

A mathematical nutrition model adequately predicts beef and dairy cow intake and biological efficiency

Phillip A. Lancaster,^{†,1} Michael E. Davis,[‡] Luis O. Tedeschi,^{||,ID} Jack J. Rutledge,[§] and Larry V. Cundiff[¶]

[†]Beef Cattle Institute, Kansas State University, Manhattan, KS 66506, USA

[‡]Department of Animal Sciences, The Ohio State University, Columbus, OH 43210, USA

^{||}Department of Animal Sciences, Texas A&M University, College Station, TX 77843, USA

[§]Department of Animal and Dairy Sciences, University of Wisconsin, Madison, WI 53706, USA

[¶]U.S. Meat Animal Research Center, Clay Center, NE 68933, USA

¹Corresponding author: palancaster@vet.k-state.edu

ABSTRACT

The beef cow-calf sector accounts for 70% of feed consumed and greenhouse gases emitted for the beef industry, but there is no straightforward method to measure biological efficiency in grazing conditions. The objective of this study was to evaluate a mathematical nutrition model to estimate the feed intake and biological efficiency of mature beef cows. Data from dams ($N = 160$) and their second and third progeny (312 pairs) were collected from 1953 through 1980. Individual feed intake was measured at 28-d intervals year-round for dams and during 240-d lactation for progeny. Body weights of progeny were measured at 28-d intervals from birth to weaning, and of dams at parturition and weaning each production cycle. The milk yield of dams was measured at 14-d intervals. Dam metabolizable energy intake (DMEI) and milk energy yield (MEL) of each cow were predicted using the Cattle Value Discovery System beef cow (CVDSbc) model for each parity. Biological efficiency (Mcal/kg) was computed as the ratio of observed or predicted DMEI to observed calf weaning weight (PWW). Pearson correlation coefficients were computed using *corr.test* function and model evaluation was performed using the *epiR* function in R software. Average (SD) dam weight, PWW, DMEI, and observed MEL were 527 (86) kg, 291 (47) kg, 9584 (2701) Mcal/production cycle, and 1029 (529) Mcal, respectively. Observed and predicted DMEI ($r = 0.93$ and 0.91), and observed and predicted MEL ($r = 0.58$ and 0.59) were positively correlated for progeny 2 and 3, respectively. The CVDSbc model under-predicted DMEI (mean bias [MB] = $1,120 \pm 76$ Mcal, 11.7% of observed value) and MEL (MB = 30 ± 25 Mcal, 2.9% of observed value). Observed and predicted progeny feed intake were not correlated ($r = 0.01$, P -value = 0.79). Observed and predicted biological efficiency were positively correlated ($r = 0.80$ and 0.80 , P -value ≤ 0.05) for parity 2 and 3, respectively, and the CVDSbc model under-predicted biological efficiency by 11% (MB = 3.59 ± 0.25 Mcal/kg). The CVDSbc provides reasonable predictions of feed intake and biological efficiency of mature beef cows, but further refinement of the relationship between calf feed intake and milk yield is recommended to improve predictions. Mathematical nutrition models can assist in the discovery of the biological efficiency of mature beef cows.

Key words: cow efficiency, metabolizable energy required, modeling

INTRODUCTION

The beef cow-calf sector requires the most feed (Johnson, 1984) and produces the most greenhouse gases (Johnson et al., 2002; Beauchemin et al., 2010; Capper, 2011) of any sector of the beef industry. Improving feed efficiency of the cow herd is one of the most effective methods to reduce beef's carbon footprint (Tedeschi et al., 2006a; Hegarty et al., 2007; Baber et al., 2020; Thompson and Rowntree, 2020). Additionally, the genotype of the most feed-efficient beef cow depends upon the nutritional environment (Jenkins and Ferrell, 1994; Jenkins and Ferrell, 2007; Hebart et al., 2018). However, measuring forage intake of grazing beef cows is difficult and impractical, such that methods of estimating or predicting the feed efficiency of beef cows have not been developed yet.

Several studies have evaluated the relationship between feed efficiency measured in young growing heifers and again as 3 to 5-yr-old cows (Arthur et al., 1999; Archer et al., 2002; Herd et al., 2006; Shaffer et al., 2011; Black et al., 2013; Freely et al., 2020). These studies indicate the phenotypic relationship is moderate ($r = 0.30$ to 0.40) when cows are

non-lactating, but weak ($r < 0.30$) when cows are lactating. Genetic correlations between feed efficiency measured in growing heifers and again as non-lactating ($r = 0.41$ and 0.98 ; Archer et al., 2002; Freely et al., 2020) and lactating ($r = 0.58$; Nieuwhof et al., 1992) cows are stronger. Generally, the weak to moderate correlations in these studies indicate that feed efficiency in growing cattle is a different trait than in mature cows, thus requiring a better estimation of feed efficiency in mature cows.

Mathematical nutrition models have been used to allocate feed intake of pen fed cattle to individual animals (mean bias [MB] of observed vs. predicted values = 2.43%) and estimate feed efficiency (MB = 1.94%) based on body weight, average daily gain, and body composition of growing cattle with reasonable accuracy (Bourg et al., 2006; Tedeschi et al., 2006a). Early work on cow efficiency found that cow body weight, condition score, and milk yield explained 84% of the variation in observed feed intake (Davis et al., 1987; Dinkel et al., 1990); all traits that can be measured or estimated with a nutrition model.

The Cattle Value Discovery System for beef cow (CVDSbc) model is based on the discovery technology proposed by [Tedeschi et al. \(2004\)](#), but it added submodels to estimate the metabolizable energy required (MER) for maintenance, gestation, and lactation of beef cows based on cow and calf performance measures and established nutrition equations ([Tedeschi et al., 2006b](#)). Cows are ranked by an energy efficiency index (EEI) that is the ratio of total MER by the cow to calf weaning weight, which has been used to identify cows that apportion more metabolizable energy (ME) toward lactation ([Reis et al., 2021](#)). The CVDSbc model has not been fully evaluated against measured cow intake and efficiency. We hypothesize that the CVDSbc model will accurately estimate total ME intake and biological efficiency in mature cows. The objective of this study was to compare CVDSbc model predicted values with observed total ME intake, milk yield, and cow efficiency and evaluate relationships among performance traits.

MATERIALS AND METHODS

Animal care and use committee approval were not required for this study because no animals were used. All data used in this evaluation were documented by [Davis et al. \(1983\)](#). The original experiments were conducted at the University of Wisconsin Agricultural Research Station located in Arlington, WI.

Data Source

Data were collected from identical and fraternal twin heifers purchased between 8 and 224 d of age in 1953, 1954, 1959, 1964, 1969, and 1974, and their progeny ([Christian et al., 1965](#); [Kress et al., 1969](#); [Kress et al., 1971a](#); [Kress et al., 1971b](#); [Hohenboken et al., 1972](#); [Hohenboken et al., 1973](#); [Towner, 1975](#); [Baik, 1980](#)). Only the data from the second and third parities were used in this analysis as the feed intake data for the first parity significantly overlapped with the postweaning growth phase of the dams prior to breeding. In 1953, 1954, and 1959, 22 dams of Hereford breeding were mated to Hereford bulls for each parity. Dams born in 1964 were straightbred Herefords except for eight dams of Hereford × dairy breed crosses, but all dams were bred to Hereford bulls for each parity. The breed composition of dams born in 1969 included 17 Herefords, 2 Hereford-Shorthorn crosses, 2 Hereford-Charolais crosses, and 24 Holsteins. Hereford and Hereford cross dams were bred to Holstein bulls, and Holstein dams were mated to Hereford bulls for each parity. In 1974, dams consisted of 14 Hereford-Holstein crosses, 14 Angus-Holstein crosses, 15 Simmental-Holstein crosses, and 13 Chianina-Holstein crosses. Dams were mated to Charolais bulls for the second and third parity.

Feeding and Management

Feeding and management of females and their progeny has been recently described in detail by [Lancaster et al. \(2021a, 2021b\)](#). Briefly, females in the 1953, 1954, and 1959 experiments were fed a common diet within experiment from 240 d of age to weaning of their third progeny. In the 1964, 1969, and 1974 experiments, females were randomly assigned within breed to either a low- or high-energy diet at 240 d of age and maintained on that diet until weaning of their third progeny. All diets were formulated to meet digestible protein

requirements and total digestible nutrients (TDN) concentration computed from values for individual feedstuffs, according to [Morrison \(1956\)](#). ME concentration of the diets was computed from diet TDN values using the National Academy of Science, Engineering, and Medicine ([NASEM, 2016](#)). Dams and their nursing progeny were individually fed throughout the experiment, and pairs were randomly assigned to separate individual self-feeders during lactation. Dams and progeny were tied to the self-feeder for 2 h in the morning and afternoon, and allowed to consume feed ad libitum. Feed offered was recorded daily. Feed refusals were weighed at 28-d intervals and feed consumption was calculated for dams and nursing progeny.

Milk yield was measured twice daily at 0800 and 1630 h at 14-d intervals throughout the lactation period by machine or hand milking one half of the udder while the calf nursed the other half. Butterfat percentage was measured and used to compute milk yield adjusted to 4% butterfat equivalent ([Davis et al., 1983](#)). Length of lactation was 240 d in all experiments except 1974, and milk yield for the 1974 dams was adjusted from 224 d to 240 d according to [Rutledge et al. \(1972\)](#).

Dams were weighed at 28-d intervals as well as within 12 h following parturition. Progeny were weighed at 28-d intervals from birth to weaning. Weaning BW was adjusted to a constant 240 days of age and weaning BW of heifers adjusted to a steer basis.

Data Calculations

Feed consumption data that were available in the datafile was the accumulated feed consumption converted to ME intake. For dams, feed consumption dam ME intake (DMEI) was accumulated from weaning to weaning (one production cycle). For nursing progeny, feed consumption progeny preweaning feed ME intake (PFMEI) was accumulated from birth to weaning.

Body weight data available in the datafile were the calf weights at weaning adjusted for age and sex and dam weights at weaning and parturition. Average dam weight (MCWT) for a given parity was computed as the average of dam weights at weaning of previous progeny, parturition, and weaning of current progeny. Weights of progeny used were those at birth and weaning. For dams, the milk yield data available in the data file was the total milk yield for the entire 240-d lactation adjusted to an energy corrected basis (4% butterfat) and was designated as milk energy yield (MEL).

Dam biological efficiency (DEFF) was computed as the ratio of observed DMEI to progeny weaning weight (PWW) such that a more efficient dam has a lesser DEFF (Mcal/kg). The simple weight ratio (WR) was calculated as ratio of PWW to dam weight at weaning such that a more efficient dam has a greater WR.

CVDSbc Model

The CVDSbc model is time-dependent calculated each day of a 365-d calving interval and partially adopted submodels developed by [Fox et al. \(1988\)](#) and [Reynoso-Campos et al. \(2004\)](#) and is illustrated in Supplementary Material. The model computes ME required for maintenance based on cow weight adjusted for conceptus weight and physiological stage (dry vs. lactation) but does not currently adjust for changes in body condition score as does the CVDS for dairy cows

(Tedeschi et al., 2010). ME required for gestation is computed using calf birth weight and day of gestation to derive the energy concentration in the conceptus and assuming an efficiency of ME use of 13%, though this efficiency may not be constant (Tedeschi and Fox, 2020). The model computes milk yield by iteratively adjusting peak milk yield (PKM) until the model-predicted weaning weight matches the observed weaning weight. Calf growth is computed from the intake of milk and forage, where forage intake is computed from a model developed from the data of Abdelsamei et al. (2005) as described by Tedeschi et al. (2006b). The ME required for lactation is computed assuming milk fat content of 4% and a protein content of 3.4% and efficiency of ME use of 0.64. The predicted MEL was computed based on a NASEM (2016) equation to predict milk energy using milk fat content. Cow MER is computed as the sum of energy required for maintenance, gestation, and lactation, and was used as the predicted DMEI. Predicted cow biological efficiency, DEFF, was computed as the ratio of cow MER to calf weaning weight (Mcal/kg) such that a more efficient dam has a lesser DEFF.

For this data analysis, the CVDSbc model was modified to accommodate differing net energy for maintenance requirements of dam and progeny of varying breed composition based on adjustment factors from NASEM (2016). For straightbred beef breeds, no adjustment to maintenance was made. For straightbred dairy breeds, maintenance was increased 20%, and for crossbred beef $\times$ dairy breeds, maintenance was increased 10%. Additionally, the model was adjusted for production cycles shorter and longer than 365 days as dams were bred at first heat after parturition until pregnant, resulting in varying lengths of the production cycle. In the CVDSbc model, gestation length was maintained at 285 days, and the length of the postpartum interval was varied.

There were 312 dam-progeny pairs over the second and third parities with all the necessary data (dam weight, calf birth weight, calf weaning weight, and calf slaughter weight) for the CVDSbc model. Each pair was modeled separately, and the outputs of ME required for maintenance, gestation, and lactation of the dam, progeny ME intake, and biological efficiency were recorded.

Model Evaluation

Data for parities 2 and 3 were combined into a single dataset for CVDSbc model evaluation. Model evaluation was performed using R statistical software. First, Pearson correlation coefficients were computed within parity to evaluate the relationships among observed and predicted performance and efficiency traits. Correlation coefficients were considered significant at $P \leq 0.05$.

Second, a comparison of predicted DMEI, MEL, calf feed intake, and cow EEI with observed values was performed using several model evaluation techniques. Linear regression of observed values on predicted values was performed using the *lm* function of the base statistical package. A linear hypothesis test was performed using the *linearHypothesis* function with $P \leq 0.05$, resulting in rejection of the null hypothesis that intercept and slope are simultaneously equal to zero and one, respectively. The concordance correlation coefficient (CCC), bias correction factor (Cb), and MB were computed using the *epiR* package, root mean square error of prediction (RMSEP) was computed, and the coefficient of model

determination (CD) and modeling efficiency statistics were computed according to Tedeschi (2006).

RESULTS AND DISCUSSION

The dataset used to evaluate the CVDSbc model may impact the relevance to current cattle genotypes, but is unique in the type and quantity of data. Few studies have collected individual feed intake on cows and calves for two complete production cycles, and bi-weekly milk yield of cows. The value for net energy for maintenance used by NASEM (2016) and in the CVDSbc model is based on data of Lofgreen and Garrett (1968), the milk yield equation used by NASEM (2016) and in the CVDSbc model is based on Jenkins and Ferrell (1984), and the growth equation used by NASEM (2016) and in the CVDSbc model is based on comparative slaughter experiments conducted between 1960 and 1980 (Garrett 1980). A recent analysis of the growth equation (National Academies of Sciences, Engineering, and Medicine, 2016) indicated that predicted retained energy explained 95% of the variation in observed retained energy in current cattle genotypes (2001 to 2010) even though the growth equation was developed from cattle between 1960 and 1980. Equations developed from cattle genetics during the same timeframe as data in this study are still used and accurate with current cattle genetics.

Average MCWT (515 and 552 kg) and PWW (287 and 294 kg; Table 1) in Production Cycles 2 and 3, respectively, are similar to previous studies evaluating feed intake and efficiency in beef cows age 3 to 6 yr that have reported cow weight ranging from 435 to 757 kg (Basarab et al., 2007; Black et al., 2013; Lawrence et al., 2013; Wood et al., 2014; Broleze et al., 2020), and calf weight ranging from 160 to 240 kg at 205 d of age (Jenkins and Ferrell, 1994; Mourer, 2012; Andresen et al., 2020). Previously, we estimated dam daily dry matter intake to be 13.21 (SD = 1.27) kg/d (Lancaster et al., 2021a) and PKM to be 10.03 (SD = 5.21) kg/d (Lancaster et al., 2021b) in this dataset, which is within the range reported by previous studies with DMI ranging from 9.08 to 12.97 kg/d, and energy-corrected milk yield ranging from 4.7 to 11.6 kg/d (Basarab et al., 2007; Black et al., 2013; Lawrence et al., 2013; Wood et al., 2014; Broleze et al., 2020).

Mature cow weight and observed MEL were strongly, positively correlated ($r > 0.50$) with observed DMEI in both parity 2 and 3 (Tables 2 and 3). Progeny feed ME intake was moderately, negatively correlated with observed MEL in both parities as would be expected given that feed intake increases as milk yield decreases (Baker et al., 1976; Holloway et al., 1982; Tedeschi and Fox, 2009). Additionally, PWW was strongly, positively correlated with observed MEL and DMEI in both parities as expected (Clutter and Nielsen, 1987; Meyer et al., 1994; Cortés-Lacruz et al., 2017). Likewise, predicted MEL was strongly positively correlated with observed MEL, DMEI, and PWW in both parities, and predicted DMEI was strongly, positively correlated with observed MCWT, MEL, DMEI, and PWW in both parities. A strong correlation between predicted MEL and PWW was expected because the calculation of predicted MEL in the CVDSbc model is directly related to PWW. However, the correlation between predicted MEL and PWW (0.85 to 0.89) is stronger than the correlation between observed MEL and PWW (0.68) in the current dataset, as well as previous studies correlating milk yield

Table 1. Summary statistics of observed growth, intake, lactation, and feed efficiency traits of dams and progeny, and CVDS beef cow model outputs for parities 2 and 3

Trait	N	Mean	SD	Min	Max
Observed data					
Production cycle 2					
Dam LW parturition, kg	152	497	83	313	791
Dam LW weaning, kg	152	534	86	343	879
Dam ME intake, Mcal	152	9,440	2,719	4,483	19,263
Dam milk ME, Mcal	147	1,009	538	229	2,719
Dam efficiency, Mcal/kg	152	32.69	7.17	18.87	53.83
Progeny BW, kg	152	39.4	7.7	24.1	63.9
Progeny WW, kg	152	287	49	182	405
Progeny feed ME intake, Mcal	152	1,281	336	412	2,377
Progeny slaughter weight, kg	152	459	62	257	650
Weight ratio, kg WW/kg dam LW	152	0.545	0.089	0.288	0.798
Production cycle 3					
Dam LW parturition, kg	159	536	88	346	830
Dam LW weaning, kg	160	568	91	364	923
Dam ME intake, Mcal	160	9,721	2,686	4,772	18,267
Dam milk ME, Mcal	139	1,051	521	188	2,759
Dam efficiency, Mcal/kg	160	32.87	6.84	18.97	59.71
Progeny BW, kg	160	40.0	7.3	26.5	62.6
Progeny WW, kg	160	294	44	194	389
Progeny feed ME intake, Mcal	160	1,309	320	462	2,074
Progeny slaughter weight, kg	160	464	51	372	614
Weight ratio, kg WW/kg dam LW	160	0.525	0.086	0.325	0.819
Model outputs					
Production cycle 2					
Dam ME maintenance, Mcal	152	5,995	1,259	4,027	10,535
Dam ME pregnancy, Mcal	152	594	115	363	963
Dam ME lactation, Mcal	152	1,703	527	494	2,866
Dam ME required, Mcal	152	8,292	1,618	5,402	13,704
Dam efficiency, Mcal/kg	152	29.02	4.30	22.10	51.47
Progeny feed ME intake, Mcal	152	1,714	314	1,031	2,549
Production cycle 3					
Dam ME maintenance, Mcal	160	6,301	1,372	4,103	10,823
Dam ME pregnancy, Mcal	160	592	119	293	945
Dam ME lactation, Mcal	160	1,733	525	524	2,880
Dam ME required, Mcal	160	8,626	1,702	5,466	13,601
Dam efficiency, Mcal/kg	160	29.35	4.01	22.34	44.09
Progeny feed ME intake, Mcal	160	1,756	260	1,200	2,278

LW, live weight; ME, metabolizable energy; milk ME, ME available to the calf after consuming the milk; BW, birth weight; WW, weaning weight

with weaning weight ($r = 0.30$ to 0.60 ; Clutter and Nielsen, 1987; Marston et al., 1992; Mallinckrodt et al., 1993). The stronger correlation of PWW with predicted MEL than in previous studies is likely due to the inaccuracy and imprecision of predicting feed intake of nursing calves using the available equations (Lancaster et al., 2021b). Additionally, the strong correlation of predicted DMEI with MCWT was expected because maintenance energy requirements and cow weight account for the largest proportion of variation in beef cow intake (Johnson, 1984; Dinkel et al., 1990). The strong correlations of predicted with observed MEL and predicted with observed DMEI are indicative of the adequacy of the

CVDSbc model to appropriately rank cows based on milk yield and total energy intake, and should result in accurate ranking based on biological efficiency.

Observed DEFF was moderately to strongly, positively correlated with MCWT and observed MEL, and strongly, positively correlated with observed DMEI such that more efficient cows were lighter, produced less milk, and consumed less ME. Likewise, predicted DEFF was moderately to strongly positively correlated with MCWT and observed DMEI in both parities, but was not correlated or weakly correlated with observed MEL. In contrast, Dinkel and Brown (1978) reported no significant correlation of biological efficiency

Table 2. Pearson correlations among dam and progeny performance and efficiency traits, and CVDS beef cow model outputs for parity 2

Trait1	oMEL	oDMEI	oDEFF	oPFMEI	PWW	PSLW	WR	pMEL	pDMEI	pDEFF
MCWT	0.47*	0.63*	0.47*	-0.31*	0.47*	0.07	-0.44*	0.43*	0.68*	0.37*
oMEL		0.71*	0.42*	-0.41*	0.68*	0.19*	0.26*	0.58*	0.63*	0.06
oDMEI			0.78*	-0.36*	0.69*	0.08	0.06	0.65*	0.93*	0.42*
oDEFF				-0.52*	0.11	-0.18*	-0.39*	0.19*	0.67*	0.80*
oPFMEI					0.02	0.39*	0.30*	-0.19*	-0.30*	-0.46*
PWW						0.30*	0.56*	0.85*	0.71*	-0.25*
PSLW							0.25*	-0.21*	0.04	-0.35*
WR								0.44*	0.07	-0.61*
pMEL									0.70*	-0.08
pDMEI										0.48*

oMEL, observed milk metabolizable energy (ME) yield; oDMEI, observed dam ME intake; oDEFF, observed biological efficiency (Mcal ME/kg WW); oPFMEI, observed progeny preweaning feed ME intake; PWW, observed progeny weaning weight; PSLW, progeny slaughter weight; WR, ratio of observed progeny weaning weight to dam weight at weaning; pMEL, model predicted ME required for lactation; pDMEI, model predicted dam ME intake; pDEFF, model predicted biological efficiency.

* $P \leq 0.05$

Table 3. Pearson correlations among dam and progeny performance and efficiency traits, and CVDS beef cow model outputs for parity 3

Trait	oMEL	oDMEI	oDEFF	oPFMEI	PWW	PSLW	WR	pMEL	pDMEI	pDEFF
MCWT	0.52*	0.65*	0.57*	-0.37*	0.44*	0.06	-0.53*	0.38*	0.66*	0.47*
oMEL		0.77*	0.55*	-0.52*	0.68*	0.19*	0.18*	0.59*	0.69*	0.25*
oDMEI			0.85*	-0.39	0.66*	0.15*	-0.04	0.57*	0.91*	0.58*
oDEFF				-0.48*	0.18*	0.07	-0.39*	0.14	0.70*	0.80*
oPFMEI					-0.03	0.16*	0.33*	-0.09	-0.26*	-0.33*
PWW						0.17*	0.49*	0.89*	0.72*	-0.05
PSLW							0.10	-0.28*	0.13	-0.01
WR								0.44*	0.04	-0.47*
pMEL									0.64*	-0.04
pDMEI										0.65*

oMEL, observed milk metabolizable energy (ME) yield; oDMEI, observed dam ME intake; oDEFF, observed biological efficiency (Mcal ME/ kg WW); oPFMEI, observed progeny preweaning feed ME intake; PWW, observed progeny weaning weight; PSLW, progeny slaughter weight; WR, ratio of observed progeny weaning weight to dam weight at weaning; pMEL, model predicted ME required for lactation; pDMEI, model predicted total ME required; pDEFF, model predicted biological efficiency

* $P \leq 0.05$

with cow weight, and a weak negative correlation with milk yield, which may be due to only four measurements of milk yield using the weigh-suckle-weigh technique compared to the more intensive measurement of milk yield in the current study. Additionally, the increase in milk production may not result in large increases in calf weaning weight (Mulliniks et al., 2020) due to less efficient conversion of nutrient intake to gain of calves nursing high milking cows (van Oijen et al., 1993). Calves from low milking cows can compensate with increased nutrient intake from feed given high nutritive value of the feed (Edwards et al., 2017) as in the current dataset.

Predicted DEFF was moderately to strongly correlated with predicted DMEI, which is slightly lower than correlations between observed DEFF and observed DMEI, and was not correlated with predicted MEL in either parity, which is different from correlations between observed DEFF and observed MEL. The lack of correlation between predicted DEFF and predicted MEL is likely due to the calculation of predicted MEL in the CVDSbc model, where predicted MEL is dependent upon calf weaning weight rather than cow energy intake and mobilization of body reserves.

Milk production is dependent upon the genetic potential for milk production, the energy intake of the cow, and the level of energy reserves available (Lalman et al., 2000; Spencer, 2017). Currently, the CVDSbc model does not account for changes in body condition scores to adjust milk yield. Both observed and predicted DEFF were moderately negatively correlated with observed PFMEI, such that more efficient dams had progeny that consumed more feed. Based on this analysis, cows with greater peak milk but lesser lactation persistence may be more efficient. Cows that mobilize energy reserves in early lactation for greater peak milk would result in larger calves at 3 to 4 months of age when forage intake becomes a significant source of nutrients and greater intake of forage to increase growth. Lesser lactation persistence would allow the cow to regain condition in late lactation more efficiently than after weaning (Moe et al., 1971; Moe, 1981). However, the negative impact of greater energy demands in early lactation on reproductive efficiency could offset the efficiency of the entire herd. Additionally, the most efficient peak milk and lactation persistence may be dependent on the differences in forage nutritive value

throughout the lactation period. If forage nutritive value declines sharply later in lactation, increased forage intake by the calf could result in lesser weaning weight than if the lactation persistence was greater. Again, the most efficient cow for one environment may be different than in other environments.

WR had very different correlations with production measures in contrast to observed and predicted DEFF. WR was weakly, positively correlated with observed MEL, was not correlated with observed DMEI, and was strongly, positively correlated with PWW, as expected, such that more efficient dams produced more milk for the same intake and weaned heavier calves. Also, WR was moderately to strongly, negatively correlated with MCWT, as expected, such that more efficient dams were lighter. Similar correlations were reported by Dinkel and Brown (1978), who agreed with the analysis of MacNeil (2005).

WR was moderately, negatively correlated with observed DEFF, and predicted DEFF was strongly, positively correlated

with observed DEFF. Thus, predicted DEFF more closely matched the observed DEFF than the simple WR, probably due to the CVDSbc model adjusting for differences in net energy for maintenance per unit of MCWT, and energy requirements for gestation and lactation, whereas WR does not account for these differences.

Summary statistics of observed variables for the combined parity dataset are presented in Table 4. Regression of observed MEL on predicted MEL resulted in an intercept and slope not different than zero or one ($P = 0.50$), but a low r^2 and large RMSE (Table 5). The CCC was moderate and the CD was far from 1, but the Cb was high and the MB was low at 2.91%. Collectively, these results indicate that the CVDSbc model prediction of MEL was accurate but imprecise. In contrast, the CVDSbc model more precisely predicted DMEI and DEFF but was somewhat inaccurate. Regression of observed DMEI or DEFF on predicted DMEI or DEFF resulted in intercepts less than zero and slopes greater than 1, but r^2 of 0.842 and 0.638, respectively. The CCC was moderate to strong and CD were closer to 1, but the MB was high at 11.69 and 10.95% for DMEI and DEFF, respectively, indicating an underprediction. Unlike MEL, DMEI, and DEFF, the CVDSbc model prediction of PFMEI was both inaccurate and imprecise. Regression of observed PFMEI on predicted PFMEI resulted in a slope not different from zero, and an r^2 and CCC near zero. The Cb was low, and the MB was -33.98% , indicating a large overprediction. The equations to predict nursing calf feed intake have previously been evaluated by our laboratory (Lancaster et al., 2021b). When milk intake is known, these equations adequately predict calf weaning BW, but poorly predict calf feed intake.

The CVDSbc model successfully ranked cows according to feed intake and biological efficiency. The small discrepancies among correlations of production measures with model outputs compared with observed traits is likely due to additional variation in maintenance energy requirements, partial efficiencies, feed digestibility, and estimation of milk yield not accounted for by the CVDSbc model. Maintenance energy requirements vary with body composition, both dependent (Ferrell, 1988) and independent (Birnie et al., 2000)

Table 4. Summary statistics of observed variables in the combined parity dataset

Parameter	N	Mean	SD	Min	Max
Mature cow weight, kg	312	527	86	328	901
Dam milk energy yield, Mcal	286	1,029	529	188	2,759
Dam feed ME intake, Mcal	312	9,584	2,701	4,483	19,263
Progeny weaning weight, kg	312	291	47	182	405
Progeny feed ME intake, Mcal	312	1,295	328	412	2,377
Dam efficiency, Mcal/kg	312	32.78	7.00	18.87	59.71

ME, metabolizable energy.

Table 5. Model evaluation of CVDS beef cow model in predicting total feed metabolizable energy intake of dams for a full production cycle, milk energy yield and progeny feed metabolizable energy intake during a 240-d nursing period, and dam biological efficiency

Item	MEL	DMEI	PFMEI	DEFF
RC β_0	26.54 $\pm$ 87.24	-3,000 $\pm$ 315	1,266 $\pm$ 114	-6.49 $\pm$ 1.70
RC β_1	1.003 $\pm$ 0.083	1.487 $\pm$ 0.036	0.017 $\pm$ 0.065	1.345 $\pm$ 0.057
r^2	0.337	0.842	0.000	0.638
Pr > F	0.502	<0.0001	<0.0001	<0.0001
RMSE	431.9	1,074	328.3	4.21
RMSEP	431.41	1,749	617	5.71
CCC	0.502	0.729	0.007	0.586
Cb	0.865	0.794	0.491	0.734
MB	29.99 $\pm$ 25.49	1,120 $\pm$ 76	-440 $\pm$ 25	3.59 $\pm$ 0.25
CD	2.957	1.806	0.387	1.621
MEF	0.334	0.579	-2.556	0.331

MEL, observed milk metabolizable energy (ME) yield; DMEI, observed dam ME intake; DEFF, observed biological efficiency (Mcal ME/kg WW); PFMEI, progeny preweaning feed ME intake; RC simple linear regression coefficient; r^2 , simple coefficient of determination; Pr > F, P-value for simultaneous test of intercept = 0 and slope = 1; RMSE, root mean square error; RMSEP, root mean square error of prediction; PRESS, predictive residual sum of squares; CCC, concordance correlation coefficient; Cb, bias correction factor; MB, mean bias; CD, coefficient of model determination; MEF, modeling efficiency statistic.

of visceral organ mass, and this could affect accuracy of estimating maintenance energy requirements in the CVDSbc model since measurements of body condition were not available. Additionally, visceral organ mass is influenced by the plane of nutrition and forage or neutral detergent fiber (NDF) intake (Ferrell et al., 1986; Reynolds et al., 1991), and the level of milk production (Montaño-Bermudez et al., 1990). Some previous attempts to model changes in maintenance energy requirements have been published (Williams and Jenkins, 1998; Williams and Jenkins, 2003; Oltjen, 2005), but none have been adopted by the committee on Nutrient Requirements of Beef Cattle (NASEM, 2016). Currently, the CVDSbc model does not adjust net energy for maintenance requirements other than for breed differences and does not attempt to adjust ME required for maintenance based on milk production or diet characteristics as this information is not commonly available at the farm level.

The CVDSbc model uses a constant efficiency of ME use for lactation of 0.64. Recent evidence indicates that some variation (13%) in the efficiency of ME use for lactation exists among dairy cattle (Guinguina et al., 2020), but Veerkamp and Emmans (1995) suggest that there is minimal variation in the partial efficiency of ME use for lactation. Little data are available to determine whether variation in partial efficiency exists, and much less data on the factors that may influence the partial efficiency are available, making the prediction of partial efficiency difficult. Based on the accuracy of predicted MEL an average partial efficiency of 0.64 seems appropriate, but the imprecise prediction of MEL indicates that variation in partial efficiency may exist. The current dataset includes beef, dairy, and beef × dairy cross dams which may influence the partial efficiency of ME use for lactation. Freely et al. (2006) reported a partial efficiency of ME use for lactation of 0.72 in beef cows compared with the 0.60 to 0.67 reported in dairy cows (Moe et al., 1971; Yan et al., 1997). In contrast, Reynolds and Tyrell (2000) reported a partial efficiency of 0.64 in beef cows, which is more similar to the value of 0.61 when these authors re-evaluated the data of Moe et al. (1972) in dairy cows. Thus, whether the partial efficiency of ME use for lactation should be adjusted between beef and dairy breeds in the current dataset is inconclusive, but additional research to ascertain any variation in and factors affecting partial efficiency is warranted.

Another reason for the discrepancies between model-predicted and observed biological efficiency is the poor precision with which the CVDSbc model predicts milk yield and progeny feed intake. In the calf growth submodel, milk intake and feed intake are related through an empirical equation to predict feed intake based on days in milk, calf body weight, and daily milk yield (Tedeschi and Fox, 2020). Daily milk yield is calculated from peak milk and days in milk using the NASEM (2016) milk yield equation. The peak milk value used in the milk yield equation is iterated until the predicted weaning weight matches the observed weaning weight. The issue with the calf growth submodel is that there are two unknowns: milk intake and feed intake, and multiple combinations of the two could result in the correct weaning weight. Unfortunately, a solution has not yet been identified. Lancaster et al. (2021b) recently evaluated several equations to predict feed intake of nursing calves assuming milk intake was known, and none of the available equations adequately predicted feed intake. Additionally, the relationship between milk intake

and feed intake in the dataset varied depending upon the calf breed composition. Furthermore, a recent analysis of published data (Hildebrand and Lancaster, unpublished) indicates that the relationship between retained energy and empty body gain is different in calves less than 200 kg compared to growing cattle over 250 kg likely due to the greater proportion of less energy-dense protein and water in the gain of lighter weight calves. This result suggests that the standard growth equation (NASEM, 2016) may not accurately predict the growth of preweaning calves, which could affect the amount of milk and feed intake required to reach the observed weaning weight. Therefore, further research is needed to improve equations for ME intake and growth of preweaning calves.

In conclusion, the CVDS beef cow model estimated DMEI and biological efficiency of a wide variety of cow types under differing nutritional environments reasonably well; however, accuracy and precision could be further improved to rank cows within contemporary groups for biological efficiency. Prediction of dam milk yield and calf feed intake were imprecise and for feed intake inaccurate, which likely represents the greatest imprecision of estimating DMEI and biological efficiency. However, further research is needed to better account for variation in net and metabolizable energy required for maintenance, and partial efficiency of metabolizable energy use for maintenance and lactation.

Supplementary Data

Supplementary data are available at *Translational Animal Science* online.

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Conflict of interest statement

None declared.

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