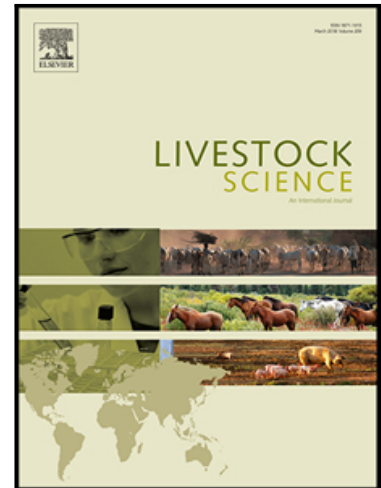


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Quantification of cow milk yield and pre-weaning calf growth response in temperate pasture-based beef suckler systems: A meta-analysis

D. Sapkota , A.K. Kelly , P. Crosson , R.R. White , M. McGee

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Highlights

- Cow genotype and parity are primary factors influencing milk yield and pre-weaning calf growth.
- Cow milk yield and corresponding pre-weaning calf growth for Dairybeef, Beef, Early-maturing and Late-maturing genotypes were 8.64, 6.38, 6.78, 8.20 kg/day and 960, 894, 890, and 965 g, respectively.
- Multiparous cows produced proportionately 14.8% (1.05 kg/day) more milk and their calves had a 92 g higher daily growth rate than primiparous cows.
- Calf growth response to an additional kg of milk was 47, 53, 51 and 55 g for Dairybeef, Beef, Early-maturing and Late-maturing genotypes, respectively.

Quantification of cow milk yield and pre-weaning calf growth response in temperate pasture-based beef suckler systems: A meta-analysis

D. Sapkota^{a,b}, A.K. Kelly^b, P. Crosson^a, R.R. White^c and M. McGee^{a,*}

^aTeagasc, Animal & Grassland Research and Innovation Centre, Grange, Dunsany, Co. Meath, Ireland

^bSchool of Agriculture and Food Science, University College Dublin, Belfield, Dublin 4, Ireland

^cDepartment of Dairy Sciences, Virginia Tech, Blacksburg 24061, USA

*Corresponding author.

E-mail address: mark.mcgee@teagasc.ie (M. McGee)

Abstract

The objectives of this study were to quantitatively summarize factors associated with cow milk yield (MY) and calf growth response in pasture-based beef cow-calf suckler systems and to discern how cow genotype and parity influenced these responses. A dataset of 344 treatment mean observations was compiled from 69 studies that reported data on cow MY, and calf pre-weaning average daily live weight gain (ADG) and/or weaning weight (WW). Data were analysed using linear mixed effects models with study and region included as random effects. Models were developed for cow MY, calf ADG and WW response and each model was evaluated based on different model fit statistics. The final cow MY model included cow origin (Dairybeef or Beef), cow maturity (early-maturing (EM) or late-maturing (LM) genotypes) and parity. Dairybeef produced 35.4% more milk (8.64 vs. 6.38 kg/day) than Beef cows, and LM produced 20.9% more milk (8.20 vs. 6.78 kg/day) than EM genotypes ($P < 0.001$). Multiparous cows had a 14.8% higher MY (8.11 vs. 7.06 kg/day) compared to primiparous cows ($P < 0.001$). Lactation curve persistency was

better ($P < 0.05$) for Beef and EM compared to Dairybeef and LM genotype cows, respectively. The final models of calf ADG and WW included cow origin, cow maturity and parity. Calves from Dairybeef and LM cows were 14 and 20 kg heavier ($P < 0.001$) at weaning (210-day adjusted) compared to those from Beef and EM genotype cows, respectively. Calves from multiparous cows were 13 kg heavier at weaning than those from primiparous cows ($P < 0.001$). The response in calf ADG associated with a 1 kg increase in cow daily MY was 47 and 53 g for Dairybeef and Beef cows, respectively ($P < 0.001$). Corresponding responses for EM and LM cows were 51 and 55 g ($P < 0.001$). In conclusion, the relationships between cow MY and calf pre-weaning growth, as well as the quantitative impact of cow genotype and parity were determined for pasture-based beef suckler systems; the coefficients generated can be used for improving beef cow-calf management strategies, beef cattle breeding programmes and bio-economic modelling purposes.

Key words: beef cow; calf growth; pasture-based systems; milk yield; meta-analysis.

1. Introduction

Internationally, the vast majority of beef suckler cow-calf production systems are pasture-based and tend to be seasonal calving with parturition occurring at, or around, the time of onset of seasonal pasture growth (Drennan and McGee, 2009; Walmsley et al., 2018). Within these systems, calves are generally allowed continuous and unlimited nursing of the dam for approximately 6 to 8 months until weaning, typically at the end of the grazing season (Jouven et al., 2008; Drennan and McGee, 2009). Pasture, either grazed or conserved, is usually the major dietary input and grazing is generally the cheapest source of nutrients (Finneran et al., 2012;

Mulliniks et al., 2015). Pasture-based grazing systems vary tremendously across unique environments that differ in climate, topography and production levels, and can range from intensively-managed lowland pasture with high-nutritive value herbage to marginal land often comprised of low-quality herbages (Drennan and McGee, 2009; Mulliniks et al., 2015). This study will focus on 'temperate' pasture-based production systems.

In beef suckler cow-calf systems the weight of calf at weaning is the primary output; therefore, most definitions of cow-calf efficiency or 'maternal productivity' include calf weaning weight (WW) (Walmsley et al., 2018). Consequently, pre-weaning average daily gain (ADG) of beef calves is often positively associated with the profitability of these systems (Minick et al., 2001; Åby et al., 2012; Crosson and McGee, 2012), although this is not always clearly evident (Miller et al., 2001; Mulliniks et al., 2020).

Milk is the primary source of nutrients for the newborn calf in early postnatal life and remains a significant component of the diet until weaning (McGee et al., 2005; Grings et al., 2008; Roca Fraga et al., 2018). Beef suckler cows with higher milk yield (MY) generally produce heavier calves at weaning (Arthur et al., 1997; Murphy et al., 2008a; Minchin and McGee, 2011; Vaz et al., 2016; McCabe et al., 2019a); MY can account for up to *ca.* 74% of the variance in calf WW (Arthur et al., 1997). Furthermore, research has generally shown that, due to limited compensatory growth post-weaning (Drennan and McGee, 2004), the additional weight gain of suckled calves at weaning due to higher MY of cows is largely retained until slaughter (Miller et al., 1999; Murphy et al., 2008b). This demonstrates the importance of milk as a key factor influencing life-time live weight gain in calf-to-beef systems. Pre-weaning gain is also a critical factor in breeding replacement heifers as

target weights at puberty and first breeding need to be attained; in this respect, pre-weaning gain generally has a larger positive impact on age at puberty than post-weaning gain (Perry, 2016).

Many individual studies have evaluated beef suckler cow MY and calf pre-weaning performance; however, the calf growth response obtained varied widely and was influenced by factors such as cow genotype (McGee et al., 2005; Murphy et al., 2008a; McCabe et al., 2019b), cow parity (Villalba et al., 2000), calf sex (Manninen et al., 2004) and other environmental factors including, cow nutrition level (McGee and Caffrey, 1998) and grassland management (Arthur et al., 1997; Drennan and McGee, 2008), associated with different temperate pasture-based systems worldwide. In the context of beef cattle breeding programs and bio-economic modelling of beef suckler systems (Crosson and McGee, 2012), as well as determination of efficient management strategies (Ramsey et al., 2005; Mulliniks et al., 2020), it is necessary to more accurately quantify calf growth response to cow MY under different biological and management regimes within pasture-based systems. In particular, there is comparatively little research explaining variation in calf growth responses to MY and, to our knowledge, no quantitative summarisation of the available literature in this area. In this regard, a meta-analytical approach can integrate the results from previous studies to generate robust estimates and to quantify the associated responses (Sauvant et al., 2008).

Therefore, the objectives of this study were to quantitatively summarize factors associated with cow MY and calf growth response and to discern how cow genotype and cow parity influenced these responses in temperate pasture-based, beef suckler cow-calf production systems.

2. Materials and methods

2.1. Data collection, inclusion and exclusion criteria

The literature search was conducted for published studies up to November, 2019 using public data search generators that included Science Direct, Web of Science, SCOPUS and Google Scholar, to compile published studies related to cow MY and calf performance pre-weaning. Search terms were selected based on the titles and key words used in known eligible published studies. The following terms in different combinations were used: “milk”, “milk production”, “milk yield”, “milk intake”, “lactation”, “lactating beef cow”, “calf”, “nursing calf”, “suckling calf”, “calf performance” “calf pre-weaning growth”, “calf daily live weight gain”, “calf weaning weight”, “live weight gain”, “beef cow”, “suckler cow”, “cow performance”, “cow-calf productivity”, “maternal productivity”, “cow-calf systems”, “suckler beef systems”, “beef cattle” and “beef systems”. Following the initial search, we reviewed individual titles and abstracts to remove irrelevant studies. The search was supplemented by manual searching of citations from retrieved studies and publications of known authors in the research area.

In order to be included in the dataset, studies must have reported cow daily MY and calf ADG or WW. In addition, the studies included had to be; written in English, conducted in predominantly pasture-based grazing production systems mainly using temperate sward species, and with *Bos taurus* genotypes. Studies that evaluated cow MY and calf performance within full-time ‘indoor’ or ‘housed’ production systems or used only concentrate-based diets, were excluded. Study-related variables collected included: authors, journal, year, country, cow genotype, sire breed, cow parity (classified as primiparous: first-parity cows and multiparous \geq second-parity cows), calf birth weight and calf sex. As there were insufficient data to permit

analysis on the basis of individual breed type and their crosses, cow breed types were classified into distinct genotype; based on cow 'origin', either Dairybeef (whereby the dam of the cow is a dairy breed, primarily Holstein-Friesian, Jersey, Ayrshire, and the sire is a beef breed) or Beef (whereby both the dam and sire are beef breeds). In addition, cow genotypes were further categorized based on cow maturity, either early-maturing (EM; primarily Angus, Hereford, Blue grey, Welsh, Galloway and/or their crossbreds) or late-maturing (LM; primarily Charolais, Limousin, Simmental and/or their crossbreds) genotypes. The density of observation of data (cow MY) based on cow origin and maturity differentiated by cow parity are shown in Figure 1. The sire breed types were classified into two categories; EM and LM. Similarly, the countries where the research studies were located were grouped based on geographical location into regions; Europe, North America and Oceania (Australia and New Zealand), although it is acknowledged that within regions production systems can vary widely.

Cow MY data were classified by stage of lactation based on the day of measurement as; early- (0-70 d), mid- (71-140 d) and late- (>141 d) lactation. This permitted the generation of lactation profile curves for the beef cow genotypes. In practice, it is generally not possible to routinely measure cow MY on a daily basis unless an automated system is used (Sepchat et al., 2017), and particularly in pasture grazing environments. At least three point estimates were generated for each cow genotype utilizing different studies and these values were adjusted to the Woods equation (Wood, 1967) to develop genotype-specific lactation curves. The MY data were further classified based on how it was measured; an indirect method (i.e. weigh-suckle-weigh; WSW) and direct methods (e.g. machine- or hand-milking

techniques with or without oxytocin injection). Milk composition was not widely reported and therefore not considered for inclusion in the analysis.

2.2. Data cleaning

The dataset was explored to verify the biological coherence of response variables. Age of weaning initially varied from 50 to 244 days due to differences in production systems in the different geographic regions. To account for this variation, the WW data were adjusted to a common weaning age of 210 days (Hudson et al., 2010; Syrucek et al., 2017), which is a duration more reflective of general commercial practice worldwide. The studies that reported weaning age of 50 days were excluded because it was deemed to be excessively young to 'adjust' to 210 days.

A challenge with meta-analysis is the inconsistency in reporting the parameters of interest across different studies. Although, the initial database included sire genotype and calf sex, including those variables in the final dataset would reduce the number of treatment observations by almost half, thus limiting ability to characterize variation; therefore, these variables were not taken into consideration for the current analysis. Similarly, 25% of the studies in the initial dataset did not report cow parity and/or used a mixture of primiparous and multiparous cows; including those studies would either underestimate or over-estimate the effect of parity, thus they were excluded from the final dataset. Another challenge with meta-analysis is that studies often fail to report standard error of mean (SEM) for the parameter of interest. Where this occurred, those variables were given average pooled SEM for the respective parameter of interest. Similarly, the data for response variables were weighted by $1/SEM$ as a weighing factor in the model so as to prevent overweighting of studies due to extremely low or high standard error (Liebe and White, 2018).

Graphical examinations were used at each stage of the analysis to check for extreme data and biological coherence. Outliers were ascertained through examination of Cook's distance (Cook, 1979) where values with >1 Cook's distance are removed. The final dataset included 344 treatment means from 69 studies that satisfied the above criteria. The summary statistics for key variables reported within the dataset are provided in Table 1 and the list of references used for this meta-analysis is provided in Supplementary Material S1.

2.3. Statistical analysis and model derivation procedure

The linear mixed effects model was performed using lme4 (Kuznetsova et al., 2013) and lmerTest packages (Pinheiro et al., 2014; Kuznetsova et al., 2015) of the statistical software R version 3.1.2 (Team, 2014). In the analysis, the variables or factors of interest were considered as fixed effects. The study and region effects were considered as random because the data was retrieved from multiple studies conducted over various years encompassing different conditions (St-Pierre, 2007; Sauvant et al., 2008). The general form of the mixed effects model was:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\boldsymbol{\gamma} + \boldsymbol{\varepsilon}$$

Where \mathbf{y} represents a vector of observed data, $\boldsymbol{\beta}$ is an unknown vector of fixed effects parameters with known design matrix \mathbf{X} , $\boldsymbol{\gamma}$ is an unknown vector of random effects parameters with known design matrix \mathbf{Z} and $\boldsymbol{\varepsilon}$ is an unknown random error vector. Differences between means or relationships with $P < 0.05$ were considered as statistically significant for all models, and $P < 0.10$ were accepted as representing a tendency for statistical significance. Additionally, the collinearity (multicollinearity) between independent variables was ascertained according to variance inflation factor (*VIF*) through faraway package in R (Faraway, 2016) and values over 10 were

considered to indicate a significant collinearity (Dohoo et al., 2009). Therefore, to avoid the collinearity problem, the variables showing $VIF > 10$ were omitted from the model. Birth weight of calves was removed from cow MY model as it was highly correlated to cow MY.

The initial models of cow MY and birth weight, ADG and WW response of calves were generated based on the theoretical understanding of biological relationships to quantify them. Therefore, the model developed contained different starting explanatory variables. The models for characterizing cow MY were developed by initially including terms for cow origin, cow maturity, cow parity, calf birth weight and MY measurement technique. In addition, MY response based on different lactation stage of production was tested separately to generate the lactation curve for each genotype (Figure 2) using the lactation curve developed by Wood (1967). Models for calf birth weight, ADG and WW were developed including biologically relevant variables such as cow origin, cow maturity and cow parity. While developing models, all the variables with the greatest non-significant P -value ($P > 0.05$) were iteratively eliminated from the model until only statistically significant ($P < 0.05$) variables remained. Each model was evaluated based on different model fit statistics described below. In addition, to discern genotype-specific responses in calf pre-weaning growth to milk, MY data were nested within the respective suckler cow genotype. The correlation between cow MY and calf ADG were investigated using Pearson correlations.

2.4. Model evaluation

Once the statistical analysis was performed, a visual examination of residual plots (observed minus predicted values) was used to assess the normality of residuals and homogeneity of variances. Model accuracy and precision was

evaluated mainly using the concordance correlation (CCC; Lawrence and Lin (1989), and root means square error (RMSE, with slope and intercept bias). Concordance correlation coefficient measures the agreement between variables used in the model, and higher values of CCC represent better model fit. Improved RMSE is also indicated by a lower value; therefore, the lower mean and slope bias are preferred to claim a model with better fit.

3. Results

Summary statistics of the parameters used in this study are presented in Table 1. As expected, there was large variation in cow MY and calf performance (Table 1). Mean daily MY was 8.94, 6.04, 6.45 and 8.35 kg for Dairybeef, Beef, EM and LM cows, respectively. Mean calf ADG was 920 g and ranged from 445 to 1449 g. The large variation in calf ADG reflects differences in genetic potential for growth and prevailing dietary nutrition (milk and non-milk). Mean calf WW was 224 kg and ranged from 124 to 372 kg, which additionally reflects the large variation in age of weaning, from 90 to 244 days. Only the model parameters that were statistically significant are presented.

3.1. Cow milk yield

The model characterizing cow MY, parameter estimates, and model fit statistics are shown in Table 2. The model showed that cow MY was influenced by cow origin, cow maturity and parity. Beef cows produced 2.26 kg less milk per day than Dairybeef cows ($P < 0.001$), and LM genotypes produced 1.42 kg more milk than their EM counterparts ($P < 0.001$). The least square means (corrected for parity) of MY for Dairybeef, Beef, EM and LM genotypes were 8.64, 6.38, 6.78 and 8.20 kg/day, respectively (Table 3). Daily MY for multiparous cows was 1.05 kg higher

than primiparous cows ($P < 0.001$) (Tables 2 and 3). Method of milk measurement had no effect ($P > 0.05$) on cow MY. The fit statistics for the cow MY model showed a CCC values of 0.93 with RMSE (% of mean) of 11.75 and almost no mean (< 0.001) and slope (0.58 % MSE) bias.

Daily MY was highest in early-lactation and lowest in late-lactation ($P < 0.05$) for all four cow genotypes (Table 4); however, unlike Dairybeef and LM genotypes, daily MY did not differ ($P > 0.05$) between mid and late-lactation for Beef and EM. Lactation curves generated for the different cow genotypes are presented in Figure 2. The decline in daily MY was greater ($P < 0.05$) for the higher-producing genotypes, Dairybeef and LM, than their lower-producing counterparts, Beef and EM i.e. persistency of lactation was better for Beef and EM genotypes.

3.2. Calf performance

Factors contributing to calf birth weight, ADG and WW, their estimates, and model fit values are shown in Table 2. Calf birth weight was significantly affected by cow maturity and cow parity. Compared to calves from EM genotypes, calves from LM genotypes were 2.70 kg heavier ($P < 0.001$) at birth, whereas calves from Dairybeef and Beef genotypes were not different ($P > 0.05$). The least square means (corrected for parity) of calf birth weight for Dairybeef, Beef, EM and LM genotypes were 36.62, 37.38, 35.71 and 38.41 kg, respectively (Table 3). Calves born from multiparous cows were 3.54 kg heavier than those born from primiparous cows ($P < 0.001$). The fit statistics of the calf birth weight model resulted with CCC value of 0.87 with RMSE (% of mean) of 8.5 with almost no mean bias (< 0.001) and very small slope bias (0.78 % MSE).

Calf ADG was significantly affected by cow origin, cow maturity and cow parity (Table 2). The calf pre-weaning ADG for Dairybeef and LM genotypes were 66 and 75 g higher ($P < 0.001$) compared to Beef and EM genotypes, respectively. The least square means (corrected for parity) of calf ADG for Dairybeef, Beef, EM and LM genotypes were 960, 894, 890, and 965 g, respectively (Table 3). Calves from multiparous cows had a 92 g higher ($P < 0.001$) ADG compared to those from primiparous cows (Table 2). The calf ADG model fit statistics returned CCC values of 0.89 with RMSE (% of RMSE) of 9.21 and a very minimal mean (0.04 % MSE) and slope (0.82 % MSE) bias.

Correlations between cow MY and calf ADG for the different cow genotypes were moderately high; 0.68, 0.61, 0.58, and 0.65 for Dairybeef, Beef, EM and LM, respectively. Similarly, the correlations between daily cow MY and calf pre-weaning ADG were 0.63 and 0.55 for primiparous and multiparous cows, respectively. Correlations between cow daily MY and calf pre-weaning ADG for early-, mid- and late-lactation were 0.67, 0.59, 0.52, respectively.

The regression coefficients of calf ADG from birth-to-weaning on each additional kg of daily MY (g/kg) were higher ($P < 0.001$) for Beef (53 g) compared to Dairybeef (47 g), and higher ($P < 0.001$) for LM (55 g) compared to EM (51 g) genotypes and resulted in an additional 11.2, 9.8, 11.6 and 10.7 kg, respectively, of live weight at weaning. Furthermore, there was a quadratic or curvilinear relationship between calf ADG and cow MY for Dairybeef genotypes ($P < 0.05$) but not Beef genotypes. The response in calf ADG per kg additional milk was higher ($P < 0.001$) for multiparous (53 g) compared to primiparous (48 g) cows. The calf pre-weaning ADG response to each additional kg of milk during the particular lactation period was highest ($P <$

0.001) in late-lactation (48 g), followed by mid-lactation (44 g) and lowest in early-lactation (41 g) (Table 4).

Calf WW was significantly affected by cow origin, maturity and parity (Table 2). Calves from Dairybeef and LM genotypes were 14 and 20 kg heavier at weaning compared to those from Beef and EM genotypes, respectively. The least square means (corrected for parity) of calf 210-d adjusted WW for Dairybeef, Beef, EM and LM genotypes were 235, 223, 221, and 241 kg, respectively (Table 3). Calves from multiparous cows were 13 kg heavier than calves from primiparous cows ($P < 0.001$) at weaning (Table 2). The calf WW model fit statistics returned CCC values of 0.92 with RMSE (% of mean) of 7.50% and almost no mean (0.21 % MSE) and minimal slope (0.92 % MSE) bias.

4. Discussion

To our knowledge this study is the first published meta-analysis to synthesize data on beef suckler cow MY and calf performance and to determine the quantitative effect of cow MY on calf growth in temperate pasture-based systems. The objectives of this meta-analysis have been met, with the derivation of empirical models of cow MY, calf ADG and WW response with additional quantification of the effects of suckler cow genotype and cow parity. Factors influencing cow MY and calf performance are numerous; the development of multiple regression equations highlighted the most important variables and the response achieved from changes in these variables. The magnitude and range of data used in this analysis has enabled the development of models with a satisfactory level of accuracy for pasture-based beef suckler cow-calf systems operating under conditions similar to those in the dataset.

4.1. Cow milk yield

The current study showed a 35.4% greater daily MY for Dairybeef compared to Beef genotypes, which is broadly consistent with results (external to the current dataset) comparing Beef breed x Holstein-Friesian dams with their beef counterparts (42%, McCabe et al., 2017; 23%, McCabe et al., 2019a) or other purebred beef breeds (24-59%, McGee et al., 2005). In a comparison of Limousin, Limousin x (Limousin x Holstein-Friesian) and Limousin x Holstein-Friesian cows Murphy et al. (2008) found that increasing the proportion of Holstein-Friesian ancestry resulted in a 27% and 76% increase in cow daily MY, respectively, compared to the beef purebred. The higher MY of cows with dairy ancestry is a primary reason why beef crossbred replacement heifers are sourced from the dairy herd (beef x dairy) in many countries, as opposed to the alternative strategy of obtaining - purchased or homebred - heifer replacements from within the beef suckler herd (McGee, 2012; Roca Fraga et al., 2013; Law et al., 2013).

The 20.9% higher daily MY from LM genotypes than EM genotypes is consistent with breed rankings, albeit for peak daily MY, from NASEM (2016) whereby LM breeds such as Simmental, Charolais, and Limousin produced 12, 9, 9 kg, respectively, and EM breeds such as Angus and Hereford produced 8 and 7 kg of milk daily reflecting overall the higher production potential from LM genotypes. A positive relationship between cow body weight and MY within beef breeds has been noted (Petit et al., 1992), and, in general, LM genotype cows are comparatively heavier (Cundiff et al., 1993). It is accepted however that there can be relatively large differences in cow MY within both the LM and EM breed categories. For example, from a comprehensive analysis of French data Sepchat *et al.* (2017) reported daily MY of 5.9, 6.9 and 8.2 kg for Limousin, Charolais and Salers breeds,

respectively; similarly, an Irish study found 5.5 kg for Limousin and 6.9 kg for Charolais (Murphy et al., 2008). In particular within LM genotype cows, the 'dual-purpose' breeds, such as Simmental, are often recognised as having relatively higher MY (Murphy et al., 2008; NASEM, 2016). Additionally, breed rankings for MY may differ or change across countries depending on the emphasis placed on 'maternal' trait selection, such as MY or its proxy, calf (maternal) WW (Minogue et al., 2013), within breed-specific cattle breeding programs. Breeding indexes offer a potential strategy to identify genetically elite beef females with superior milk production (McHugh et al., 2014; McCabe et al., 2017).

The 14.8% higher MY for multiparous compared to primiparous cows is intermediate to parity differences reported for the main French beef breeds (20%, Petit and Agabriel 1989; 11%, Sepchat et al., 2017). The relatively lower MY of primiparous cows can be partially attributed to the fact that they are still growing compared to more mature, multiparous cows and require additional energy for their own growth (Freetly et al., 2006).

Milk yield of beef cows is mostly measured using indirect methods; in this dataset 73% of studies used the WSW technique. In effect, by using this method milk intake by the calf rather than MY of the cow is measured (Sepchat et al., 2017). French authors have reported that from shortly after birth the milk intake of a calf is limited by the milk production of its dam (Le Neindre and Vallet, 1992), whereas other studies have suggested that milk production is limited by the capacity of the calf (McGee et al., 2005; Roca Fraga et al., 2013); however, the former would generally apply to lower-yielding cow genotypes, whereas the latter applies to studies with higher-yielding, beef x dairy genotypes (McGee et al., 2005). In terms of calf growth

however, milk consumption, rather than potential production of the dam, is more important.

Unlike dairy cows, MY of beef suckler cows is not routinely measured in individual experiments; thus, relatively few studies have reported lactation curves suited for suckler cows (Wood, 1967; Jenkins and Ferrell, 1984) compared to dairy cows (e.g. Wood, 1967; Ali and Schaeffer, 1987; Quinn et al., 2005). Studies that have compared lactation curves for beef suckler cows have concluded that the equation developed by Wood (1967) was the most suitable (Hohenboken et al., 1992; Hirooka, 2010). Using the lactation curve of Wood (1967) peak MY occurred at an earlier stage of lactation in Dairybeef (4 to 6 weeks) compared to Beef (5 to 8 weeks) cows, both of which are within the 4 to 10 week range reported by Petit et al. (1992) and Roca Fraga et al. (2013). Previous research that involved the measurement of MY indoors and subsequently at pasture within seasonal grass-based production systems have shown the emergence of second higher peak in MY following turn-out to pasture in spring (McGee et al., 2005; Sepchat et al., 2017). This secondary peak mainly reflects differences in feed nutrient supply to the cow, which is usually higher when grazing pasture. Indeed, there is evidence that the increase in MY following turn-out to pasture is greater in higher-yielding (beef x dairy) compared to lower yielding (beef) genotypes (McGee et al., 2005).

Similarly, compared to Dairybeef, the daily MY of Beef genotypes increased relatively slowly after calving and also declined more slowly resulting in a flatter lactation curve (Figure 2). As the calf grows and its ability to suckle milk increases, MY stabilizes (Roca Fraga et al., 2013). The persistency of lactation curves from low-producing cows such as Beef and EM (-0.44 kg per month) is in agreement with the study by Sepchat et al. (2017) who reported 0.5 vs. 0.9 kg less daily MY per

month for 'low-producing' compared to 'high-producing' cows, respectively, in their dataset. However, milk production persistency varies according to other factors such as cow nutrition as well as consumption capacity of the calf (Le Neindre and Vallet, 1992; Vaz et al., 2016). Therefore, more research is warranted to develop more accurate and precise models to explain variation in MY by accounting additional factors, such as cow nutrition, within grazing systems.

4.2. Calf performance

Birth weight is the single most important risk-factor for occurrence of dystocia (Hickson et al., 2006; Ahlberg et al., 2016) and it is well known that the birth weight of calves varies with genotype. The 8% higher birth weight of calves from LM cow genotype than their EM counterpart's is consistent with recent findings by Nelson et al. (2016), who reported a higher mean birth weight of Norwegian calves from LM cow genotypes such as Charolais, Limousin and Simmental (45.6, 43.3, 45.6 kg, respectively) compared to EM cow genotypes such as Angus and Hereford (40.4 and 42.9 kg, respectively). Similarly, in their review, NASEM (2016) reported that the estimated mean birth weight of calves (born to Angus or Hereford cows) from Angus, Hereford, Charolais, Limousin and Simmental sires ranged from 26-31, 35-37, 39-43, 37-39 and 39-43 kg, respectively. Calf birth weight is positively correlated with cow mature weight and LM genotype cows are heavier and larger in frame size compared to EM genotypes (Bennett and Gregory, 1996).

The current study showed that calves born to multiparous cows were 10% heavier (3.54 kg), at birth than calves from primiparous cows (Table 2). Likewise, other studies have shown that the birth weight of calves from primiparous cows are lighter than those from multiparous cows (Johanson and Berger, 2003; Cundiff et al., 2010; Toušová et al., 2014); results indicating the opposite are infrequent (Nelson et

al., 2016). Lighter calves from primiparous cows is mainly attributed to the fact that younger dams allocate relatively more consumed energy towards growth and less towards the development of foetus in comparison to multiparous cows (Holland and Odde, 1992).

A higher pre-weaning growth rate and WW of beef calves is generally a key factor determining the profitability of beef production systems (Davies et al., 2009; Taylor et al., 2018). Calf pre-weaning growth was markedly different between the cow genotypes and is determined by both 'maternal' (mainly due to milk production) and by direct genetic (growth capacity transmitted to calves) effects, as well as environmental factors (Cortés-Lacruz et al., 2017; Walmsley et al., 2018). The 66 g higher calf pre-weaning ADG from Dairybeef compared to Beef genotypes is in line with results from other studies (72-110 g, McGee et al., 2005; 141-205 g, Murphy et al., 2008). The 14 kg heavier calves at weaning (210-day adjusted) from Dairybeef compared to Beef genotypes is in close agreement with a recent analysis of an Irish national database (McCabe et al., 2019b) and a cow genotype evaluation (McCabe et al., 2019a), which found that calves from beef x dairy cows were ca. 18 kg heavier at weaning (240-days) than beef genotypes. Similarly, Law et al. (2013) reported that 'high milk line' cows (e.g. Angus x Holstein-Friesian, Angus x Kiwicross) produced heavier (224 vs. 197 kg) calves at weaning (ca. 160-days) than 'low milk line' (straight-bred Angus) cows.

The 75 g higher calf ADG and 20 kg heavier calf at weaning from LM compared to EM cow genotypes in the current study are in agreement with other studies, who reported a higher pre-weaning growth rate for calves from LM genotypes - such as Charolais - cows compared to calves from EM genotypes - such as Hereford - (Jakubec et al., 2003; Krupa et al., 2005; Seppä-Lassila et al., 2017). The higher

values from Seppä-Lassila et al. (2017) and Krupa et al. (2005) may be due to a record of calf performance for short period of time as opposed to full-weaning period. In fact, the superior WW from LM genotype cows was a combination of a heavier birth weight (+2.70 kg), a higher cow MY (1.42 kg/d) resulting in a higher ADG (+75 g) of calves (Table 2), and additionally likely superior direct genetic effects (Cortés-Lacruz et al., 2017).

The 92 g higher calf pre-weaning ADG and a 13 kg heavier WW from multiparous cows compared to calves from primiparous cows in the current study are in close agreement with other studies outside of our dataset (Goyache et al., 2003; Linden et al., 2014; Toušová et al., 2014) who reported higher calf pre-weaning ADG and WW from multiparous cows. The superior WW of calves from multiparous compared to primiparous cows is due to a combination of a heavier birth weight (+3.54 kg) and superior growth, partly attributed to higher milk consumption (1.05 kg). Additionally, the higher growth response for each additional kg of milk from multiparous cows (53 vs. 48 g) reflected a higher growth potential from those calves compared to calves from primiparous cows.

The positive correlation of MY and calf pre-weaning ADG, and thus WW, is well documented although correlation coefficient values reported vary widely; 0.2 to 0.9 (Fiss and Wilton, 1993; Wright et al., 1994; Arthur et al., 1997; Liu et al., 2015). This large variance is likely due to the differences in factors such as cow nutrient environment, dietary proportion and nutritive value of forage consumed by the calf, as well as cow genotype, parity and stage of lactation effects. The current study synthesized the wider correlation between cow MY and calf pre-weaning ADG across the total lactation and reported moderately-high correlation coefficients ranging between 0.58 and 0.68 for the four genotype categories. The observed

correlation also depended on lactation stage with higher correlations detected in early-lactation (0.67) than late-lactation (0.52). The strength of this relationship declines with lactation stage as dependence by the suckling calf on non-milk nutrient sources, such as pasture, increases as it gets older (Tedeschi and Fox, 2009).

Calf growth is a key factor determining the profitability of beef suckler systems (Taylor et al., 2018); thus, it is imperative to understand the efficiency of calf growth from milk consumption in pasture-based systems. The current study found that the mean calf growth response to an additional kg of milk was 47, 53, 51 and 55 g for Dairybeef, Beef, EM and LM genotypes that resulted in an additional 9.8, 11.2, 10.7 and 11.6 kg, respectively, of live weight at weaning (210-d adjusted). The current calf growth response values are somewhat inferior (47-55 g) than the estimate of 60 g / kg derived by Sepchat et al. (2017) for suckled calves from French beef (late-maturing) breeds. In terms of calf WW per kg cow MY, the current results are superior (9.8-11.6 kg) to the estimate of 7.9 kg derived from a meta-analysis of 14 North American studies presented by Mulliniks et al. (2020).

The higher calf growth response to an additional kg of milk from Beef than Dairybeef genotypes concurs with results reported by McGee et al. (2005) who found, in two experiments, a pre-weaning calf growth response to an additional kg of milk of 55.4 and 63.7 g for Charolais cows, and 17.6 and 24.1 g for Beef x Friesian cows, respectively. The difference between the genotypes partially reflects the declining growth response to increased MY, as evidenced by the quadratic response found with Dairybeef genotypes in the current analysis. The presence of a quadratic response of calf ADG to cow MY in Dairybeef genotype implies that the cow MY beyond maximal response (i.e. 10 kg) will not be beneficial biologically; however, the linear model was retained as it explained most of the variation. In case of cow

maturity, the higher growth response per kg MY from LM than EM cows is consistent with other studies (Marston et al., 1992), and at least partially reflects the higher growth potential of LM genotypes. In studies where beef calves were artificially-fed with reconstituted milk whilst grazing (ca. 60-240 days), the response in calf ADG was 50 g per additional kg of milk (Baker et al., 1976). In contrast, with artificially-reared dairy calves, regression analysis showed a calf pre-weaning (from 7 to 41 days of age) ADG response of 34 g per additional kg of milk (mean daily consumption per treatment ranged from 5.7 to 9.4 kg) (Rosenberger et al., 2017). Alternatively, growth responses to creep feeding suckled calves at pasture in mid-late lactation with energy-based concentrates can range from 60 to 190 g live weight per kg concentrate (LeNeindre and Vallet, 1992; McGee et al., 1996), which is generally higher than the aforementioned responses obtained from milk consumption. In the case of concentrate creep feeding, the calf growth response will be a function of factors such as cow milk yield and forage substitution rate.

Although, it is recommended to include energy intake of both the cow and calf (milk + forage) in order to determine beef cow-calf production system efficiency (Walmsley et al., 2018), it was beyond the scope of this study to evaluate such effects. Additionally, there are numerous other factors that affect cow efficiency, particularly reproductive performance, and thus definitions of maternal productivity can vary accordingly, as well as depending on the maternal time-scale and whether the system incorporates progeny post-weaning performance too.

5. Conclusion

This meta-analysis extends the quantitative knowledge of cow MY and calf performance and discerned how cow genotype and parity influenced these

responses in pasture-based beef cow-calf suckler systems. The Dairybeef and LM genotype cows had 35.4% and 20.9% higher MY and ultimately weaned 14 and 20 kg heavier calves at weaning (210-day adjusted) compared to Beef and EM genotype cows, respectively. Multiparous cows produced 14.8% higher MY per day, delivered 3.6 kg heavier calves at birth and weaned 13 kg heavier calves at weaning (210-day adjusted) than primiparous cows. The calf growth response per kg additional daily MY was 47, 53, 51, and 55 g for Dairybeef, Beef, EM and LM cow genotypes, respectively.

It is concluded that the values and coefficients generated from this study for cow MY and calf performance can be used for improving beef cow-calf management strategies, beef cattle breeding programmes and bio-economic modelling purposes within pasture-based grazing systems. However, future research is warranted to determine how intake-related variables might further improve the model fit values and how additional cow-related variables affect the efficiency of pasture-based beef suckler cow-calf production systems.

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Ethics statement

Not applicable.

Declaration of interest

The authors have no known conflict of interest.

AUTHOR STATEMENT

We encourage you to submit an author statement file outlining all authors' individual contributions

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Figure 1: Density of observation of cow milk yield data: a. Cow origin and b. Cow maturity differentiated based on cow parity.

Figure 2: The lactation curve for different suckler cow genotypes modelled using Wood (1967).

Table 1. Summary statistics of cow MY (differentiated by cow origin, maturity, parity and lactation stages), calf birth weight, average daily gain, age of weaning and weaning weight.

Table 2. Parameter estimates and model fit values for cow milk yield, calf birth weight, calf pre-weaning average daily gain (ADG; g) and weaning weight (WW; kg-adjusted to 210 days of age) models.

Table 3: Least square means (SE in parenthesis) with the associated P value for cow milk yield (MY; kg/d), calf birth weight (kg), pre-weaning average daily gain (ADG; g) and weaning weight (WW; kg) adjusted to 210 days of age.

Table 4. Cow milk yield (kg/d) and calf response to milk yield (ADG/MY; g) at different lactation stages.

Figure

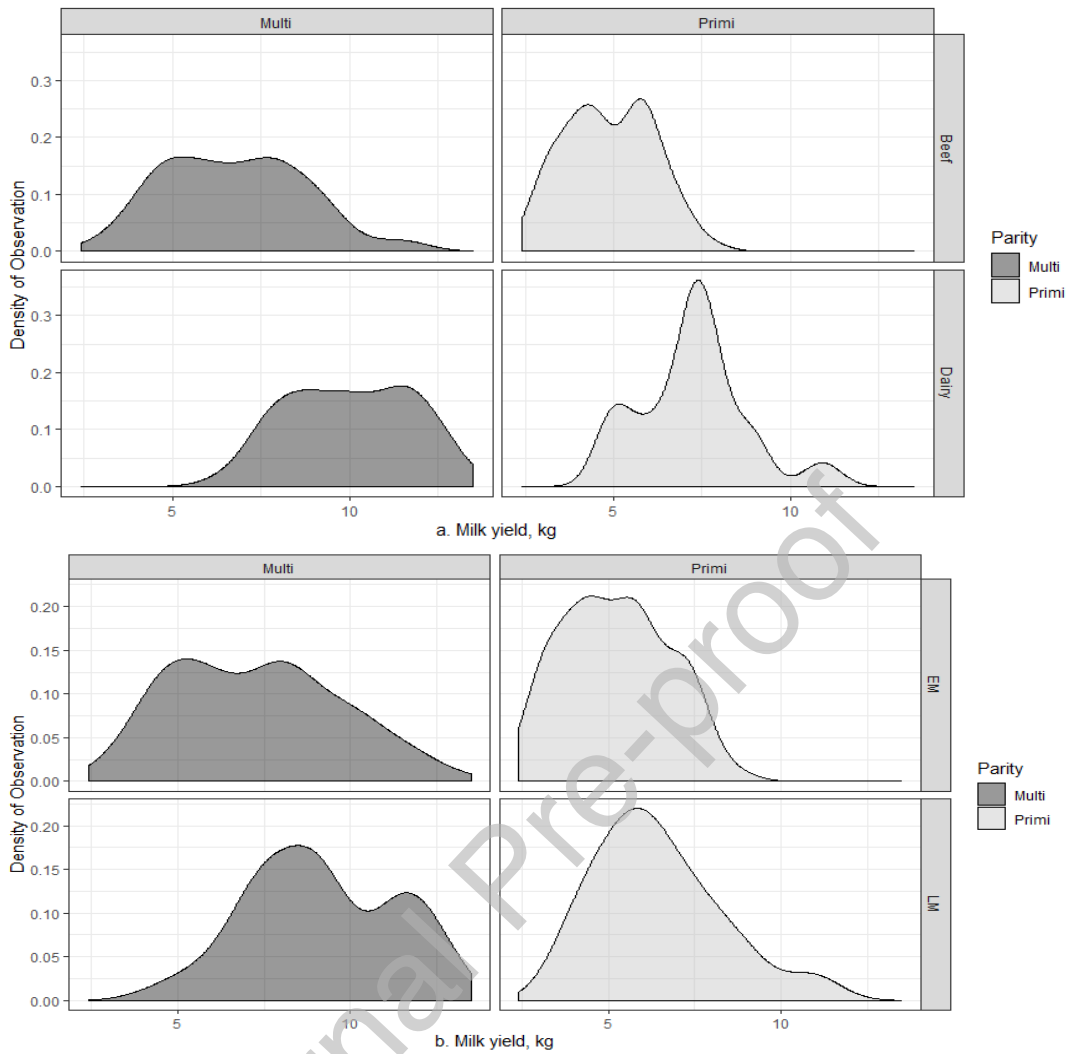


Figure 1: Density of observation of cow milk yield data: a. Cow origin and b. Cow maturity differentiated based on cow parity.

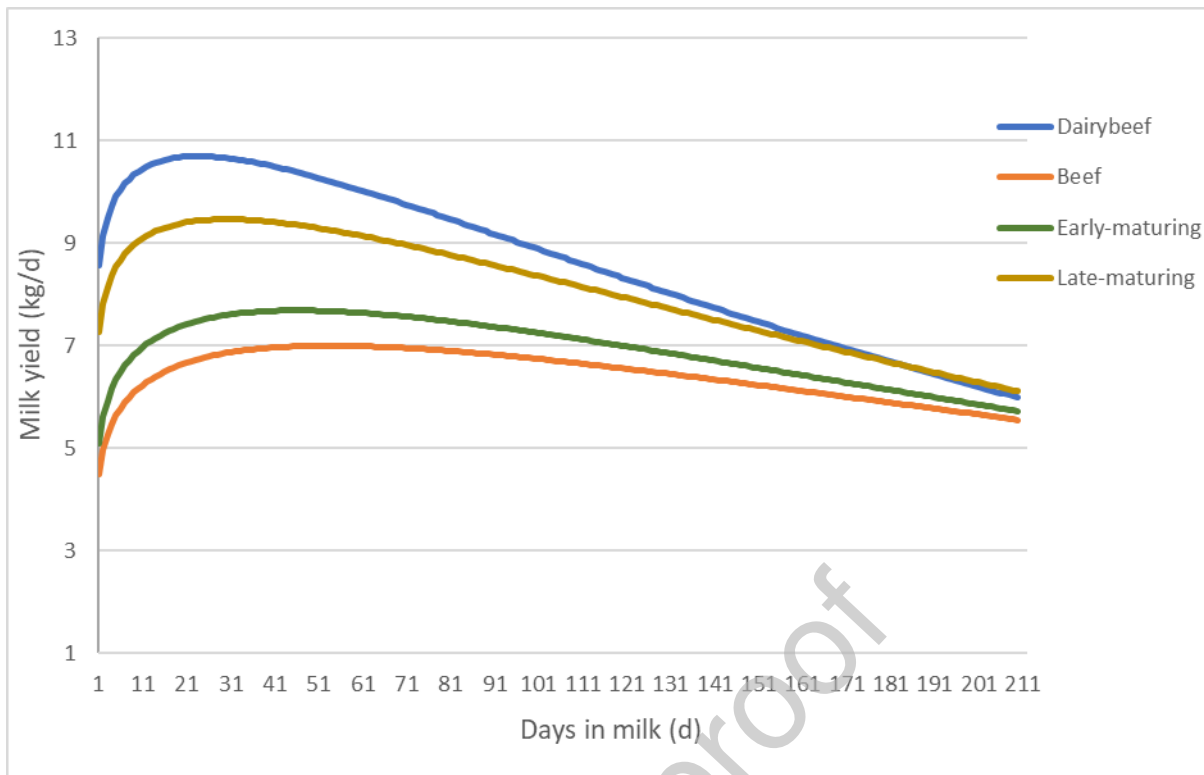


Figure 2: The lactation curve for different suckler cow genotypes modelled using Wood (1967).

Tables

Table 1. Summary statistics of cow MY (differentiated by cow origin, maturity, parity and lactation stages), calf birth weight, average daily gain, age of weaning and weaning weight.

Parameters	No of treatments	Mean	SD ¹	Minimum	Maximum
MY ² (kg/d)	344	7.12	2.482	3.10	12.80
MY by cow origin					
Dairybeef	131	8.94	2.115	4.23	12.80
Beef	213	6.03	1.941	3.10	11.58
MY by cow maturity					
Early-maturing	209	6.45	2.274	3.17	12.14
Late-maturing	135	8.35	2.389	3.80	12.71
MY by cow parity					
Primiparous	146	5.92	1.872	3.10	11.12
Multiparous	198	8.04	2.348	3.28	12.80
MY by lactation stage					
Early ³	71	9.51	2.163	4.10	12.80
Mid ⁴	113	7.05	2.079	3.19	11.67
Late ⁵	63	5.18	1.792	3.10	9.43
Calf birth weight (kg)	255	36.6	6.94	26.2	52.5
ADG ⁶ (g)	344	920	202.8	445	1449
AOW ⁷ (d)	344	188	36.2	90	244
WW ⁸ (kg)	344	224	47.4	124	372

¹SD=Standard deviation; ²MY=Milk yield of cows (kg/d); ³Early=0-70 days of lactation; ⁴Mid=71-140 days of lactation; ⁵Late=>141 days of lactation; ⁶ADG =Average daily gain of calves(g/d); ⁷AOW=Age of weaning (d); and ⁸WW=weaning weight of calves (kg).

Table 2. Parameter estimates and model fit values for cow milk yield, calf birth weight, calf pre-weaning average daily gain (ADG; g) and weaning weight (WW; kg- adjusted to 210 days of age) models.

	Milk yield (kg/d)		P-value	Calf birth weight (kg)		P-value	Calf ADG (g)		P-value	Calf WW (kg)		P-value
	Estimate	SE ¹		Estimate	SE		Estimate	SE		Estimate	SE	
	Intercept	7.41		0.412	<0.001		33.47	2.477		<0.001	878	
Cow origin												
Dairybeef	Reference											
Beef	-2.26	0.168	<0.001	0.76	0.751	0.21	-66	12.2	<0.001	-14	2.8	<0.001
Cow maturity												
Early-maturing	Reference											
Late-maturing	1.42	0.153	<0.001	2.70	0.638	<0.001	75	9.8	<0.001	20	3.7	<0.001
Cow parity												
Primiparous	Reference											
Multiparous	1.05	0.187	<0.001	3.54	0.816	<0.001	92	17.4	<0.001	13	3.5	<0.001
Model fit statistics												
r^2	344			255			344			344		
RMSE ³ , % Mean	11.75			8.52			9.21			7.54		
Unadj. RMSE, % Mean	21.61			12.21			17.33			13.70		
Mean bias, %												
MSE ⁴	<0.001			<0.001			0.04			0.21		
Slope bias, %MSE	0.58			0.78			0.81			0.92		

RSR ⁵	0.61	0.67	0.82	0.89
CCC ⁶	0.93	0.87	0.89	0.92
Unadj. CCC	0.81	0.81	0.76	0.74

¹SE=Standard error; ²n=No of treatments; ³RMSE=Root mean square error; ⁴MSE=Mean square error; ⁵RSR=RMSE/SD; and

⁶CCC=Concordance correlation coefficient.

Table 3: Least square means (SE in parenthesis) with the associated P value for cow milk yield (MY; kg/d), calf birth weight (kg), pre-weaning average daily gain (ADG; g) and weaning weight (WW; kg) adjusted to 210 days of age.

Parameters	MY	Birth weight	Calf ADG	Calf WW
Cow origin				
Dairybeef	8.64 (0.408)	36.62 (2.438)	960 (33.4)	236 (6.5)
Beef	6.38 (0.417)	37.38 (2.422)	894 (34.1)	222 (6.8)
<i>P</i> value	<0.001	0.21	<0.001	<0.001
Cow maturity				
Early-maturing	6.78 (0.191)	35.71 (2.403)	890 (33.8)	221 (5.7)
Late-maturing	8.20 (0.217)	38.41 (2.437)	965 (35.2)	241 (5.9)
<i>P</i> value	<0.001	<0.001	<0.001	<0.001
Cow Parity				
Primiparous	7.06 (0.219)	35.26 (2.422)	883 (33.9)	225 (6.4)
Multiparous	8.11 (0.241)	38.80 (2.467)	975 (34.7)	238 (6.6)
<i>P</i> value	<0.001	<0.001	<0.001	<0.001

Table 4. Cow milk yield (kg/d) and calf response to milk yield (ADG/MY; g) at different lactation stages.

Suckler cow genotypes	Lactation stage			SE ⁴	P-value
	Early ¹	Mid ²	Late ³		
Cow origin					
Dairybeef	10.16 ^a	8.47 ^b	6.67 ^c	0.713	<0.05
Beef	7.47 ^a	6.04 ^b	5.39 ^b	0.481	<0.05
Cow maturity					
Early-maturing	9.01 ^a	6.56 ^b	5.12 ^b	0.417	<0.05
Late-maturing	9.38 ^a	8.13 ^b	7.25 ^c	0.622	<0.05
ADG/MY	41 ^a	44 ^b	48 ^c	1.648	<0.001

¹Early=1-70 days; ²Mid=71-140 days; ³Late=>141 days; ⁴SE=Standard error; superscript ^{a, b, and c}=means within a row without a common superscript differ significantly (P<0.05).