Genetic parameters for production and feeding behaviour traits in crossbred steers fed a finishing diet at different ages

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[1]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada T6G 2P5 (e-mail: Zhiquan.Wang@ales.ualberta.ca); [2]Agriculture and Agri-Food Canada, Brandon, Manitoba, Canada R7A 5Y3; [3]International Livestock Research Institute (ILRI) P.O. Box 30709 Nairobi 00100, Kenya; [4]7604 Northport Avenue, Kalamazoo, MI 49009, USA; [5]Alberta Agriculture and Rural Development, Lacombe Research Centre, 6000 C&E Trail, Lacombe, Alberta, Canada T4L 1W1; and [6]Queensland Alliance for Agriculture and Food Innovation, The University of Queensland Brisbane Qld 4072 Australia.

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Durunna, O. N., Mujibi, F. D. N., Nkrumah, D. J., Basarab, J. A., Okine, E. K., Moore, S. S. and Wang, Z. 2013. **Genetic parameters for production and feeding behaviour traits in crossbred steers fed a finishing diet at different ages**. Can. J. Anim. Sci. **93**: 79–87. Because cattle can be raised postweaning under several feeding regimes, this study examined the consistency of phenotypic and genetic parameters of some production and feeding behaviour traits between two feeding periods that beef cattle received a finisher diet. Crossbred steers ($n=851$) were used for feeding trials from 2002 to 2009 where the steers received a finisher diet either during the fall–winter season (FP1) or during the winter–spring season (FP2). The steers evaluated in FP2 received a backgrounding diet in FP1. Traits examined include dry matter intake (DMI), average daily gain (ADG), gain: feed ratio (G:F), residual feed intake (RFI), and ultrasound measures of backfat thickness (UBF), rib-eye area (UREA) and marbling (UMB). Others include feeding duration (FD), headdown time (HDT) and feeding frequency (FF). As expected, there was no difference ($P=0.90$) between the RFI measured in the two periods. The two periods were similar for UBF ($P=0.87$) and UREA ($P=0.25$),while DMI, ADG and UMB were greater ($P<0.04$) in FP2 than in FP1. The FD, HDT and FF were greater ($P<0.0001$) in FP1 compared with FP2. Heritability estimates were calculated in FP1 and FP2, respectively, for ADG (0.38, 0.28), DMI (0.52, 0.42), RFI (0.16, 0.27), G:F (0.18, 0.33), HDT (0.35, 0.18) and FF (0.26, 0.46). More importantly, genetic correlations between FP1 and FP2 were estimated for DMI (0.61), RFI (0.65) and G:F (0.60). The results may indicate the influence of age or feeding period or both on these traits, which may suggest the need for multi-environment genetic evaluations to identify superior animals.

Key words: Steers, finisher diet, feeding period, residual feed intake, feeding behaviour, genetic parameters

Durunna, O. N., Mujibi, F. D. N., Nkrumah, D. J., Basarab, J. A., Okine, E. K., Moore, S. S. et Wang, Z. 2013. **Paramètres génétiques des traits de caractères liés à la production et à l'alimentation chez les bouvillons hybrides nourris avec une ration de finition à divers âges**. Can. J. Anim. Sci. **93**: 79–87. Les bovins pouvant être élevés selon plusieurs régimes après le sevrage, les auteurs ont examiné la cohérence des paramètres génotypiques et phénotypiques de certains traits de caractère associés à la production et aux habitudes alimentaires pendant deux périodes d'engraissement durant lesquelles les animaux ont reçu une ration de finition. Ils ont recouru à des bouvillons hybrides ($n=851$) pour les essais d'engraissement effectués de 2002 à 2009. Les sujets ont reçu une ration de finition pendant la saison automnale-hivernale (FP1) ou la saison hivernale-printanière (FP2). Les bouvillons évalués pendant la FP2 avaient reçu une ration de semi-finition durant la FP1. Les traits de caractère examinés incluaient l'ingestion de matière sèche, le gain quotidien moyen, le ratio gain:aliments, l'ingestion résiduelle d'aliments ainsi que l'épaisseur du gras dorsal, la surface du faux-filet et le persillé. Les auteurs se sont aussi intéressés à la durée des repas, au temps passé la tête en bas et à la fréquence des repas. Tel que prévu, l'ingestion résiduelle d'aliments est la même ($P=0{,}90$) pour les deux périodes. L'épaisseur du gras dorsal ($P=0{,}87$) et la surface du faux-filet ($P=0{,}25$) sont également similaires pour les deux périodes, mais l'ingestion de matière sèche, le gain quotidien moyen et le persillé étaient plus élevés ($P<0{,}04$) pendant la FP2. La durée des repas, le temps passé la tête en bas et la fréquence des repas sont plus élevés ($P<0{,}0001$) pendant la FP1 que la FP2. Les auteurs ont estimé l'héritabilité des caractères examinés pour la FP1 et la FP2. Elle s'établit respectivement comme suit : gain quotidien moyen (0,38, 0,28), ingestion de matière sèche (0,52, 0,42), ingestion résiduelle d'aliments (0,16, 0,27), ratio gain:aliments (0,18, 0,33), temps passé la tête en bas (0,35, 0,18) et fréquence des repas (0,26, 0,46). Le point principal est que la corrélation génétique entre la FP1 et la FP2 a été estimée à 0,61 pour l'ingestion de matière sèche, à 0,65 pour l'ingestion

Abbreviations: **ADG**, average daily gain; **DMI**, dry matter intake; **FD**, feeding duration; **FE**, feed efficiency; **FF**, feeding frequency; **GF**, gain: feed ratio; **HDT**, headdown time; **MWT**, metabolic mid-weight; **RFI**, residual feed intake; **UBF**, ultrasound measure of backfat thickness; **UMB**, ultrasound measure of marbling; **UREA**, ultrasound measure of rib-eye area

résiduelle d'aliments et à 0,60 pour le ratio gain:aliments. Ces résultats pourraient indiquer que l'âge, la période d'engraissement ou les deux influent sur ces traits de caractère, ce qui laisse supposer qu'il faudrait procéder à des évaluations génétiques dans de multiples conditions pour identifier les animaux supérieurs.

Mots clés: Bouvillons, ration de finition, période d'engrais, ingestion résiduelle d'aliments, habitudes alimentaires, paramètres génétiques

Beef cattle can be raised postweaning under several feeding regimes. Two common scenarios in Western Canada are: (1) those that receive a high-energy diet immediately after weaning during the fall–winter season and (2) those that receive a backgrounding diet prior to being finished on a high-energy diet during winter–spring season. Current research indicates that feed intake, growth and feed efficiency (FE) of steers are affected by various environmental factors such as diet, age and weather condition (Crews et al. 2003; Mujibi et al. 2010; Durunna et al. 2011a). Residual feed intake (RFI) is gaining popularity as the preferred measure of FE in cattle and is calculated as the difference between the actual feed intake and predicted feed intake based on body weight, production (Arthur et al. 2001a, b) and any other measurable energy sink, such as body composition (Richardson et al. 2001; Basarab et al. 2003) and feeding activity (Durunna et al. 2011c). Previous studies have shown that RFI is moderately repeatable over two successive diet regimes (Crews 2003; Kelly et al. 2010; Durunna et al. 2011a). Kelly et al. (2010) reported that RFI and feeding behaviours were repeatable in heifers during the yearling and finishing phases while Crews et al. (2003) and Durunna et al. (2011b) reported that RFI is repeatable in steers fed backgrounding and finishing diets, successively in two feeding periods.

It is important to know whether feed intake, growth, FE and feeding behaviour traits measured in steers fed a finisher diet in the fall–winter season are similar to those measured in the steers that were first backgrounded in the fall–winter, before receiving a finisher diet in the winter–spring season. Even though the timing of these performance tests is important to producers with respect to animal ranking and environmental impact, little information is available on young crossbred steers that received energy-dense finishing diet in these two seasons. Such information will add to the growing literature on environmental influence on beef cattle performances. It will also consolidate existing knowledge from other studies about the consistency of these traits over different environmental and mature phases.

MATERIALS AND METHODS

Animals and Management

The steers used in this study were born in the springs of 2002 to 2008 from hybrid, Angus or Charolais sires ($n = 114$) mated to hybrid dams ($n = 660$). Goonewardene et al. (2003) gave the details on the breed composition of the hybrid dam line. Because the matings were made in a multi-sire pasture, sire identification was performed via genotyping. Ear tissues or blood samples or both were collected from all steers for DNA extraction. Details on the genotyping and sire identification are contained in Nkrumah et al. (2007) and Durunna et al. (2011a). The steers were castrated within 24 h after calving and they grazed with their dams until weaned at approximately 184 ± 17d of age in October of each year. All steers had been vaccinated for infectious bovine rhinotracheitis, parainfluenza-3 virus, bovine viral diarrhoea, bovine respiratory syncytial virus, *Haemophilus somnus*, *Pasteurella multocida* and clostridial diseases 4 wk before entering the test facility. Upon arrival at the test facility, the steers were treated with a pour-on parasiticide that controls warble larvae, mites, lice and horn fly. Subsequently, each steer was identified with a radio frequency transponder button (half duplex RFID, Alflex USA, Inc., Dallas/Ft. Worth Airport, TX 75261-2266) in the right or left ear. All animals were located at the University of Alberta research ranch at Kinsella, Alberta, and were cared for according to the Canadian Council on Animal Care (1993) guidelines.

Each year, there were two feeding periods whereby the first feeding period (FP1) ran from November to January (fall–winter season), and the second feeding period (FP2) was from February to April (winter–spring season). Within each year's test, cohorts were developed from steers from the same calf-crop and tested within the same feeding period. The mean ambient temperatures from November 2003 to April 2009 were obtained from the Kinsella meteorological station, Kinsella, Alberta. Because the weather station at Kinsella was not installed until October 2003, the weather data from November 2002 to April 2003 were obtained from Viking AGCM (about 20 km from Kinsella). The mean ambient temperatures for FP1 for 2002, 2003, 2004, 2006, 2007 and 2008 were -8.46, -11.78, -8.73, -8.97, -10.87, and -10.74°C, respectively, and in FP2, the mean ambient temperatures were -6.00, -1.41, -1.33, -4.66, -5.05, and -6.02°C for 2003, 2004, 2005, 2007, 2008 and 2009, respectively. Figure 1 shows the daily maximum and minimum temperatures during the months of the trials. The ambient temperatures within the two feeding periods across the 6 yr were relatively constant.

Feed intake and feed bunk activities (measures of feeding behaviour) of each steer were measured daily using the GrowSafe automatic feeding system (GrowSafe Systems Ltd., Airdrie, AB). In FP1, these observations were collected on 80, 73, 78, and 88 steers

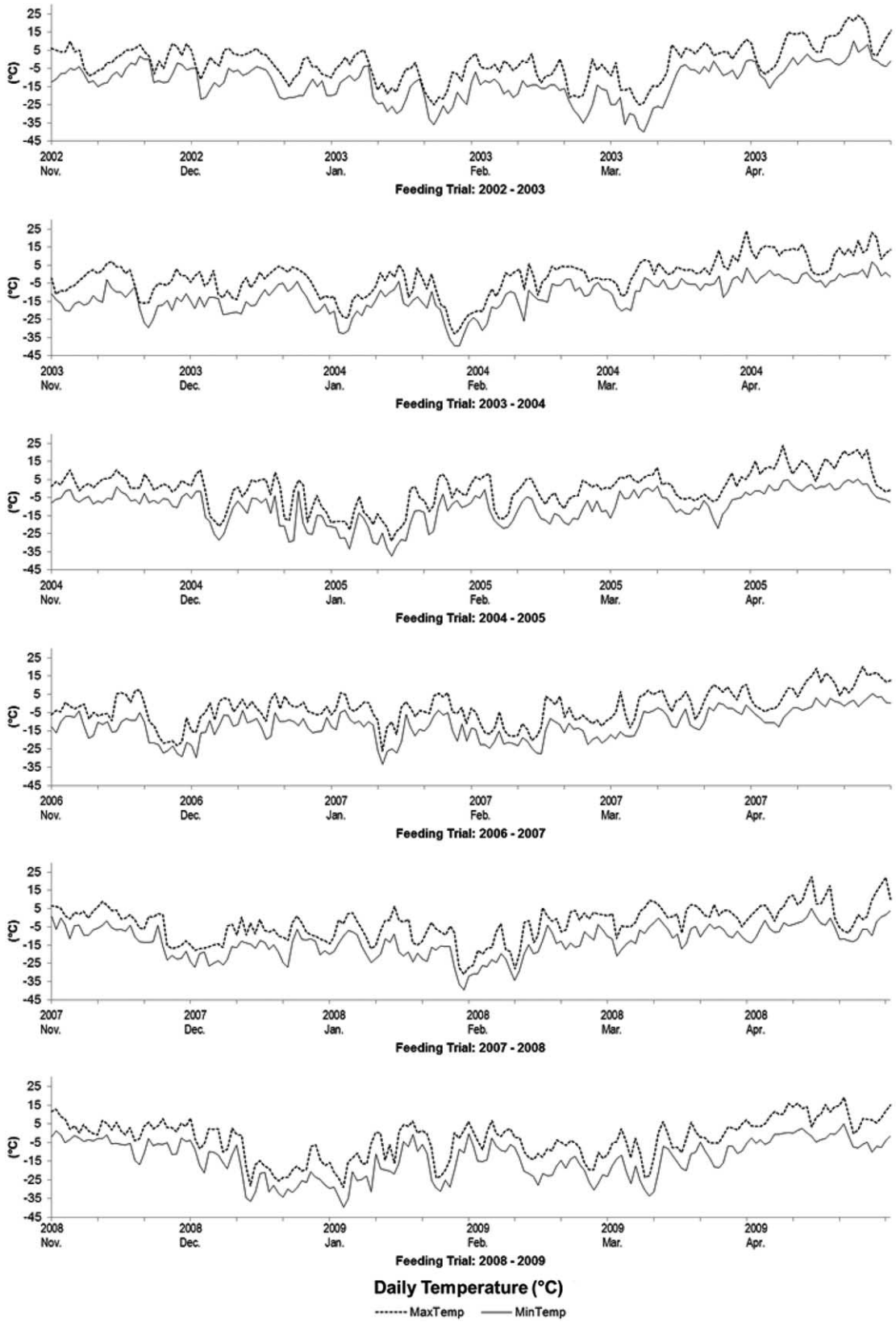

Fig. 1. Maximum and minimum daily temperature across the test periods.

in 2002, 2004, 2005 and 2007, respectively, while the observations from FP2 were collected on 61, 68, 73, 174, 84, and 72 steers in 2003, 2004, 2005, 2006, 2007 and 2008, respectively. Prior to being tested in FP2, steers were kept on a backgrounding diet that contained 20% grass hay, 74% oat grains and 6% feedlot supplement.

The diet composition and nutritive value of the finisher diets provided to the steers are shown in Table 1. For all years, the steers were adjusted to their trial rations for at least 21 d before the commencement of feed intake data collection. This adjustment period enabled the animals to adapt to the automatic feeding units and test rations, and minimized carry-over effects from the previous diet.

Data Collection, Trait Definitions and Statistical Analyses

Within each period, the data on feed intake and feed bunk activity were collected over 71 to 93 d. The feed bunk activities recorded by the GrowSafe System include feeding duration (FD), headdown time (HDT) and feeding frequency (FF), which were collected within feeding events. A feeding event is an uninterrupted detection of a steer's transponder (Basarab et al. 2003). Feeding interruptions arise when the time of non-detection of a steer's transponder is over 300 s or when another ear tag is detected at the same bunk. Each independent feeding event is one count for FF, while the FD is the total time spent within feeding events. The FD can also be defined as the time difference between the first and last electronic tag reads for any steer at a particular bunk as long as there is no feeding interruption. The FD can also be the length of time animals spent at the bunk for feeding related activities such as eating, chewing, licking, socializing, etc. (Nkrumah et al. 2007).

Table 1. The ingredients (as-fed) and composition of the finisher diets

Feed composition	2002[z]	2003[z]	2004[z]	2006[y]	2007[y]	2008[y]
Dry-rolled corn	80.0	–	–	–	–	–
Alfalfa pellets	13.5	9.0	9.0	10.0	10.0	10.0
Oat grains	–	20.0	20.0	28.3	28.3	28.3
Barley grains	–	64.5	64.5	56.7	56.7	56.7
Canola oil	1.5	1.5	1.5	0.0	0.0	0.0
Feedlot-32 Supplement[x]	5.0	5.0	5.0	5.0	5.0	5.0
ME content (MJ kg^{-1})	12.1	12.2	12.2	12.1	12.1	12.1
Chemical composition (% of DM)						
DM (%)	90.5	88.9	88.9	87.0	87.0	87.0
CP (%)	12.5	14.0	14.0	13.5	13.5	13.5
Crude fat (%)	5.32	–	–	3.3	3.3	3.3
ADF (%)	5.61	9.5	9.5	10.3	10.3	10.3
NDF (%)	18.3	21.49	21.49	29.5	29.5	29.5

[z]Obtained from digestibility trials Nkrumah et al. (2004, 2006).
[y]Obtained from Durunna et al. (2011a).
[x]Contained 440 mg kg^{-1} of Monensin, 1.6 mg kg^{-1} of selenium, 5.0% Ca, 0.58% P, 0.76% K, 16 mg kg^{-1} I, 80 mg kg^{-1} Fe, 170 mg kg^{-1} Cu, 480 mg kg^{-1} Mn, 485 mg kg^{-1} Z, 4.3 mg kg^{-1} Co, 1.98% Na, 0.17% S, 0.38% Mg, 80500 IU kg^{-1} vitamin A, 8000 IU kg^{-1} Vitamin D, 1111 IU kg^{-1}.

The HDT was calculated as the number of times the electronic tag of a particular steer was read by the system multiplied by the scanning time (1 s).

The live weights of all steers were measured once every 2 wk throughout the test periods. Ultrasound backfat (UBF) thickness, ultrasound ribeye area (UREA) and ultrasound marbling (UMB) were measured at the beginning and at the end of the feeding period using an Aloka 500V real-time ultrasound with a 17.5 cm 3.5 MHz probe (Overseas Monitor Corporation Ltd., Richmond, BC). The end observations for UBF, UREA and UMB were used for analyses. The linear regression procedure was used to compute the average daily gain (ADG), initial weight and mid-test body weight for each animal in SAS (Version 9.2, SAS Institute, Inc., Cary, NC). The mid-test body weight was converted to metabolic mid-weight (MWT) by $BW^{0.75}$. Each steer's average daily feed intake (as fed) was multiplied by the dry matter content of the feed to derive the dry matter intake (DMI), which was standardized to 10 MJ ME kg^{-1} DM. The RFI was calculated within cohorts (Mujibi et al. 2010) as the difference between the actual standardized DMI (sDMI) and the predicted DMI based on ADG, MWT and UBF using the GLM procedure of SAS.

$$\text{RFI} = \text{sDMI} - (\beta_0 + \beta_1\text{ADG} + \beta_2\text{MWT} + \beta_3\text{UBF})$$

where RFI is the residual feed intake, sDMI is the standardized DMI, β_0 is the regression intercept, β_1 is the ADG regression coefficient, β_2 is the MWT regression coefficient and β_3 is the UBF regression coefficient. Each steer was assigned to an RFI class based on 0.5 standard deviations above or below the mean. There were three classes namely Low (RFI <0.5 SD), Medium (± 0.5 SD) and High (>0.5 SD). The G:F ratio was calculated for each steer as the ratio of ADG to average daily DMI.

The T-test procedure in SAS was initially used to determine whether there were significant differences between the two periods for each trait. Then within each period, multiple comparisons of least-squares means for each trait were tested with the Mixed procedure of SAS using the PDIFF option. This latter model included RFI group (Low, Medium and High), breed of sire and year-of-test as fixed effects while the start-of-test age (within each feeding period) was included as a linear covariate.

Genetic analyses were implemented in ASReml (Gilmour et al. 2008) using a bivariate animal model which included year-of-test and breed of sire as fixed effects while the age of steer was fitted as a linear covariate. The model equation is shown below:

$$\begin{bmatrix} \boldsymbol{y}_1 \\ \boldsymbol{y}_2 \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_1 & 0 \\ 0 & \boldsymbol{X}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_1 \\ \boldsymbol{b}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{Z}_1 & 0 \\ 0 & \boldsymbol{Z}_2 \end{bmatrix} \begin{bmatrix} \boldsymbol{a}_1 \\ \boldsymbol{a}_2 \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_1 \\ \boldsymbol{e}_2 \end{bmatrix}$$

where $\mathbf{y}_1$ and $\mathbf{y}_2$ are the vectors of multiple phenotypic measurements for any trait (for example ADG1 and ADG2) measured in FP1 and FP2, respectively. $\mathbf{X}_1$ and

$\mathbf{X}_2$ are incidence matrices relating the fixed effects to records in y_1 and y_2, respectively; $\mathbf{b}_1$ and $\mathbf{b}_2$ are vectors of fixed effects (year and sire-breed) in FP1 and FP2, respectively;. $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are incidence matrices relating the phenotypic observations to the vectors of polygenic (a) effects for the FP1 and FP2, respectively. $\mathbf{e}_1$ and $\mathbf{e}_2$ are vectors of random residuals in FP1 and FP2, respectively.

The expectations and variances were:

$$E\begin{bmatrix}\boldsymbol{y}_1\\ \boldsymbol{y}_2\end{bmatrix} = \begin{bmatrix}\boldsymbol{X}_1 & 0\\ 0 & \boldsymbol{X}_2\end{bmatrix}\begin{bmatrix}\boldsymbol{b}_1\\ \boldsymbol{b}_2\end{bmatrix}$$

and

$$V\begin{bmatrix}a_1\\ a_2\\ e_1\\ e_2\end{bmatrix} = \begin{bmatrix}A\sigma^2_{a1} & A\sigma^2_{a1} & 0 & 0\\ A\sigma_{a21} & A\sigma^2_{a2} & 0 & 0\\ 0 & 0 & I\sigma^2_{e1} & 0\\ 0 & 0 & 0 & I\sigma^2_{e2}\end{bmatrix}$$

a and e were assumed to be normally distributed with mean of zero and (co)variances $A\sigma^2_a$, $I\sigma^2_e$ for a and e, respectively. A is the additive relationship matrix based on a pedigree with known sires and dams, σ^2_a is the random polygenic effect variance, I_n is an identity matrix with order equal to the number of animals. The residual errors between the two environments were assumed independent because the animals expressing the trait in FP1 were different from those expressing the trait in FP2. Heritability estimates and the genetic correlation between the expressions of a trait in FP1 and in FP2 were obtained from the bivariate analyses.

RESULTS AND DISCUSSION

This study investigated whether differences exist in phenotypic and genetic parameters in steers that received a finisher diet in either FP1 or FP2, which represent finishing phases in the beef feedlot. These phases are marked by differences in age, body weight and weather conditions especially ambient temperature. Any observed differences in the phenotypic and genetic parameters may be attributed to the influence of different genes or genomic regions that are activated as a result of the feeding period or stage of maturity which may indicate that phenotypes measured within these two periods may not represent the same trait. Even though the age of the animal in each period was included as linear covariate, a limitation of this study was the inability of the experimental design to separate these confounding factors while maintaining a sufficient sample size for analysis. There should be caution in interpreting and extrapolating these results to purebreds or other beef populations given that the animals used here were crossbreds.

The R-squares from the model predicting DMI ranged from 50 to 76% with UBF accounting for about 2 to 5% of the variation in DMI. Data integrity checks were performed (Durunna et al. 2011a; Mujibi et al. 2011); however, the average feed disappearance was not available for the steers tested in 2002–2005.

Phenotypic Differences

The differences between the mean performance measured in FP1 and FP2 are shown in Table 2. The average initial weights on test were 293 and 390 kg, for FP1 and FP2, respectively. Significant ($P<0.0001$) differences were found between the two feeding periods for DMI, ADG, and MWT whereby the values in FP2 were greater than those in FP1. The UMB was also greater ($P=0.03$) in FP2 than in FP1. There was no difference between the two feeding periods for UBF ($P=0.87$) and UREA ($P=0.25$). There were fewer ($P<0.0001$) observations for FD, HDT and FF in FP2 than in FP1. As expected, there was no difference ($P=0.90$) between the RFI from the two feeding periods, while there was a trend ($P=0.09$) for greater G:F in FP2 than in FP1.

Limited studies have reported feedlot performance of young steers of about 200 d of age. Basarab et al. (2003) reported feed intake of about 6 to 8 kg DM d^{-1} in composite steers, which weighed an average of 297 kg and were 238 d old at the beginning of the test.

Table 2. Simple means (SD) of traits measured in the two feeding periods

Trait	First feeding period	Second feeding period	*P* value[z]
Start of test age (d)	209 (17)	291 (15)	<0.0001
Start of test weight (kg)	293.4 (37.5)	389.7 (42.3)	<0.0001
Dry matter intake (kg d^{-1})	9.13 (1.33)	11.11 (1.56)	<0.0001
Average daily gain (kg d^{-1})	1.46 (0.25)	1.69 (0.31)	<0.0001
Metabolic mid-weight (kg)	81.0 (6.3)	99.0 (7.2)	<0.0001
Ultrasound backfat thickness (mm)	8.54 (3.71)	8.50 (2.64)	0.87
Ultrasound rib eye area (cm^2)	77.98 (14.97)	76.93 (9.02)	0.25
Ultrasound marbling	4.94 (0.88)	5.07 (0.68)	0.03
Gain to feed ratio	0.157 (0.026)	0.161 (0.031)	0.09
Residual feed intake (kg DM d^{-1})	−0.01 (0.67)	−0.00 (0.91)	0.90
Feeding duration (min d^{-1})	78.4 (20.6)	66.7 (15.4)	<0.0001
Head-down time (min d^{-1})	43.8 (13.5)	32.7 (11.8)	<0.0001
Feeding frequency (events d^{-1})	35.1 (8.6)	22.3 (6.6)	<0.0001

[z]The *P* value of the difference between the means is equal to zero.

The steers in their study had a lower DMI despite receiving a ration similar to the diet in this study. The DMI and ADG for steers in FP2 were similar to that reported by Hicks et al. (1990). The authors reported an average DMI of 10.31 kg d^{-1} for yearling steers weighing 322 kg at the beginning of the test with an ADG of 1.6 kg d^{-1}, which were similar to the DMI and ADG in FP2. The greater ADG in FP2 may be due to compensatory gain (Fluharty et al. 2000) because of the previous dietary regime.

Arthur et al. (2001a) used Angus bulls of 268 ± 23 d of age for their study and reported a mean DMI of 9.65, which was similar to the DMI from FP1 but the ADG (1.26 kg d^{-1}) was lower compared with the ADG in FP1. Even though the average age of the bulls used in Arthur et al. (2001a) was similar to those in FP1, the diet used in that study contained 2.5 Mcal kg^{-1}, which was lower than the ME content of this study. The average DMI (10.4 kg d^{-1}) and ADG (1.61 kg d^{-1}) of Charolais bulls at 15 mo (Arthur et al. 2001b) were similar to those of the steers in FP2.

The similarity between the two periods in the mean observations on the UBF and UREA agreed with Fluharty et al. (2000), who reported that feeding energy dense diet to early-weaned calves increased the rate of growth in those steers by accelerating the rate of adipogenesis. Schoonmaker et al. (2002) reported that calves that entered the feedlot at 111 d had greater backfat and longissimus area by the 202 d than those that entered the feedlot at 202 d, but there was no difference between the two groups for backfat thickness at slaughter. However, they reported that calves that entered the feedlot as yearlings had the greatest backfat thickness at slaughter. Such increase of backfat thickness may be expected because the yearling calves were 534 d at slaughter, while those that entered the feedlot at 111 and 202 were 333 and 391 d, respectively, at slaughter. The difference in the UREA observed in this study was contrary to the reports of Schoonmaker et al. (2002) who reported greater longissimus area at target fat level for calves placed in the feedlot at an older age.

There were differences ($P<0.0001$) among the three RFI-classes within the two feeding periods for DMI, RFI, G:F and FD as shown in Table 3. There were no differences ($P>0.12$) among the RFI classes within each feeding period for initial weight on test, ADG and MWT. For HDT in the FP1, there was no difference ($P=0.15$) between the high and medium classes, while the low class was significantly different ($P<0.0001$) from the high and medium classes (Table 3). During FP2, the three RFI classes were significantly different ($P<0.0001$) for the HDT. There was no difference ($P=0.13$) between the low and medium RFI classes for the FF in FP1, while the low RFI-class had fewer ($P<0.01$) FF than either the medium or the high RFI-class in P2.

For DMI, G:F and RFI, differences observed among the RFI-classes were in agreement with previous studies (Nkrumah et al. 2004, 2007; Meyer et al. 2008; Bingham et al. 2009) irrespective of the feeding period. The less-efficient (positive RFI) steers had greater feed-intake, smaller G:F, longer FD, longer HDT and more FF, than the more-efficient (negative RFI) steers.

Table 3. Least-squares means of the RFI-classes of steers in both feeding periods

	First feeding period				Second feeding period			
Trait	High	Medium	Low	*P* value	High	Medium	Low	*P* value
Start of test weight	300.1 ± 3.0	292.5 ± 2.6	295.1 ± 2.9	0.150	393.5 ± 3.7	389.3 ± 3.0	392.0 ± 3.5	0.540
Average daily gain (kg d^{-1})	1.45 ± 0.03	1.44 ± 0.02	1.47 ± 0.02	0.686	1.62 ± 0.03	1.64 ± 0.02	1.64 ± 0.02	0.673
Metabolic mid-weight (kg)	82.1 ± 0.7	80.7 ± 0.5	81.3 ± 0.6	0.170	98.7 ± 0.7	98.2 ± 0.5	98.6 ± 0.6	0.716
Dry matter intake (kg d^{-1})	10.28 ± 0.11*a*	9.30 ± 0.09*b*	8.80 ± 0.10*c*	<0.0001	11.47 ± 0.10*a*	10.59 ± 0.08*b*	9.67 ± 0.10*c*	<0.0001
Ultrasound backfat thickness, (mm)	8.87 ± 0.27*a*	8.00 ± 0.23*b*	8.72 ± 0.26*ab*	0.027	7.70 ± 0.23	8.18 ± 0.19	7.97 ± 0.22	0.155
Ultrasound rib eye area (cm^2)	79.47 ± 0.76	78.48 ± 0.65	79.21 ± 0.74	0.571	77.99 ± 0.70	78.22 ± 0.58	78.84 ± 0.67	0.547
Ultrasound marbling	5.01 ± 0.07*a*	4.77 ± 0.06*b*	4.94 ± 0.07*ab*	0.018	4.80 ± 0.06*a*	4.96 ± 0.05*b*	4.93 ± 0.06*ab*	0.040
Residual feed intake (kg DM d^{-1})	0.78 ± 0.04*a*	−0.02 ± 0.03*b*	−0.72 ± 0.03*c*	<0.0001	1.01 ± 0.04*a*	−0.01 ± 0.04*b*	−1.08 ± 0.04*c*	<0.0001
Gain to feed ratio	0.14 ± 0.002*a*	0.16 ± 0.001*b*	0.17 ± 0.002*c*	<0.0001	0.14 ± 0.002*a*	0.16 ± 0.002*b*	0.17 ± 0.002*c*	<0.0001
Feeding Duration (min d^{-1})	85.1 ± 1.5*a*	78.0 ± 1.3*b*	70.3 ± 1.5*c*	<0.0001	70.0 ± 1.3*a*	64.3 ± 1.0*b*	56.1 ± 1.2*c*	<0.0001
Head-down time (min d^{-1})	47.9 ± 1.2*a*	45.0 ± 1.1*a*	37.8 ± 1.2*b*	<0.0001	39.1 ± 1.0*a*	33.19 ± 0.9*b*	25.3 ± 1.0*c*	<0.0001
Feeding frequency (events d^{-1})	38.0 ± 0.7*a*	35.3 ± 0.6*b*	33.6 ± 0.7*b*	<0.0001	24.5 ± 0.5*a*	23.4 ± 0.4*a*	20.7 ± 0.5*b*	<0.0001

a–c Within each period, different letters indicate differences among feed-efficiency classes at $P<0.05$.

Genetic Parameters

Table 4 shows the phenotypic variances, and heritability estimates for both feeding periods as well as the genetic correlations between the traits in FP1 and FP2. Using the 95% confidence interval approach (Estimate $\pm 2 \times$ SE), the sizes of the phenotypic variances for DMI and ADG in FP1 may be similar to those in FP2, while the size of the heritability estimates for ADG and DMI obtained in the FP1 may also be similar to those in FP2. The FE traits (RFI and G:F) had greater phenotypic variances in FP2 compared with FP1, but the heritability estimates may be similar. Based on the intervals, the heritability estimates in the two feeding periods may be similar for FD, HDT and FF, while the phenotypic variances may also be similar for the two periods for HDT but not for FD and FF.

The genetic correlations (Table 4) between FP1 and FP2 may indicate that a similar set of genes may be influencing ADG or HDT measured in the two feeding periods. Given that the genetic correlations between the two periods were greater than 90% (Crews et al. 2003), it may also indicate that ADG or HDT measured during these two feeding periods may be the same traits. The size of the estimates of the genetic correlations for DMI, RFI, G:F, FD and FF suggest that these traits measured in FP1 may be different from those measured in FP2 despite the steers receiving similar diets in the two feeding periods. These results may also suggest that apart from FF, all traits measured in FP1 were related to their subsequent measurement in FP2.

The age of animals at which selection decisions are made may influence profitability of the beef sector. Early identification of the potential candidates is preferred in order to reduce the cost associated with keeping and testing possible rejects. An important question from producers, which is yet to be addressed by the scientific community, is regarding the appropriate time to conduct genetic evaluations on selection candidates whose ranking for certain traits are likely to change. A suggestion is conducting multi-environment genetic evaluations in order to identify candidates that perform better within specific environments. Such evaluations may also identify candidates whose relative ranking in both environments did not change.

Few researchers have conducted genetic studies using crossbred cattle of about 200 d of age for feed intake and FE (Arthur et al. 2001b; Crews et al. 2003; Durunna et al. 2011a; Kelly et al. 2010) or feeding behaviour (Durunna et al. 2011c). Fan et al. (1995) carried out performance tests on Hereford and Angus bulls (under 200 d of age) using high- and medium-energy diets. They reported pooled heritability estimates for ADG (0.26), DMI (0.24) and RFI (0.14) in the two breeds, which were lower than the estimates from the estimates in FP1. The differences between their results and those reported here may be due to the physiology and breed of the animals. The results here were similar to the heritability estimates from Robinson and Oddy (2004) for ADG (0.23) and RFI (0.18), but their estimate for FD (0.36) was greater than the result from this study, while their estimate for feed conversion ratio (0.06) was lower. Nkrumah et al. (2007), in their previous study on this crossbred population, did not consider the genetic parameters in cohorts or feeding periods due to limited sample size. The increased sample size enabled this study to estimate the genetic parameters within feeding periods.

Arthur et al. (2001b) reported greater phenotypic variances for feed intake, ADG and RFI in bulls at 19 mo than at 15 mo and that the heritability estimate was slightly greater at 19 mo (0.43) than at 15 mo (0.39) for RFI. The trend for ADG in this study disagreed with the reports of Cucco et al. (2010) but agreed with Sarmiento and Garcia (2007), Prince et al. (2010) and Chen et al. (2010) in Romosinuano cattle, Avikalin sheep and Duroc pigs, respectively. Cucco et al. (2010) reported a slightly higher heritability estimate for weight gain measured at 365 d (0.18) versus 450 d (0.21). Observing the results made at different stages of maturity in mice, Archer et al. (1998) reported a slightly greater heritability for RFI measured postweaning (0.27) than at maturity (0.24).

These authors (Sarmiento and Garcia 2007; Prince et al. 2010; Chen et al. 2010), observed the decline of additive genetic component for postweaning weight traits in different species as the animals advanced in age. This may imply that the genes controlling such traits had smaller effects on the expression of the traits

Table 4. Phenotypic and genetic parameters of traits expressed in two feeding periods

		First feeding period		Second feeding period	
Trait	r_g^z	σ_p^2	h^2	σ_p^2	h^2
Average daily gain (kg d^{-1})	0.92 ± 0.36	0.06 ± 0.005	0.38 ± 0.18	0.07 ± 0.005	0.28 ± 0.12
Dry matter intake (kg d^{-1})	0.61 ± 0.28	1.32 ± 0.11	0.52 ± 0.19	1.52 ± 0.10	0.42 ± 0.14
Residual feed intake (kg DM d^{-1})	0.65 ± 0.51	0.46 ± 0.04	0.16 ± 0.17	0.83 ± 0.05	0.27 ± 0.12
Gain to feed ratio	0.60 ± 0.51	0.0004 ± 0.00003	0.18 ± 0.16	0.0005 ± 0.00003	0.33 ± 0.13
Feeding duration (min d^{-1})	0.84 ± 0.53	237.7 ± 19.4	0.22 ± 0.14	187.9 ± 11.8	0.14 ± 0.10
Head-down time (min d^{-1})	0.97 ± 0.34	150.4 ± 12.6	0.35 ± 0.19	134.1 ± 8.5	0.18 ± 0.11
Feeding frequency (events d^{-1})	0.05 ± 0.44	46.13 ± 3.81	0.26 ± 0.17	25.11 ± 1.71	0.46 ± 0.16

[z]The genetic correlation between the two feeding periods for each trait.

as the animals mature or that the environmental influences were greater at older ages. In the Avikalin sheep, Prince et al. (2010) suggested that the environment plays a larger role for growth rate as the animal advances in age, especially after 6 mo of age. The mechanism by which this occurs is unclear; however, Middelbos et al. (2009) investigated the influence of age on the gene expression profiles of dogs, and they reported that age influenced the mRNA abundance of the skeletal tissue where there was down regulation (with advancing age) of genes involved in cellular organization and development, signalling mechanisms, calcium and lipid transport. In chickens, a decline in heritability due to increasing environmental variance was observed for body and egg traits (Dana et al. 2011) indicating that reduced heritability was not only due to declining additive genetic variance but also due to increasing environmental variance.

The genetic correlations reported here were lower than the reports of Arthur et al. (2001b) for RFI (0.75) and daily feed intake (0.90), but were greater than their report for ADG (0.46) and feed conversion ratio (0.42). These results were in agreement with Durunna et al. (2011b), who reported high genetic correlations for ADG (0.80) in steers fed grower and finisher diets in successive feeding periods. While the authors reported a greater genetic correlation for G:F (0.78) and DMI (0.78), their report for RFI was lower (0.50). The high genetic correlation for ADG and HDT in this study may indicate the absence of genotype by environment interactions for these traits between the two feeding periods. On the other hand, the results suggest that the expression of the other traits (DMI, RFI, G:F, FD and FF) may be dependent on the age and feeding period and may be considered as different traits within each feeding period.

CONCLUSION

This study investigated the possible effects of feeding period and age on production, feed efficiency and feeding behaviour traits using crossbred steers that were fed the finisher diet in one of two finishing regimes. There was no consistent trend for the heritability estimates in FP1 and FP2. The 95% confidence intervals suggest that the size of the heritability estimates for each trait evaluated was similar from FP1 to FP2. The results from the genetic correlation may support the argument that postweaning performance of DMI, RFI, G:F, FD and FF in cattle may be affected by age and feeding period, but ADG and HDT measured in both environments may be devoid of the influence of genotype by environment interactions.

The mechanisms that reduce or increase the influence of genes at older ages in cattle need to be explored. Genomic studies may be required to investigate these differences using genetic marker panels or micro-arrays.

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