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Genetic Analysis of Early Growth of Crossbred Dairy Cattle in Central Ethiopia Using Random Regression Model

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የዲቃላ ጥጆችን የዕድገት ባህሪ የሚያሳዩ የጋራ ልይይት ክፍሎችን (covariance components) እና የጀነቲክስ ልኬቶችን (genetic parameters) ለመገመት፣ እንዲሁም ልኬቶቹ በከብቶቹ የዕድገት ወቅት የሚያሳዩትን አዝማሚያ ለማወቅ ጥናት ተካሂዷል፡፡ ለዚህ ጥናትም በሆለታ ምርምር ማዕከል ከተወለዱ 50 በመቶ የሆልስቴን ፍሬዥያን ደም ባላቸው ዲቃላ ጥጆች ላይ በየወሩ በተሰበሰበ 13,839 በሆነ የክብደት መረጃ ላይ ተስማሚ ስታስቲካዊ ሞዴልን በመጠቀም ትንተና ተከነውኗል፡፡ ለዲቃላ ጥጆች ዕድገት ምክንያት የሆነው ከወላጆቻቸው የሚያገኙት የዘር ውርስ መጠን በ0.16 እና 0.30 መካከል እንደሆነና ከልደት እስከ 120 ቀን ዕድሜያቸው ድረስ የመጨመር አዝማሚያ እንደሚያሳይ ጥናቱ አሳይቷል፡፡ የዲቃላ ጥጆች ከእናት የሚያገኙት የዘር ውርስ መጠንም ከተወለዱበት ጊዜ ጀምሮ እስከ 540 ቀን ዕድሜያቸው ድረስ የመቀነስ አዝማሚያ እንዳለው ተረጋግጧል፡፡ ከተራራቁ የጥጆች ዕድሜዎች በተወሰዱ ክብደቶች መካከል የታየው ጀነቲካዊ ዝምድና በተከታታይ የጥጆች ዕድሜዎች መካካል ከተወሰዱ ክብደቶች ጋር ሲነፃፀር አንስተኛ ሆኖ ተገኝቷል፡፡ የዝምድና መጠኑም ከ0.03 እስከ 1.00 ነበር፡፡ ዲቃላ የወተት ከብቶችን በወተት ማቆሚያ ዕድሜያቸው መረጣ በማካሄድ የቁም ክብደታቸውን ወይም ዕድገታቸውን ማሻሻል እንደሚቻል ጥናቱ አመልክቷል፡፡

Abstract

The study was carried out to estimate the covariance components and genetic parameters associated with growth traits of crossbred cattle using random regression models as well as to examine their trend over trajectories. The study encompassed a total of 13,839 body weight records taken across different months from birth up to 540 days of age on 902 F_1 HFB (Holstein Friesian Boran) crossbred growing calves born at Holetta Agricultural Research Center (HARC) between 1978 and 2003. Random Regression Models (RRM) were fitted to cubic Legendre polynomials (LP) of age at recording for additive genetic and permanent environmental effects of the animals and linear LP of age for their maternal genetic effects. The findings indicated that the additive direct heritability ranged between 0.16 and 0.30 and increased from birth until the age of 120 and then decreased from the age of 150 - 300 days and slightly increased again until the age of 450 days followed by slight decrease at the end of the trajectory. Maternal heritability patterns showed a decreasing trend from birth (0.07) to the age of 270 days (0.002) and continued declining to value closer to zero at the end of growth period (540 days). Genetic correlation estimates were higher between consecutive weight records as compared to records that were far apart from each other. The correlation estimates ranged from 0.03 to unity (1.00). Selection on crossbred dairy cattle can be done at weaning age for better genetic improvement of body weight traits.

Introduction

Genetic evaluation of growth traits are generally focused on beef cattle since growth is the major economical trait associated with the beef industry. However, growth traits are also important as goals in breeding dairy cattle and these goals need to be assessed in any breeding program. In dairy cattle, stocks can be selected earlier only if growth rates are better than those of their contemporaries as such heifers can calve at younger age and increase their lifetime productivity, (Hohenboken, 1985 as cited in Gizachew *et al*. 2003).

Some studies (Sendros *et al*., 2003b; Kefena *et al*., 2006) have been conducted on relative performances and genetic parameters pertaining to growth traits viz. birth weight (BW), weaning weight (WWT), six month weight (SMWT) and yearling weight (YWT) of indigenous breeds and their crosses. Moreover, several studies (Beyene, 1992, Sendros *et al*., 2003a; Kefena *et al*., 2006; Kefena *et al*, 2011; Kefena *et al*., 2013) have been made to improve some of the economically important traits of crossbred cattle associated with milk production and reproduction performances.

Growth in cattle has also been described using univariate and multivariate models, in which weight of individual animals were accessed at a particular age assuming constant variances between ages (Haile-Mariam and Kassa-Mersha, 1995; Sendros *et al*., 2003b; Wasike, 2006). In these analyses, the ages describing the traits were predefined to certain landmarks ages and adjustment of the weights are made to the closest landmarks and weights farthest from the landmark ages were discarded (Nobre *et al*., 2003). Consequently, there can be loss of information following elimination of some animals in the evaluation process and a reduction in accuracy of estimates due to pre-adjustments of the records (Tier and Meyer, 2004). On the other hand, in multivariate analysis as the over-parameterization problem is encountered, the information about covariance structure of repeated records and trend of change of a trait over time cannot be provided when a large number of longitudinal measurements are considered (Meyer and Hill, 1997; Fischer et al., 2004). Due to these restrictions, a more flexible and accurate method namely, random regression models (RRM) are described by orthogonal polynomials which are used for the estimation of parameters for traits that change continuously over time in beef cattle (Meyer, 2004). Furthermore, studies by Coffey *et al*. (2006) on the growth of Holstein Friesian heifers investigated the genetic associations among birth weight, weaning weight, and calving weight using RRM.

The patterns of variance components of growth traits for crossbred growing dairy cattle from birth to puberty age have substantial economic implication and greatly contribute to the dairy cattle genetic improvement programs. However, in

Ethiopia, nearly all available evidences on crossbred dairy cattle focused on the post-calving traits such as productive and reproductive performances. So far, no empirical evidence was available on the trajectories of genetic parameters of early growth traits for growing crossbred dairy cattle produced in Ethiopia. Therefore, the objectives of this study were to estimate variance components and genetic parameters for early growth traits in crossbred cattle and examine their patterns over trajectory.

Material and Methods

The study site

The Holetta Agricultural Research Center (HARC) is situated 35 km west of Addis Ababa at 38.5°E longitude and 9.8° N latitude. It is situated at about 2400 m above the mean sea level. The average annual rainfall is about 1200 mm and an average maximum temperature is 21.3 (18.6-24˚C). Common livestock species reared around the study area are cattle, sheep, goats, and equines.

Animal management

All calves were weighed immediately after birth and allowed to suckle their dams for the first 24 hrs. Then after, the calves were taken to calf rearing pen and the colostrum feeding continued up to their 4th days of age and feeding of whole milk was carried out until weaning (98 days) by bucket feeding. The offer of milk was 10% of calves' body weight. Each calf was fed a fixed amount of 260 kg of whole milk mixed from different cows during the pre-weaning period. Weaned calves were kept indoors until 6 months, during which they were fed ad lib on natural pasture hay made from andropogon and hyperina dominated grass species and supplemented with approximately 1 kg per day per animal of concentrate, which was composed of 30% wheat bran, 32% wheat middling, 37% noug seedcake (*Guizoita abysinica*) and 1% salt. Heifers older than six months of age were allowed to graze on natural pasture for about 8 hrs during daytime. At night, all animals were housed in an open shade and supplemented with natural pasture hay. Treatment and vaccination of the herd for common diseases such as foot and mouth disease (FMD), black leg, anthrax, lump skin diseases (LCD) and pasteurolosis were carried out by the animal health research division of the HARC.

Data source and traits

Repeated records of growth data and pedigree information were filtered from growing F1 HFB (50% HF and Ethiopian Boran) crossbred calves born between 1978 and 2003 at Holetta Agricultural Research Center, using HF bull semen imported from Sweden. Due to incomplete data records and differences' in the management of the calves, weight data from calves born before 1978 and after 2003 were excluded from the analysis. One of the reasons was that F1 crossbred calves born before and after the aforementioned years were reared by suckling their dams. The calves used for this study were managed similarly and weighed every month from birth to 540 days of age. The initial data set consisted of 15,112 weight records on 902 F1 HFB (Holstein Friesian Boran) crossbred calves. All the data were checked for reliability of pedigree information and correct dates of birth and weighing. Records with inconsistent pedigree information and dates were discarded. Only records of animals with at least four weight records were considered. The edited data set included 13, 839 weight records from 902 calves. These calves were progeny of 91 Holstein Friesian sires and purchased 398 Ethiopian Boran dams with 1245 animals in the pedigree.

Statistical analysis

Preliminary data analysis

Preliminary least squares mean analysis was carried out to identify fixed effects that significantly affect the growth traits using GLM model of the Statistical Analysis System (SAS, 2008). The fixed effects considered were sex, season of birth, year of birth and parity.

Random regression analysis

To determine the most appropriate polynomial order to be fitted as fixed effect, preliminary analyses with ordinary polynomials of second to fifth order were carried out until non- significant change in R^2 values of consecutive regression model was also obtained. Weight as a function of age in days at weighing was included as a fixed regression of orthogonal polynomial of order four. This fixed regression describes the average growth curve of all animals with records. Individual crossbred calves were allowed to deviate from this overall curve and thus have different growth coefficients for additive genetic, permanent environmental and dam genetic effect levels.

Three random effects such as additive genetic, maternal genetic and permanent environmental effects were modeled using random regression model (RRM) with Legendre polynomials (LP) of different orders (k). The reason why we included the genetic effects of the dam was to estimate pre-natal maternal genetic effect on consecutive calves’ growth. The environmental effects of the dams were not taken into account in the analysis as calves were reared by bucket milk feeding and sucked for the first 24h only. Quadratic, cubic and quartic polynomials were used for additive direct (a) and animal permanent environmental (p) effects and constant (order 1), linear, quadratic and cubic were used to model the maternal genetic (m) effect. Residual variances were modeled considering one, i.e., assuming homogeneity of variances across all ages or 7 age classes divided as follows: 0, 1 to 60, 61 to 150, 151 to 240, 241 to 330, 331 to 420 and 421 to 540 days of age.

Model of analysis

The random regression model can be described as:

$$Y_{ijk} = \mu + SX_i + BS_j + \sum_{m=0}^{3}\beta_m\phi_m(\alpha^*{}_{ijk}) + \sum_{m=0}^{K_{A-}1}(\alpha_{pm}\phi_m(\alpha^*{}_{ijk}) +$$

$$\sum_{m=0}^{K_m-1}\gamma_{pm}\phi_m(\alpha^* ijk) + \sum_{m=0}^{k_c-1}\delta_{pm}\phi_m(\alpha^* ijk) + \varepsilon_{ijk}$$

where Y_{ijk} = any of weight records; μ =total average, Sx_i = fixed effects of ith sex , BS_l = fixed effects of lth season, a* *ijk*= standardized age in range of +1 to -1; Φ_m (α* *ijk*) = the mth Legendre polynomial of age; β_m= mth fixed regression coefficients; α*pm*, γ*pm and* δ*pm* are mth random regression coefficients for direct additive genetic, maternal additive genetic, animal permanent environmental effects, respectively, related to pth animal. K_A, k_M *and* K_p denote the corresponding orders of fit; and ε*ijk* = the temporary environmental effect related to Y_{ijk}. The matrix form of above statistical model is as follows:

$$Y = XB + Z_1\alpha + Z_2\gamma + W_1\delta + \varepsilon$$

$$V\begin{bmatrix}\alpha\\ \gamma\\ \delta\\ \varepsilon\end{bmatrix} = \begin{bmatrix}K_A\otimes A & 0 & 0 & 0\\ 0 & K_M\otimes A & 0 & 0\\ 0 & 0 & Kp\otimes I & 0\\ 0 & 0 & 0 & R\end{bmatrix}$$

Y= vector of observations; B = the vector of fixed effects (including fixed effects and fixed regression coefficients) α= the vector of additive genetic direct random coefficients; γ= the vector of maternal additive genetic random coefficients; δ= the vector of animal permanent environmental coefficients. X, Z_1, Z_2 and W_1 are incidence matrices; and Σ is the vector of residuals; k_A, k_M *and* k_P are the matrices of coefficients of the covariance function for additive direct, maternal genetic and permanent environmental effects, respectively. A is the additive numerator relationship matrix and I is identity matrix. All available pedigree information was used in the building of the relationship matrix (A) for evaluation of the animal additive genetic effects

Variance and covariance functions

Parameters estimated in RR analysis were the K matrices containing variances and co variances between the random regression (RR) coefficients. The covariance function for the random effects were obtained by pre- and post multiplying K by a matrix containing orthogonal polynomials (Φ) pertaining to a set of specific ages directly from the data by REML. This resulted in an estimated matrix for the random effect for the specific ages defined by Φ. For the direct additive genetic effect, the matrix notation of the equation to estimate variance components was $\mathbf{G_0 = \Phi K \Phi'}$. Covariance matrices for the other random effects can be expressed in similar manner. These components and their patterns over the age of animals were estimated by using VCE-6 (Groeneveld *et al.*, 2010) and IML (Interactive matrix language) of SAS procedures, version 9.2 (SAS, 2008).

Model comparison

A total of eight models varying in the order of polynomial fit (from quadratic to quartic) for additive genetic and animal permanent environmental and (from constant polynomial to cubic) for maternal genetic were compared. Repeated analyses were done using likelihood ratio test (LRT) (Ch-square) until non-significant change between log likelihood values of two consecutive runs obtained to determine the best model. Selection of models was based on the log-likelihood ratio test and Akaike's Information Criterion (AIC). A model with significantly the highest ($P<0.05$) LRT and with the lowest AIC and AIC difference values was considered to be the most appropriate model.

AIC = -2LogL + 2.q where, **LogL** is Likelihood value and q is No. of model parameters.

Results and Discussion

Weight data characteristics

The numbers of weight records, mean body weight, standard deviation (SD) and coefficient of variation (CV) for various ages of animals are shown in Fig 1. A decrease in the number of records was observed after weaning age (98 days). This indicated the mortality of calves and occurrence of culling for crossbred growing cattle at young ages, especially for bull calves which were culled after weaning age, except these retained for candidate bulls. Mean body weights had an increasing pattern over age from birth to 540 days as it is expected. A decrease in growth rate after weaning (98 days of age) due to weaning stress was observed and after that it followed an approximate linear trend. The trend of SD was found to be similar across the growth trajectory of the calves. However, the trend of CV showed that variability remained almost similar across the period of growth.

Fixed effects

The result of preliminary analysis showed that fixed effects such as sex and birth season significantly affected body weight of crossbred growing calves. These fixed effects were included in the genetic analysis of growth trajectories of growing crossbred cattle. Other fixed effects like year of birth and parity of dams did not significantly affect body weight of calves and were excluded in the analysis.

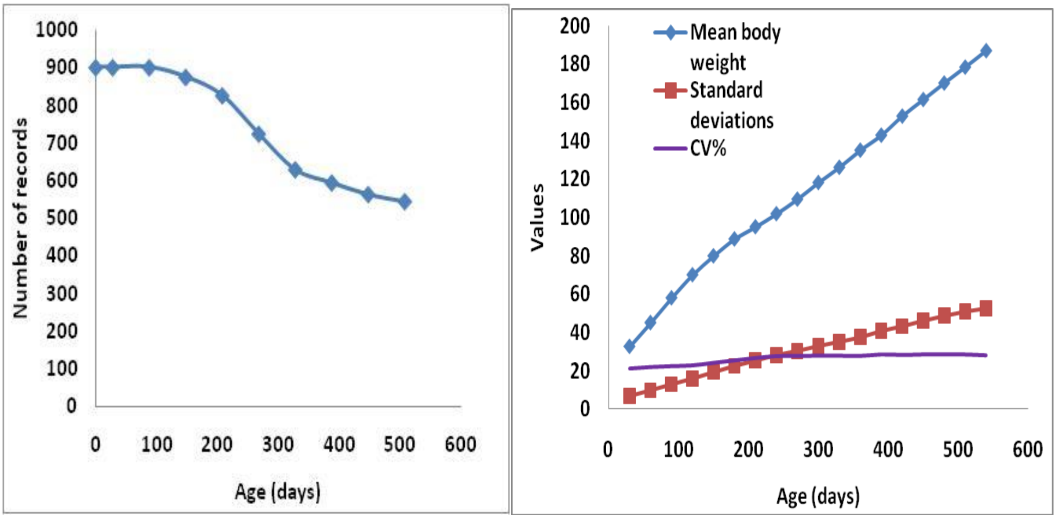

Figure 1.Number of weight records, mean body weights, Standard deviations (SD) and Coefficients of variation (CV) for Body weight at various ages from birth up to 540 days.

Random effects

Eight models were fitted to the data and a description of each with the corresponding LogL and AIC values are given in Table 1. Increasing the order of fit for direct additive genetic and, animal permanent environmental effects from 3 to 4 (Model 6) improved the fit to the data as indicated by a decrease in AIC and AIC difference values. Both LRT and AIC suggested a model at $K_A = 4$, $K_D= 2$, $K_P= 4$, and error variance (r) = 3, with a total of 26 parameters which were considered to be the most appropriate model (M424-3). Thus, variance and covariance components of growth trait were analyzed using this model.

Variance component estimates

Estimates of phenotypic, additive genetic, maternal genetic, animal permanent and temporary environmental (residual) variances were obtained using random regression model (RRM) and are presented in Figure 2. Additive genetic variance showed an increasing trend from birth up to the end of trajectory (540 days). The variance showed strongly increasing trend from birth up to about 98 days of age followed by a slightly decreasing trend up to the age of 210 days and again strongly increased up to the age of 510 days and decreased again at the end of trajectory. The increasing trend in additive genetic variance up to weaning age was because of better feeding management of calves and at this age period the permanent environmental effect was supposed to be lower as compared to post weaning period. The observed declined trends after weaning could be due to weaning stress and the exposure of animals to outdoor management in which growing calves were not fed based on their requirement to express their genetic potential for growth. This implies that nutritional intervention at post- weaning stage can influence the growing crossbred calves which can be ascribed to reduction in maternal and permanent environmental effects and the same can have a carryover effect at later ages. The additive genetic variance trend in this study was found to be similar with findings obtained on growth trait of Kenyan Boran cattle using RRM (Wasikie *et al.*, 2007). Albuquerque and Meyer (2001) also obtained the same results on the growth of Nellore Cattle evaluated from birth up to 630 days of age. Another study on the growth of Brazilian Nelore cattle (Boligon *et al.*, 2010) indicated increment in the additive genetic variance from birth till 800 days of age. The enhancement in the values of additive genetic variance from birth to weaning age (98 days) also implies that response to selection may be higher if selection were based on weight taken at the age of weaning rather than other latter age points.

Table 1. Order of fit for random effects, total number of parameters (q), log likelihood function (log L), AIC, change in AIC (ΔAIC), number of parameter (p) and number of parameters for residual (r)

Model	K_A	K_P	K_D	p	r	q	2q	LogL	AIC	ΔAIC
1	3	4	1	17	3	20	40	-38817.2	77674.46	1214.4
2	3	4	2	19	2	21	42	-38789.3	77620.54	1160.48
3	3	3	4	22	3	25	50	-38250.4	76550.50	90.44
4	**4**	**4**	**2**	**23**	**3**	**26**	**52**	**-38204.1**	**76460.06**	**0**
5	4	5	1	26	3	29	58	-39804.6	79667.2	3207.14
6	5	4	2	28	3	31	62	-39125.0	78312.00	1851.94
7	4	4	4	30	3	33	66	-38966.9	77999.76	1539.7
8	4	5	3	31	3	34	68	-39805.0	79678.04	3217.98

q= k(k+1)/2+ r , for k= order of fit for each random effects. (ΔAIC)= The deviation of smallest AIC value from each AIC values.

Phenotypic, permanent, and temporary environmental (residual) variances increased along trajectory of age with greater increase of permanent environmental variance than additive genetic variance. These trends were similar with the result obtained on growth of Kenya Boran cattle (Wasike *et al.*, 2007). In addition, some studies undertaken using RRM for body weight of cattle at different ages showed large increases of variances, (Albuquerque and Meyer, 2001; Nobre *et al.*, 2003; Meyer, 2005). However, the findings from the present study indicated a gradual increasing trend of variances throughout the trajectory when compared to the findings in Nellore cattle (Boligon *et al.*, 2010), which showed strongly increasing trends from birth up to the age of 500 days and then gradually decreased up to the end of trajectory. The difference could be due to the crossbred growing calves used in this study reared under bucket milk feeding system up to their weaning age (98 days) and then exposed to weaning stress. Whereas those used in the report had a chance of suckling, their dams until their weaning age (240 days) since they are raised in pasture (Boligon *et al.*, 2010).

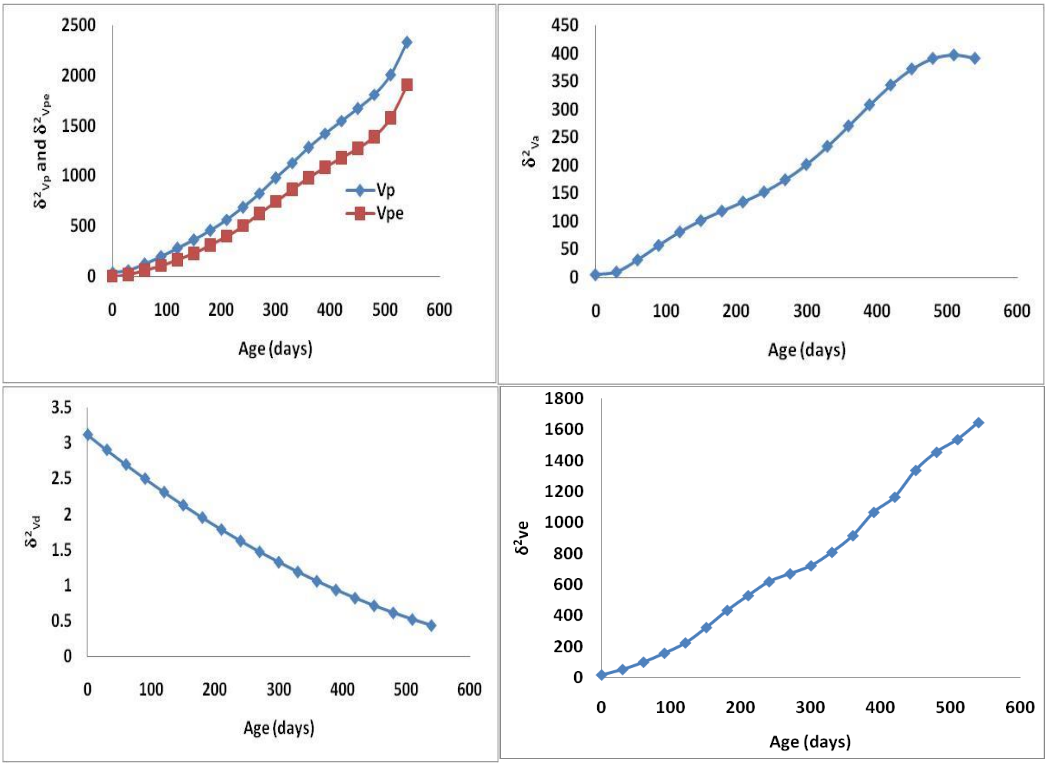

Figure 2. Phenotypic and permanent environmental variances (top left), additive genetic variance, (top right), maternal genetic variance (bottom left) and residual variance (bottom right) of body weight traits estimated using (M442-3) model over ages.

The present study also indicated that dam variance had strongly declining trend from birth throughout the trajectory. This result was not supported by other reports (*e.g.* Albuquerque and Meyer, 2001; Boligon *et al*., 2010), which indicated that maternal variances had increasing trend from birth up to weaning age and then decreased up to the end of trajectory. The difference is due to the reason that the animals used in the reports suckled their dam where as these used in this study did not suckle their dams. The variance due to prenatal dam effect (maternal genetic variance) showed lower contribution to total variance when compared to other sources of variances in this study. Thus, the additive genetic variance could not be inflated much if random dam effect was not included in the genetic evaluation of growing crossbred cattle reared using bucket milk feeding system.

Proportions of phenotypic variance

Direct and maternal heritability and permanent environmental variance as proportion of phenotypic variance estimates for body weight of crossbred replacement cattle are presented in Figure 3. The result indicated direct heritability estimates increased after birth (0.1) until the age of 120 days (0.30) and then decreased to the end of trajectory. This heritability was found to be comparable with result of Albuquerque and Meyer (2001) who obtained on Nellore cattle (0.14 -0.32) and Wasike *et al*. (2007) on Kenyan Boran beef cattle (0.11 - 0.33), but lower than the findings of Boligon *et al*. (2010) on Nellore cattle (0.32 – 0.42) raised on pasture using RRM. The difference in heritability between this study and the reports may be due to the difference in environment under which the animals were managed. The increase of direct heritability observed before weaning in this study may be resulted due to relatively better and uniform management of calves and at this growth period the contribution of additive gene effect is more expressed. The reason why the direct heritability of growing crossbred cattle showed decreasing trend from the age of about 98 up to 300 days may be due to environmental effect (weaning stress) which means the heritability of weight trait is affected by high animal permanent environmental effect. High heritability of growth trait at about weaning age (98 days) was of the interest for selection purpose. At these ages' intervals, high rate of response would be achieved if selection were carried out given the high heritability estimates and relatively low proportions of environmental influence than at later ages.

Additive heritability and animal permanent environmental variance as proportion of phenotypic variance showed opposite trend from weaning age up to the end of trajectory. Similar pattern was observed for Boran Kenyan cattle (Wasikie *et al*, 2007). The decrease in direct heritability from the age of about 120 days up to 300 days caused by increase of permanent environmental variance in proportion of phenotypic variance. This implies that the management of crossbred calves should be improved at this period so that to reduce negative influence of permanent environmental effect on growth performance of animals.

Maternal heritability decreased rapidly from birth (0.07) to the age of 270 days (0.002) and after that continued declining to value closer to zero at the end of growth period (540 days). The findings are in close accordance with those of Sendros *et al*. (2003b) who reported the values to be (0.07±0.02) for birth weight), (0.04±0.02) weaning weight) and (0.04±0.02) on pre weaning average daily gain) on Ethiopian Boran cattle and their crosses with Holstein Friesian breed using different alternative animal models. This is expected since the calves used for those studies did not suckle their dams. However, the findings pertaining to heritability are not in accordance with the findings of Albuquerque and Meyer, (2001) in Nellore cattle, which showed that maternal heritability estimates increased from birth (0.02) to about 120 d of age (0.25) and decreased with age thereafter. The reason was due to Nellore cattle were raised under Ranches where the calves were allowed to suck their dams for extended period. The studies by Meyer, (2005) also found that the maternal heritability estimates in Angus cattle using RRM were lower than those found in the report using multivariate methods of analysis. This lower maternal heritability found in this study is related with calves rearing system i.e., less post- natal contribution of dam to their progeny since crossbred calves had no chance of suckling their dam.

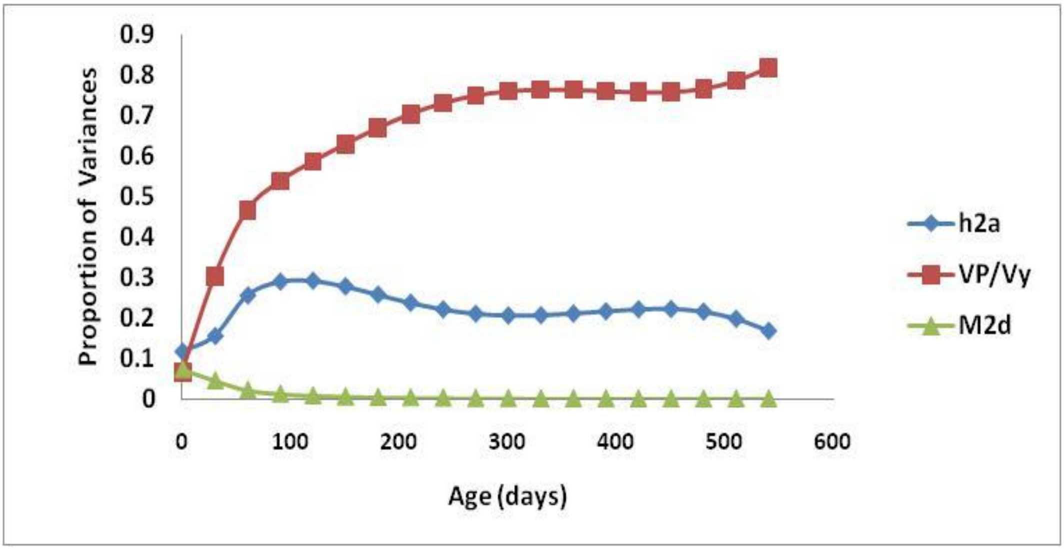

Figure 3. Changes of animal direct genetic heritability (h^2_a), animal permanent environmental variance as proportion of total Variance (Vp/Vy) and maternal genetic heritability (M^2_d) over ages.

Covariance functions

Estimates of covariance function (CF) for additive genetic, permanent environmental and dam genetic effects and their corresponding correlations and eigenvalues are presented in Table 2. The variance of random regression coefficients was the highest at intercept and the lowest at cubic term. Estimates of permanent environmental variance were higher than additive genetic variances for intercept, linear, quadratic, and cubic coefficients. Correlation estimates between the intercept and linear coefficients were positive and high for additive genetic and permanent environmental effects, but negative for maternal genetic effects. The corresponding correlations between the intercept and the quadratic coefficients were negative and medium for additive genetic effects, but low for permanent environmental effects. The correlation between intercept and cubic coefficients was also negative and low for additive genetic and permanent environmental effects. The first eigenvalues of the coefficient matrices explained 87.6%, 87.1%, and 100% of additive genetic, permanent environmental and dam genetic variances, respectively. The second eigenvalues accounted for 11.6%, 10.3% and 0% of these three variances, respectively, while the third eigenvalues explained 0.69% and 2.5% of the variation and the fourth explain 0.1 and 0.01% of the variances of additive and permanent effects, respectively.

The covariance and correlation structure between random regression coefficients obtained in this study showed strong relationship between the intercept and the linear and quadratic coefficients. The present study indicated higher covariance and correlations between the RR coefficients for the permanent environmental effects than for additive genetic effects. This was due to the high environmental influence on growth performance of crossbred growing dairy cattle on Holetta research farm. This means, the high permanent environmental effect influences the expression of desirable genes in a negative manner. It indicates that proper management interventions are required for crossbred calves to improve their growth performances. The observations too are in accordance with the findings of Wasikie *et al*, (2007) on Kenyan Boran beef cattle for both permanent environmental and additive genetic effects. However, the observations are not in accordance with those of (Arango *et al.*, 2004; Albuquerque and Meyer, (2005) and Meyer, (2005). The resulted variation may be due to relatively less permanent environmental effect on these beef calves that were reared by suckling their dam up to about 8 months of age as compared to crossbred calves which were reared under bucket milk feeding up to weaning age (98 days) and exposed to weaning shock thereafter.

Table 2. Estimates of variances (diagonal), covariance's (below the diagonal), and correlations (above the diagonal) between random regression coefficients and eigenvalues (λ) of the (co)variance matrix obtained with models M424-3 for additive genetic, maternal genetic and animal permanent environmental effects

Effect	Order of fit	0	1	2	3	λ
Additive genetic	0	267.60	0.77	-0.51	-0.06	336.04
	1	125.48	99.06	0.11	-0.60	44.61
	2	-24.42	3.06	8.57	-0.53	2.65
	3	-2.83	-17.26	-4.53	8.47	0.38
Additive maternal	0	2.4	-1.00			2.71
	1	-.85	0.30			-5.78E-06
Animal permanent environment	0	938.84	0.86	-0.30	-0.31	1210.20
	1	479.48	333.89	0.12	-0.33	143.65
	2	-89.73	21.42	92.48	0.57	34.94
	3	-47.11	-29.10	26.88	23.76	0.18

M424-3= Polynomial model with order of fit at K_A*= 4,* K_D*= 2,* K_P*= 4, error variance= 3 for additive genetic, additive maternal, animal permanent environmental and error variances, respectively.*

Eigen values and eigenfunctions of genetic covariance functions provide an insight into the way selection affects the mean growth trajectory (Kirkpatrick *et al.*, 1990; Lewis and Brotherstone, 2002). The high estimate of the leading eigenvalue of the additive genetic coefficient matrix in this study indicates that selection on the basis of the corresponding eigenfunction would result in a rapid response. On the other hand, response to selection associated with the second and third eigenvalues would be slow as each account for very little additive genetic variation. Similar observation was also obtained in studies evaluating growth performance of beef cattle in the tropics (Albuquerque and Meyer, 2001; Meyer, 2005).

The additive genetic and phenotypic correlation estimates between body weights from birth to 540 days of age obtained with model (M424-3) are shown in Table 3. The genetic correlation estimates decreased as the distance between times at which repeated records taken increased. The estimates ranged from 0.03 between birth and later age points to unity (1.00). The findings are in close accordance with the observations of Wasikie, *et al*., (2007); Meyer, (2005) on Kenyan Boran cattle using RRM. Another report indicated genetic correlations were moderate to high (0.47 to 0.91) for birth, weaning and yearling weights (Pico, 2004) using multivariate model. This difference may be due to analysis model and breeds of animals as well as the management environment. In the present study, genetic correlation between birth weight and other weights was low due to difference in genetic control of weight at these sets of ages. Under the present condition of selection for growth of crossbred replacement cattle using birth weight can be misleading, but the correlation between weaning weight (about 90 days) and other weights up to 240 days of age is found to be higher (>0.80) because of pleiotropy and linkage. Early selection of growing replacement cattle can be done in these age ranges (90 -240 days), especially, at weaning age to reduce heifer rearing cost.

Phenotypic correlation patterns were found to be inconsistent between early ages, but moderately to highly positive between intermediate and later ages. This implies that animals that had higher weights at intermediate ages (180-330 days of age) could reliably be expected to have higher weights at later ages. Similar patterns were observed in growth of Bonsmara cattle (Nephawe, 2004) and Kenyan Boran cattle (Wasikie *et al*, 2007) using RRM. Another study using multivariate model (Pico, 2004) revealed smaller estimates of phenotypic correlations as compared to this study.

Table 3. Genetic (below diagonal) and phenotypic (above diagonal) correlation between weights at different age points

Ages	0	30	60	90	120	150	180	210	240	270	300	330	360	390	420	450	480	510	540
0	-	0.13	0.05	0.02	0.02	0.02	0.03	0.04	0.06	0.08	0.09	0.11	0.12	0.13	0.15	0.16	0.17	0.17	0.17
30	0.11	-	0.60	0.61	0.60	0.58	0.54	0.50	0.45	0.41	0.37	0.33	0.30	0.28	0.27	0.26	0.26	0.27	0.27
60	0.16	0.96	-	0.79	0.79	0.77	0.73	0.68	0.62	0.56	0.50	0.45	0.41	0.38	0.35	0.33	0.32	0.32	0.31
90	0.22	0.93	0.99	-	0.86	0.85	0.82	0.78	0.72	0.66	0.61	0.56	0.51	0.47	0.44	0.41	0.39	0.37	0.34
120	0.23	0.91	0.98	1.00	-	0.90	0.88	0.85	0.80	0.75	0.70	0.65	0.61	0.57	0.53	0.50	0.46	0.43	0.39
150	0.20	0.89	0.96	0.98	0.99	-	0.92	0.90	0.87	0.83	0.79	0.74	0.70	0.66	0.62	0.58	0.54	0.49	0.43
180	0.16	0.85	0.92	0.95	0.97	0.99	-	0.93	0.92	0.89	0.85	0.82	0.78	0.74	0.71	0.66	0.61	0.55	0.47
210	0.10	0.80	0.86	0.89	0.93	0.96	0.99	-	0.94	0.93	0.91	0.88	0.85	0.81	0.78	0.73	0.68	0.60	0.51
240	0.04	0.73	0.78	0.82	0.87	0.92	0.96	0.99	-	0.95	0.94	0.92	0.90	0.87	0.84	0.79	0.73	0.65	0.55
270	0.03	0.64	0.68	0.73	0.79	0.85	0.91	0.96	0.99	-	0.96	0.95	0.93	0.91	0.88	0.84	0.78	0.70	0.59
300	0.09	0.55	0.58	0.63	0.70	0.77	0.84	0.91	0.96	0.99	-	0.97	0.96	0.94	0.92	0.88	0.82	0.74	0.63
330	0.13	0.46	0.48	0.53	0.61	0.69	0.77	0.85	0.92	0.97	0.99	-	0.97	0.96	0.94	0.91	0.86	0.78	0.67
360	0.17	0.38	0.40	0.45	0.53	0.61	0.71	0.80	0.88	0.94	0.98	1.00	-	0.97	0.96	0.94	0.89	0.82	0.71
390	0.19	0.32	0.33	0.38	0.46	0.55	0.65	0.75	0.84	0.91	0.96	0.98	1.00	-	0.97	0.96	0.92	0.86	0.76
420	0.19	0.27	0.28	0.33	0.41	0.51	0.61	0.71	0.81	0.88	0.94	0.97	0.99	1.00	-	0.97	0.95	0.90	0.81
450	0.18	0.23	0.25	0.30	0.38	0.48	0.58	0.69	0.79	0.87	0.92	0.96	0.98	0.99	1.00	-	0.97	0.94	0.87
480	0.15	0.21	0.24	0.30	0.38	0.47	0.58	0.68	0.78	0.86	0.91	0.95	0.97	0.99	0.99	1.00	-	0.97	0.93
510	0.11	0.22	0.25	0.31	0.39	0.48	0.58	0.68	0.78	0.85	0.91	0.94	0.96	0.98	0.99	0.99	1.00	-	0.97
540	0.03	0.24	0.29	0.35	0.43	0.52	0.61	0.70	0.78	0.85	0.90	0.93	0.95	0.96	0.97	0.97	0.98	0.99	-

Conclusions

The observed decreasing trend in direct genetic heritability after weaning (98 days) indicated crossbred calves were affected by unfavorable post weaning feeding and management regime. Thus, the management should be improved to reduce the negative influence of high animal permanent environmental effect that hinder the expression of gene for growth trait of crossbred growing cattle. The strongly declining trend in maternal heritability over trajectory of calves' age also implied that dams had less pre- natal contribution for post-natal growth of their progeny reared under bucket feeding system. In addition, the result indicated that direct heritability estimates increased after birth until the age of weaning. Therefore, selection of crossbred replacement herd reared under bucket milk feeding management system should be done at the age of weaning for better genetic improvement of body weight traits and to be economical through reducing the rearing cost of animals.

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