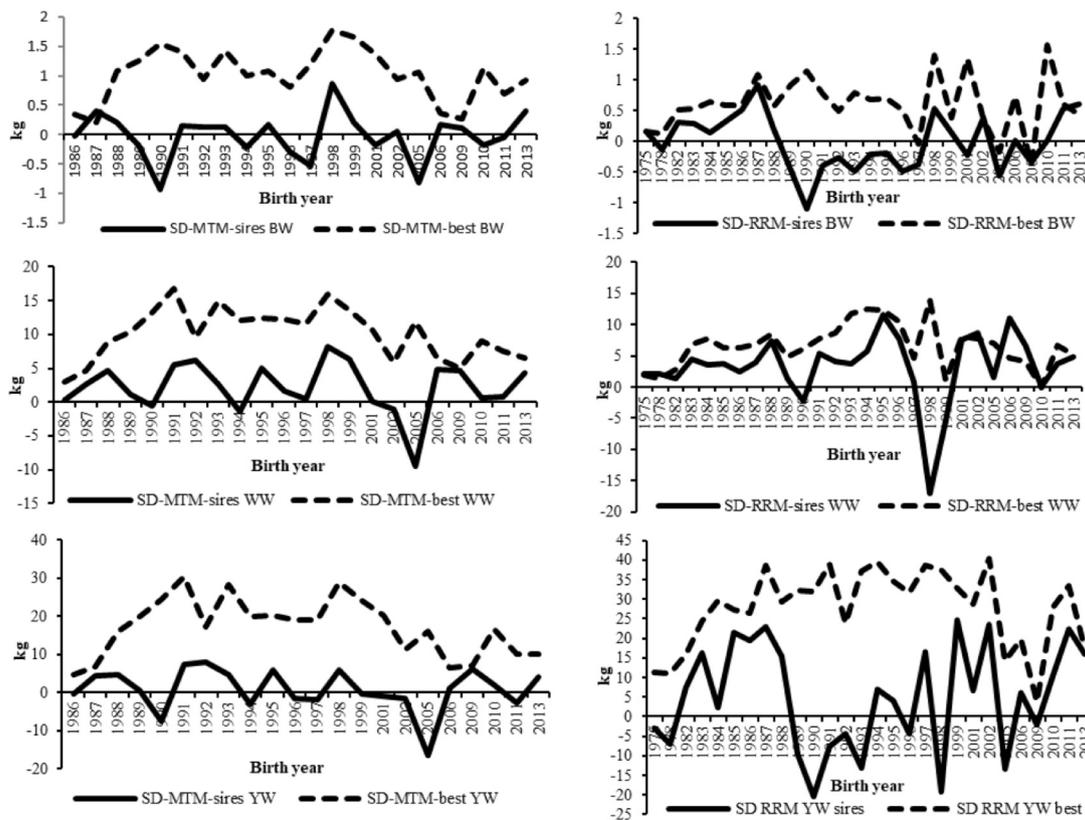


Fig. 6. Selection differentials (SD) of HC sires and best available males for BW, WW and YW in MTM-adjusted weights and RRM-433.

observations and higher orders of polynomials (de Boor 2001; Meyer 2005b; Meyer and Kirkpatrick 2005). This is consistent with the results obtained here. Moreover, in contrast to MTM, which incorporate information among traits only through linear covariances, RRM allow for more complex global consideration of information over the whole curve (Meyer 2005b). Similar results of unexpected estimates beyond biological reality have been observed for variance components analysis by RRM in other analyses of data from beef cattle (Boligon et al., 2010; Mota et al., 2013). In this study, B-spline RR models were not used as a panacea for RRM because they are also susceptible to the sparsity and irregularity of records distribution and choosing suitable knots and degrees of B-splines would not be convenient (Meyer 2005c). An increased frequency of data recording may not be feasible as it would increase the cost to weigh animals on a more frequent basis from birth to beyond a year of age. As a potential alternative, if the maximum degree of polynomials were established in advance, the ages at which to record weights in order to maximize the precision of random regression coefficients could be determined from statistical theory.

Usually, the number of weight records in beef cattle production is dependent on the length of growth trajectory which differs among breeds. For example, Nellore cattle typically show more data than European breeds (Albuquerque and Meyer 2001). Therefore, as mentioned above, in shorter times, getting more data points than BW, WW and YW would be possible if the relative costs are provided to weigh animals regularly. In this study, although there were fewer points available on the growth trajectory than those normally applied in RRM, the purpose was to see how the results deviated from MTM specially when working with local beef herds.

On the other hand, when there are more points available for longer trajectories, the frequency of data for those points are more important to affect the analysis than the number of points. For example, in a research study done by Meyer (2005a) regarding the use of RRM to analyze the growth curve of Australian Angus cattle, although there were more records available for the growth trajectory than this study,

only 1.5% of the animals had 7-9 records and they mostly showed four main critical points on average. Moreover, considering Boligon et al. (2010) and Oliveira et al. (2017) results, even with more points available, it was still possible to observe extreme values at the boundaries due to selecting a model with higher orders that matched the statistical criteria and not what might be reasonable with biological realities. In other words, if there are data with high frequency for the critical points of a growth trajectory, RRM will be more sensitive to the orders than the number of points and/or the length of the growth trajectory.

However, it could be argued that in the case of HC where weaning typically was at a younger age than the 205-d standard, RRM would allow more data to be used in prediction of a 205-d weight EBV than if weaning weights were edited to the 160 to 250 day window recommended by the Beef Improvement Federation (2018). This increase in the amount of data used is expected to increase accuracy of EBV for some selection candidates due to their own phenotypes being included in the analysis (Meyer 2004; Bohmanova et al., 2005; Mota et al., 2013). Furthermore, according to a research done by Bohmanova et al. (2005), for a specific length of growth trajectory (similar to this study), although incorporating additional records in RRM increased the accuracy compared to MTM, the change in accuracy would be small enough to conclude that both models performed similarly. Therefore, as observed in the variation results, even with fewer data points on the growth trajectory, RRM performed similar to MTM so that there may be no advantage to get more frequent data points.

Maternal effects are typically thought to be important from birth to weaning age and then gradually decreasing to the end of growth trajectory. In the present study, estimates of maternal genetic effects other than on WW were not significant. In addition, maternal permanent environmental effects accounted for negligible proportion of phenotypic variance (not shown). This may be logical in that for HC there were few calves per cow and virtually all cows produced calves in a single herd. Therefore, as opposed to Boligon et al. (2010) and

Mota et al. (2013), the exclusion of maternal permanent environmental effects not only did not affect the overall parameter estimation but also provided a better approximation for standard errors which could be considered when using RRM.

In this study, despite the usual MTM that employs adjusted weights in the analysis, other MTMs were also defined in which WW and YW records were not subjected to a priori adjustment, but rather their real ages were incorporated into the models as both linear and quadratic covariates. This increased the estimation of genetic variation and consequently estimates of direct heritability which implied that the pre-adjustments of records to defined ages in MTM and/or some standardization of ages through the process of RRM may lead to a reduction in the corresponding genetic variation.

The expanded range in ages at which weights were deemed acceptable for incorporation into the analysis (dataset 2) did not result in any specific changes of the estimated variance components and genetic parameters because the relaxed restrictions on age did not add many records to the analyses. Additionally, incorporation of ages into the model for dataset 2 as quadratic effects also did not affect the variance component estimates. This latter result may reflect the observation that weight changes across the growth trajectory were mainly linear.

Adding CG as fixed or random did not affect the overall genetic variation and other variance components except for an increase in Var (p) and consequent reduction in estimates of direct heritability. Contemporary groups are defined as a group of animals that benefit from common environmental and management factors. They are usually taken into account as fixed effects in animal models to make the results of genetic evaluations invariant and reduce biases in genetic comparisons due to the association between CG and sires (Van Vleck, 1987). However, if they are random, the prediction error variance will be reduced due to using a larger amount of data for prediction of animal breeding values (Visscher and Goddard, 1993). Today, there is no consensus about the best method of applying this effect. However, in general, CG is considered fixed in beef cattle genetic evaluations (Ramirez-Valverde et al., 2008). Likewise, many published literature regarding applications of RRM and MTM in beef cattle that have been referred to here, used CGs as fixed effects and hence the results of this study were more following and similar to them. Of course, some studies have shown that random CGs would be a better choice if there are numerous levels of this effect, small subclasses are predominant and limited use of AI in the population has led to a weak genetic connectedness among them (Schaeffer, 2009; Vostry et al., 2015). Although having several herds across Canada, the HC data for this study originated from one farm so that there were not many levels or small subclass of CGs available and regarding the similarity in MTM results, it seemed reasonable to consider CGs as fixed effects.

Fleming (2013) estimated the direct heritability of BW in HC to be 0.06 through a univariate analysis. Thus, the value reported by Fleming (2013) was slightly less than the present estimate of approximately 0.10. However, Fleming (2013) also obtained greater heritability estimates for WW (0.30) and YW (0.42) using a bivariate model than were observed in this study for RRM and MTM-adjusted weights. Estimates of maternal heritability for BW, while still near zero, were greater in Fleming (2013) (0.03 vs 0.01), but greater for WW in the present study (0.13 vs 0.04). However, the MTM for the analysis of datasets 1 and 2 with fixed CG produced similar estimates of heritability for WW and YW to those of Fleming (2013). The almost zero estimation of maternal heritability for BW might be related to the low number of calves per cow available and/or simply that in HC BW was not affected by the heritable factors influencing the uterine environment (Ferrell, 1993). However, for WW, the higher maternal heritability likely reflects differences in milk production (MacNeil and Mott, 2006).

Positive genetic correlations may result from a part-whole relationship between traits. For example, weaning weight makes up a part of yearling weight. However, the very large values in MTM may also

arise from pre-adjustment of the data before analysis (Iwaisaki et al., 2005).

According to Boligon et al. (2010) (although they did not report the standard errors), the similar direct and maternal genetic correlations in RRM suggest that these effects are likely controlled by the same genes and that are considered similar between different traits. However, although there was a weak maternal genetic correlation between BW with WW and YW in MTM, the resulting standard errors were high and similar to RRM which reflected the poor structure of HC data. Moreover, the moderate to high maternal genetic correlation between WW and YW in both models indicates that the maternal effect on YW is probably a carry-over effect from WW (Boligon et al., 2010).

With respect to RRM, BW appeared not to be very genetically correlated to WW and YW, which would be desirable from an economic point of view when selecting bulls with lower BW to facilitate ease of calving. The somewhat lower direct genetic correlation between BW and WW in RRM might be due better modeling of age in both fixed and random effects compared to MTM (Iwaisaki et al., 2005). In this study, direct additive genetic correlation between WW and YW in MTM was slightly greater than Fleming's result (0.81) in 2013.

Except for genetic correlations, the estimates of variance components and heritability for BW were approximately of the same magnitude in comparable MTM and RRM models. This reflected the importance of the fact that there are similarities in using MTM or RRM when enough data is available for each time point in the growth curve. Compared to BW and WW, there was a slightly greater difference between the two models in measuring the changes over time for YW. This may originate from the low number of actual records available for 365 days of age in RRM as an end point relative to MTM. The lower magnitude of the genetic correlation between WW and YW in RRM may have resulted in higher differences between their genetic values relative to MTM. However, despite YW, EBV trends for other traits approximately followed a similar pattern in both models. Furthermore, as there is a positive genetic correlation between WW and YW, it seemed RRM estimated a more realistic increasing trend for both traits than MTM which showed a decreasing trend for YW.

Genetic trends for weight traits in HC were directly affected by the sires selected to produce calves in each year. Sire selection did not always maximize the genetic selection differentials (Fig. 6). Sire selection always used the phenotypic records of weaning and yearling weights and there was no selection based on EBV or an index until 2014. In fact, lack of a structured management program that takes into account genetic values when selecting animals, has resulted in very little meaningful progress in genetic improvement of growth traits of a local beef breed like HC. Additionally, a large proportion of the herd was sold in 2000 leading to a meaningful reduction in the number of candidates for selection. During 2004 to 2008, little sire selection was practiced which may have also contributed to the decreasing trend in genetic values of weight traits in recent years.

7. Conclusion

Results of this study suggest similarities between RRM and MTM for most estimates of variance components and genetic trends of HC. This is mainly because records occur at standard points for both models. Currently, choosing MTM for HC genetic evaluation seems simpler. Increased weaning and yearling weights were the main objectives for HC from its inception. Tighter control of when these traits are recorded and replacement of selection based on phenotypes with selection based on EBV are expected to accelerate progress toward this goal. In these data, whether CG were considered random or fixed had little effect and thus fixed CG were deemed preferable due to their being more parsimonious with other genetic evaluations for beef cattle.

CRedit authorship contribution statement

R. Khorshidi: Software, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization. **M.D. MacNeil:** Supervision, Conceptualization, Methodology, Validation, Writing - review & editing. **D.P. Hays:** Resources, Funding acquisition. **M.K. Abo-Ismael:** Resources, Data curation. **J.J. Crowley:** Resources, Validation. **E.C. Akanno:** Validation. **Z. Wang:** Validation. **G. Plastow:** Supervision, Validation, Writing - review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that there are no conflicts of interest.

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Supplementary materials

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