Faculty Papers and Publications in Animal Science

Animal Science Department

2019

Comparison of different functions to describe growth from weaning to maturity in crossbred beef cattle

Madeline J. Zimmermann
University of Nebraska - Lincoln

Larry A. Kuehn
USDA, Agricultural Research Service

Matthew L. Spangler
University of Nebraska - Lincoln, mspangler2@unl.edu

R. Mark Thallman
USDA, Agricultural Research Service

Warren M. Snelling
USDA, Agricultural Research Service

See next page for additional authors

Follow this and additional works at: https://digitalcommons.unl.edu/animalscifacpub

Part of the Genetics and Genomics Commons, and the Meat Science Commons

Authors

Madeline J. Zimmermann, Larry A. Kuehn, Matthew L. Spangler, R. Mark Thallman, Warren M. Snelling, and Ronald M. Lewis

Comparison of different functions to describe growth from weaning to maturity in crossbred beef cattle[1]

Madeline J. Zimmermann[†], Larry A. Kuehn[‡], Matthew L. Spangler[†], R. Mark Thallman[‡], Warren M. Snelling[‡,©], and Ronald M. Lewis[†,2]

[†]Department of Animal Science, University of Nebraska – Lincoln, 68583 Lincoln, NE; and [‡]USDA, ARS, Roman L. Hruska U.S. Meat Animal Research Center, 68933 Clay Center, NE

ABSTRACT: Cow mature weight (**MWT**) has increased in the past 30 yr. Larger cows cost more to maintain, but their efficiency—and thus profitability—depends on the production environment. Incorporating MWT effectively into selection and mating decisions requires understanding of growth to maturity. The objective of this study was to describe growth to maturity in crossbred beef cattle using Brody, spline, and quadratic functions. Parameter estimates utilized data on crossbred cows from cycle VII and continuous sampling phases of the Germplasm Evaluation Program at the U.S. Meat Animal Research Center. The MWT were estimated at 6 yr from the fitted parameters obtained from the Brody (**BMWT**), spline (**SMWT**), and quadratic (**QMWT**) functions. These were defined as BMWT, SMWT, and QMWT for the Brody, spline, and quadratic functions, respectively. Key parameters from the Brody function were BMWT and maturing constant. The spline was fitted as piecewise linear where the two linear functions joined at a knot. Key parameters were knot position and SMWT. For the quadratic model, the main parameter considered was QMWT. Data were scaled for fitting such that 180 d was the *y*-intercept with the average weight at 180 d (214.3 kg) subtracted from all weights. Weights were re-expressed by adding 214.3 kg after analysis. Once data were edited, with outliers removed, there were parameter estimates for 5,156, 5,041, and 4,905 cows for the Brody, spline, and quadratic functions, respectively. The average maturing constant (SD) was 0.0023 d^{−1} (0.0008 d^{−1}). The mean MWT estimates (SD) from the Brody, spline, and quadratic functions were 650.0 kg (64.0 kg), 707.3 kg (79.8 kg), and 597.8 kg (116.7 kg), respectively. The spline function had the highest average R^2 value when fit to individual cows' data. However, the Brody function produced more consistent MWT estimates regardless of the timeframe of data available and produced the fewest extreme MWT. For the spline and quadratic functions, weights through 4 and 5 yr of age, respectively, were needed before consistent estimates of MWT were obtained. Of the three functions fitted, the Brody was best suited for estimating MWT at a later age in crossbred beef cattle.

Key words: beef cattle, Brody function, growth, mature weight, quadratic function, spline function

INTRODUCTION

There has been a well-documented increase in mature cow weight (**MWT**) and hip height since the 1970s (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016) due to an increase in desirability of cattle with heavier weaning weight (**WWT**),

yearling weight (**YWT**), and with greater ADG (Jenkins and Ferrell, 2006). Although few breeds report estimated progeny differences (**EPD**) for MWT (Kuehn and Thallman, 2016a), there are positive genetic correlations between WWT, YWT, and MWT (Brinks et al., 1964; Smith et al., 1976). Therefore, genetic trends for increased WWT and YWT since 1972 (Kuehn and Thallman, 2016b) have resulted in increased cow MWT over the past 30 yr.

Larger cows can be costly to maintain. Cow maintenance accounts for about half of an operation's feed requirements (Ferrell and Jenkins, 1984). Larger cows, requiring more energy than smaller cows (DiCostanzo et al., 1990), are thus expected to increase an operation's gross feed requirements. The relationship between cow size and calf WWT appears to be affected by environmental circumstances. For example, Scasta et al. (2015) reported that, in a semi-arid rangeland environment, cows classified into lighter weight groups weaned heavier calves in wet years but weaned lighter calves in dry years, relative to cows classified into heavier weight groups. Production efficiency relative to intake requirements of all weights varied with different levels of annual precipitation.

Since cows varying in biological type will differ in their growth patterns, effectively selecting and breeding cows of profitable size for a given environment when they are fully grown require an understanding of growth to maturity. With this understanding, a more suitable method for estimating MWT—and thus a better estimate of the cow's MWT—can be discerned. This has several benefits. Cows that do not remain in the herd long enough to be directly observed for MWT can contribute useful information for prediction of relatives' breeding values. Cows can be culled using predictions that incorporate their own phenotypes before they leave too many progeny, rendering the selection ineffective. Sires can be evaluated incorporating daughters' phenotypes before they become too old for their selection to be effective.

Growth data may be modeled by a variety of functions, including the Brody function and the spline and polynomial families; these models may facilitate understanding of how different biological types grow to maturity. The Brody function is a growth model which is asymptotic at MWT (Brody, 1945). The spline, in its most basic form, consists of two linear functions joined at a knot (Meyer, 2005). The quadratic curve is a type of polynomial consisting of a single vertex (Parks, 1982). The purpose of this study was to describe growth from weaning to maturity in crossbred beef cattle using these three different models—Brody, spline, and quadratic—and to compare the robustness of the MWT estimates generated from these functions. By determining the function that best describes growth to maturity, future efforts based on that choice can focus on estimating breed differences in MWT to enable more informed breed utilization.

MATERIALS AND METHODS

Data used were from the Germplasm Evaluation (**GPE**) program conducted at the Roman L. Hruska U.S. Meat Animal Research Center (**USMARC**) in Clay Center, Nebraska. Animals were raised in accordance with the Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching (Federation of Animal Science Societies, 2010), and their care was approved by the USMARC Animal Care and Use Committees.

Animals

A crossbred population has been developed and maintained at USMARC through eight cycles of mating and, since 2007, from continuous sampling of industry bulls. Data for this project specifically were from 2,231 cycle VII GPE cows and from 3,044 continuous sampling GPE cows, which reached a maximum age of 14 yr. Cycle VII was described by Cushman et al. (2007). Sires from the seven most common U.S. breeds—Angus, Hereford, Red Angus, Charolais, Gelbvieh, Limousin, and Simmental—were mated via artificial insemination (**AI**) to Angus, Hereford, and MARC III (¼ each Angus, Hereford, Pinzgauer, and Red Poll) dams. Half of bulls used from each breed type were influential proven sires, while the other half were young, unproven sires but considered excellent prospects (Wheeler et al., 2005; Cushman et al., 2007). All cows were exposed annually. Cows which failed to breed twice in a row, or developed substantial impairments to productivity, were culled. Cycle VII cows used for this project were born in spring calving seasons between 1999 and 2008. Continuous sampling cows were born in spring and fall calving seasons between 2007 and 2014 (Schiermiester et al., 2015). The following breed types were sampled periodically for continuous GPE: Angus, Hereford, Red Angus, Shorthorn, South Devon, Beefmaster, Brahman, Brangus, Santa Gertrudis, Braunvieh, Charolais, Chiangus, Gelbvieh, Limousin, Maine Anjou, Salers, Simmental, and Tarentaise. MARC II (¼ each Simmental, Hereford, Angus, and Gelbvieh) and MARC III composites also were

represented through the USMARC Base population. Bulls were mated via AI or natural service to purebred or crossbred cows to produce F[1], backcross, or 7/8 or higher (minimum proportion to be considered purebred) progeny.

Data

Animals lacking weights beyond 3 yr of age were removed from the data. Some cows were used in other projects requiring a restricted diet. For these cows, records were truncated at the beginning of the feed restriction. Additionally, records were truncated at any gaps between subsequent records greater than 2 yr, and at 6 yr of age. Birth weight records were not included as no weights were available to fit growth trajectories between birth and weaning.

In total, 116,305 weight records remained on 5,625 crossbred GPE cows recorded between 98 and 2,198 d of age. Most cows had three records per year, reflecting three physiological states. Weight records were generally collected at palpation to determine pregnancy status following breeding, when pregnant cows were brought in for brand clipping (third trimester) before calving, and during lactation before cows were exposed for breeding for the next calving season.

The weight collected at palpation was considered least affected by reproductive status since fetal weight was minimal and the cow was not lactating. The potential impact of changing physiological state on model fit was investigated using palpation weights only. The parameter estimates obtained, described latterly, were similar to those when the data included weights at all physiological states. The average MWT estimated from the palpation weights alone was within 50 kg of that estimated when including weights recorded at all physiological states, a difference of <7%. However, the SD of the MWT was as much as 42% larger, and the SE of the parameter values used to estimate the MWT was as much as 346% larger. Therefore, records on all physiological states were included in the analysis.

No adjustment was made for body condition (fat). Different breeds inherently differ in fatness. Therefore, breed composition and fatness were partially confounded, and it was hypothesized that adjusting for body condition would remove variation in growth and MWT across breeds. This population was highly crossbred, and these data will ultimately be used to calculate breed effects for MWT; thus, retaining this variation was deemed desirable.

Statistical Analyses

Before any models were fitted, the data were scaled. Some cows had a weight recorded as early as 98 d of age, although there was no single age at which a WWT was recorded. However, most cows had weights recorded by 180 d, which was adopted as an early boundary of the age WWT was recorded. All ages were scaled by subtracting 180 d. Furthermore, all weights were scaled by subtracting 214.3 kg, the average weight at 180 d. This allowed the intercept of two of the functional forms fitted, the spline and quadratic, to estimate a scaled WWT. The time origin for the fit of Brody function, described latterly, was also set at 180 d. By using the same average age and weight for scaling rather than actual ages and weights, data from all cows remained on an equivalent and thereby comparable scale. After parameter estimates were obtained, weight estimates were re-expressed by adding back 214.3 kg.

For all three functions, MWT was predicted at 6 yr of age from fitted parameter values. Previous studies have defined MWT at or near 6 yr of age (Koch and Clark, 1955; Smith et al., 1976; Boligon et al., 2010). Koch and Clark (1955) found that birth weight and WWT increased with dam age until 6 yr of age, after which subsequent calves were lighter. Similar results were found by Knapp et al. (1942) and Rogers (1972). Rogers (1972) also found that calving percent was greatest with 6-yr-old dams, and percent cow death loss increased rapidly after 6 yr old until 12 yr old. Preliminary analyses of the current data showed a decrease in weight after 6 yr of age, perhaps indicative of reduced productivity with transition into a geriatric phase of metabolism. Therefore, to be consistent with the earlier literature and these findings, weight at 6 yr was defined as the MWT.

The Brody function fitted is $W_t = A[1 - e^{-k(t-t^*)}]$, where W_t is the scaled BW at a certain age, in days, A is the asymptotic weight, k is the maturation constant, t is the observed age, and t^* is the time origin of the curve (St. Taylor, 1965). The deviation $t - t^*$ coincided with the scaled age. The model was fitted using the nls function (nonlinear least squares) in R (R Core Team, 2017). Starting values for A for each animal were obtained as the average of the animal's last six weight records, regardless of number of records available on a cow. Starting values for k for each animal were calculated by algebraically solving the Brody function for k, conditional on the starting value for A. Parameters A and k were estimated for each animal individually and were subsequently

used to predict MWT at 6 yr of age. This function, and those described latterly, also were fitted once combining data on all animals.

The spline function fitted was a piecewise linear function with one interior knot. The segmented package in R (Muggeo, 2008) was used with the starting value for the interior knot set at 540 scaled days for all cows. This age was chosen because, upon visual inspection, there appeared to be a change in slope of the growth trajectory around that time. Output included estimates of slopes and intercepts from both sides of the knot for each animal. Estimates of the slope and intercept after the knot were used to predict MWT at 6 yr of age. A slope after the knot of zero would indicate the arrival at MWT. The 95% confidence intervals for this slope were examined to determine how often zero was included, and thus whether cows had stopped growing after the knot. A paired t-test was conducted to determine whether the slope after the knot was significantly less than the slope before the knot, and thus whether growth slowed significantly after the knot occurred. A second internal knot also was initially fitted, but the function caused significant convergence issues with these data. For those fits that did converge, one knot was usually placed near the original, single knot, and the second knot was usually placed closer to WWT rather than closer to maturity.

The quadratic function fitted is $W_t = \beta_0 + \beta_1 \times t + \beta_2 \times t^2$, where W_t is the animal's scaled weight, t is the animal's scaled age in days, β_0 is the intercept, β_1 is the linear coefficient, and β_2 is the quadratic coefficient. The lm function (linear models) in R (R Core Team, 2017) was used for the analyses. As with the Brody and spline functions, coefficient estimates were used to predict MWT at 6 yr of age.

Data edits were applied to individual cows based on the outcome of the fit of the three functions. Cows were excluded if the model failed to converge. Such was cases 2 and 5 times for the fits of the Brody and spline functions, respectively. No cows were excluded for lack of convergence in the quadratic function. Additionally, where convergence was achieved, the distribution of estimates of MWT was assessed to identify outliers using nonparametric procedures (Ott, 1993). Separately by function, a cow's MWT was considered extreme and removed if it was >2.2 interquartile range units from the mean; that distance coincides with ~3 SD. There were 467, 579, and 720 MWT excluded as outliers from the fit of the Brody, spline, and quadratic functions, respectively. These data also are

being used to estimate breed differences and genetic parameters in a corresponding study fitting a pedigree-based animal model. Parameter estimates for cows without pedigree information were removed so that the data summarized were the same in these complementary studies.

In total, following data editing, there remained 5,156 cows with 108,957 age and weight records for the Brody function, 5,041 cows with 107,198 age and weight records for the spline function, and 4,905 cows with 104,297 age and weight records for the quadratic function. Most cows contributed to multiple functions: there were 5,022 cows in common between Brody and spline functions, 4,879 cows in common between Brody and quadratic functions, 4,796 cows in common between quadratic and spline functions, and 4,712 cows in common among all three functions. Parameter values obtained from a given function for the individual cows were averaged to obtain means and standard deviations.

The final MWT estimates were used in further analyses. Distributions of the MWT from all three functions were checked for normality using histograms, quantile–quantile plots, and skewness and kurtosis computed using the e1071 package in R (Meyer et al., 2017). Among the cows with estimates for pairs of functions, differences of MWT estimates between functions were investigated using paired t-tests. Pearson and Spearman correlations between MWT estimates from each of the three functions also were calculated.

The potential interaction between the function used to estimate MWT and the maximum age a cow attained also was investigated. Only a proportion of the cows reached 6 yr (2,190 d), the age chosen to define MWT. For those cows with shorter lifespans, the MWT estimate was an extrapolation based on the fit of the functions to their shorter-term weight data. Cows were grouped based on age at final record: 3 yr olds reached 1,095 to 1,459 d of age, 4 yr olds reached 1,460 to 1,824 d of age, and 5 yr olds reached 1,825 to 2,189 d of age. Resulting groups were mutually exclusive such that, for example, the 5-yr-old group contained only cows which were recorded into their fifth year and none of the cows with records terminating in their third or fourth years. An ANOVA was used to fit the model

$$y_{ijk} = \mu + F_i + R_j + FR_{ij} + e_{ijk}$$

where y_{ijk} is the MWT estimate for animal k, μ is the overall mean, F_i is the function used to generate the MWT estimate ($i = 1, 2,$ or 3, for Brody, spline, or quadratic, respectively), R_j is age, expressed in year, at the final record of the cow providing the MWT

estimate (j = 1, 2, or 3, for 3, 4, or 5 yr old categories, respectively), FR_{ij} is the interaction between the function and cow age, and e_{ijk} is the random residual.

RESULTS

Fit of Curves

Figure 1 shows the three functions plotted to weight-age data of all cows combined. The Brody function was asymptotic to MWT. The spline, in the form fitted, was piecewise linear with two segments joined at a single knot. The quadratic was a concave-down curve (negative second derivative). The apex was expected to occur around 6 yr of age. However, the apex of the average curve occurred at 1,864.5 d of age (about 5.1 yr of age), after which the function decreased. Likewise, depending on the extent of the data available on a cow and its pattern, the apex for the individual cow often occurred before 6 yr of age.

The fit of each curve to data on individual cows is summarized in Table 1. On average, the spline function had the greatest R^2 and smallest root mean squared error; it also, however, generated nearly five times as many extreme MWT estimates
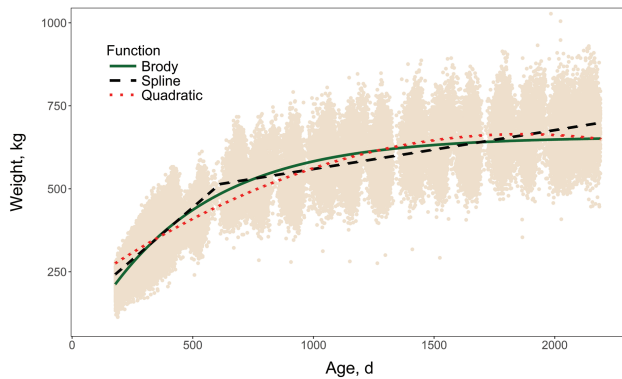

Figure 1. Average fits of Brody, spline, and quadratic curves to weight-age data of crossbred cows.

as the Brody function. The Brody function generated the fewest extreme MWT estimates with, on average, goodness-of-fit intermediate to the spline and quadratic functions. The quadratic function had the least suitable fit. It generated the greatest number of extreme MWT estimates: about 11 times as many as with the Brody function. Overall, the Brody function produced fewest extreme MWT estimates while the spline function fitted the shape of these data best.

After removing extreme values, MWT estimates were normally distributed overall. However, the distribution of MWT estimates from the quadratic function was left skewed, as shown in Figure 2. The normal quantile–quantile plots for MWT of the three functions (Figure 3), and skewness and kurtosis statistics (Table 2), also reflected their extent of departure from a normal distribution. The Brody function quantiles followed the reference line closely and had the least deviation in skewness. Negative kurtosis indicated that the distribution was somewhat more centrally concentrated than a standard normal curve. The spline function behaved similarly with some deviation in the uppermost quantiles. It had stronger measures of skewness, indicating a greater deviation from normality. The quadratic function quantiles followed the reference line near the median but showed clear deviation at data extremes. The deviation in the lowermost quantiles, corresponding to lower MWT, was most pronounced. Accordingly, the quadratic function had the strongest measures of skewness and kurtosis, with negative skewness.

The distribution of MWT estimates for cows with weight records collected up until 3, 4, and 5 yr of age was compared (Figure 4). Estimates of MWT for cows with weight data collected over shorter timeframes—3 and 4 yr—were lighter when obtained with the quadratic function. The opposite was true with the spline function; cows with records ending as 3 yr olds were estimated to have heavier

Table 1. Summary of the average quality of the fit of three growth functions to individual weight-age data on crossbred cows preceding editing (n = 5,625)

| Function | Extreme mature weight estimates[1] | | | | R^2 | | RMSE[3] | |
	Threshold low, kg	Threshold high, kg	% Low	% High	Mean	SD	Mean	SD
Brody	456.5	843.1	0.16	0.50	0.952	0.027	70.03	18.44
Spline	472.3	950.5	0.67	2.36	0.965	0.021	61.46	16.88
Quadratic	211.9	903.3	7.16	0.22	0.942	0.032	75.43	18.50

[1]Extreme was defined as exceeding 2.2 interquartile range units from the mean. Percent high and low are the percent of MWT estimates falling outside of these thresholds.

[2]R^2 values presented are the average R^2 of individual fits for all cows for a given function.

[3]RMSE is the root mean square error. RMSE values presented are average RMSE of individual fits for all cows in a given function.
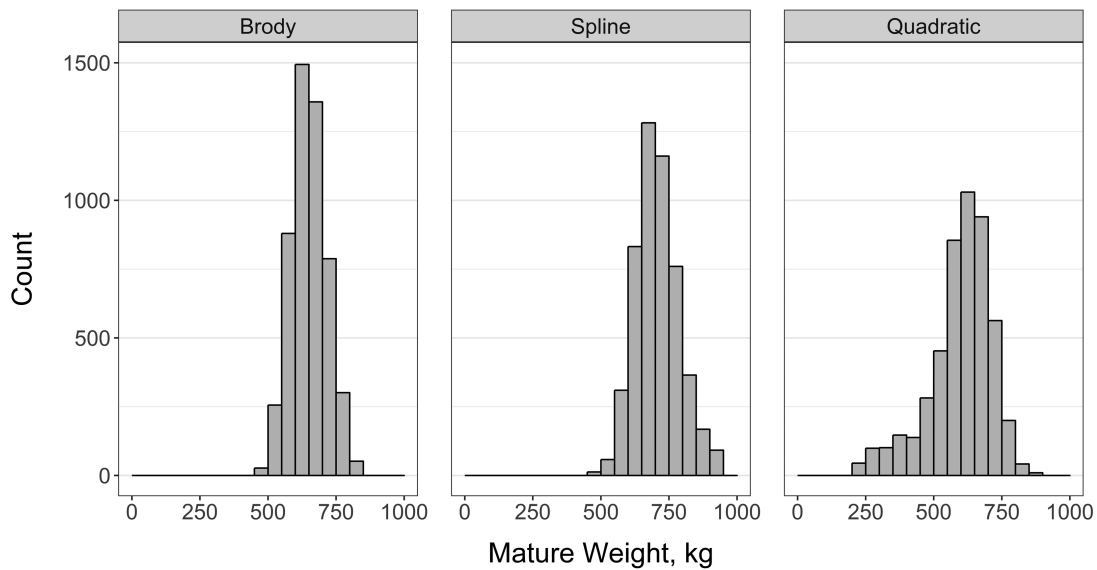
Distribution of Mature Weight Estimates

Figure 2. Distribution of mature weights estimated for crossbred cows after editing from the Brody (n = 5,156), spline (n = 5,041), and quadratic (n = 4,905) functions.
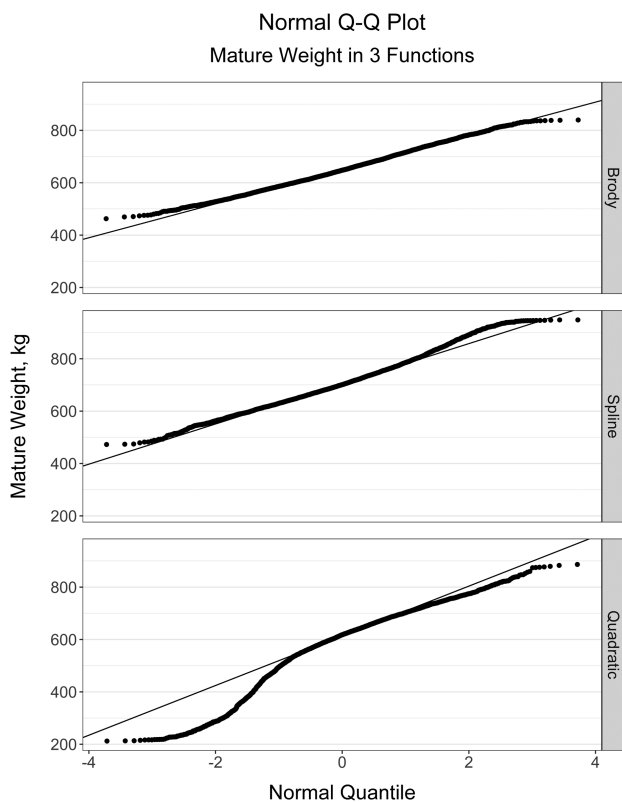

Figure 3. Quantile–quantile plots of mature weight estimates after editing from the Brody (n = 5,156), spline (n = 5,041), and quadratic (n = 4,905) functions.

Table 2. Measures of skewness and kurtosis of mature weight estimates after editing for the Brody (n = 5,156), spline (n = 5,041), and quadratic (n = 4,905) functions

Function	Skewness	Kurtosis
Brody	0.15	−0.24
Spline	0.37	0.15
Quadratic	−0.95	0.92

was a clear interaction between the functional form used to obtain MWT and the length of data available for its estimation (P < 0.001).

Pearson and Spearman correlations between MWT estimates from the cows in common between each pair of functions are presented in Table 3. Based on Spearman correlation estimates, cows were most consistent in ranking for MWT obtained with the Brody and quadratic functions. Based on Pearson correlation estimates, cows ranked similarly for MWT between the Brody function and both the spline and quadratic functions. Both types of correlations indicated that rankings of MWT based on the spline and quadratic functions were quite different.

Parameter Estimates

MWT than those with records extending to later ages. Estimates from records ending in the fourth and fifth years were similar in magnitude. The MWT estimated with the Brody function was the most consistent across all three age groups. There

Average parameter values from all three functions are summarized in Table 4. The MWT estimates ranged from 212.2 to 948.3 kg with an overall average across all functions of 652.2 kg (SD 99.6 kg). The average spline MWT was heaviest and

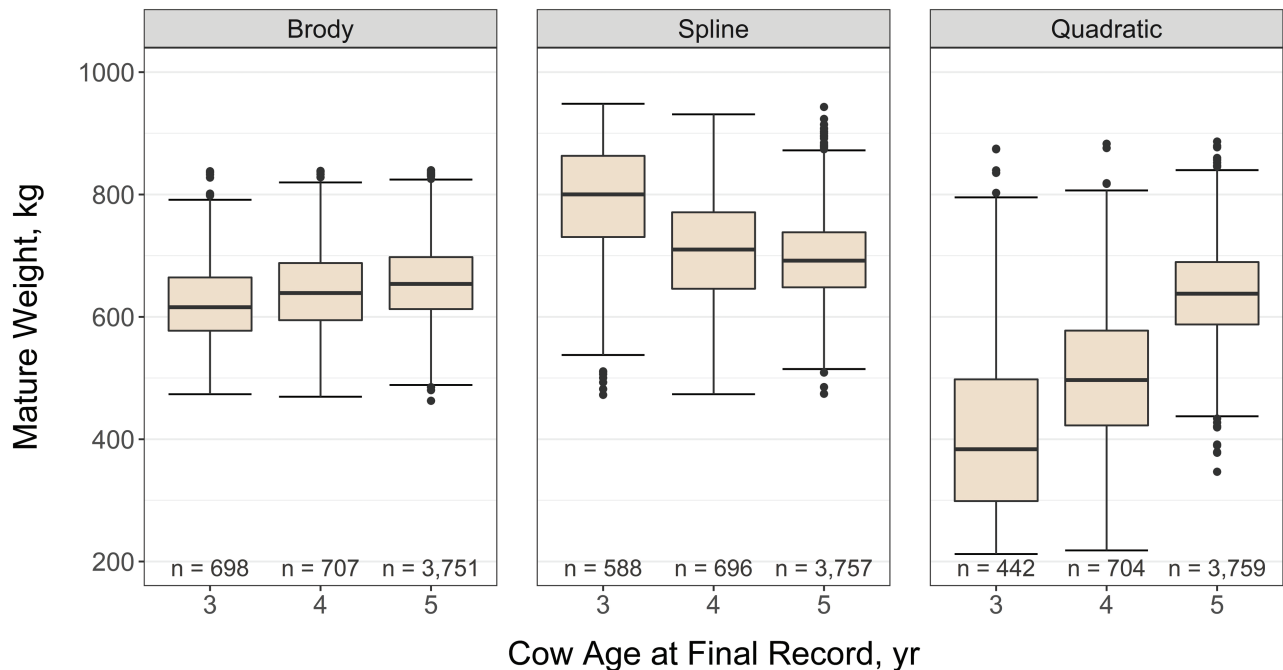## Mature Weight Estimates in 3 Functions by Maximum Age

Figure 4. Distribution of mature weights estimated for crossbred cows using the Brody, spline, and quadratic functions, separated by age at final (oldest) weight measurement (number in each category indicated on graph).

Table 3. Pearson (above diagonal) and Spearman (below diagonal) phenotypic correlations between mature weights estimated for crossbred cows from Brody, spline, and quadratic functions[1]

Function	Brody	Spline	Quadratic
Brody		0.62	0.61
Spline	0.67		0.25
Quadratic	0.71	0.46	

[1]Correlations were calculated between cows that were included in analysis for both functions being compared. There were 5,022 cows in common between Brody and spline functions, 4,879 cows in common between Brody and quadratic functions, and 4,796 cows in common between spline and quadratic functions.

the average quadratic MWT was lightest. The average Brody function MWT was intermediate and near the overall average. None of the 95% CI of the mean of each function overlapped, indicating significant differences. For cows that were included in more than one function, based on paired t-tests, the estimated MWT were significantly different between each of the functions ($P < 0.001$). The average maturing constant was 0.0023 d^{-1} (SD 0.0008 d^{-1}).

On average, the location of the spline knot, the point where the piecewise functions joined, was at 597 d of age (SD 188 d), or about 1.6 yr. The slope of the linear segment before the knot was significantly greater than that after the knot ($P < 0.001$).

The average slope before the knot was 0.74 kg/d (SD 0.21 kg/d) while the average slope after was 0.12 kg/d (SD 0.06 kg/d). For 90% of the cows, the 95% confidence interval for the slope of the linear segment after the knot did not include—and was greater than—zero.

DISCUSSION

Mature Weight

Mature weights estimated from the Brody and spline functions tended to be heavier than previously reported values. While the average MWT from the quadratic function was lightest of the three functions fitted, it was similar to previously reported estimates. Kaps et al. (1999) reported an average MWT of Angus cows of 600.8 kg (SD 75.3 kg). This value is similar to our average quadratic MWT of 597.8 kg (SD 116.7 kg). However, Kaps et al. (1999) obtained that estimate from the Brody function, and our Brody function estimate of MWT was about 50 kg heavier. DeNise and Brinks (1985) published even lighter Brody-derived MWT estimates in inbred and linecrossed Hereford- and Red Angus-sired cows: 509.7 ± 4.5 kg overall and 522.3 ± 5.6 kg for linecross cows. Nephawe et al. (2004) reported mean MWT of crossbred GPE cows aged 4 yr and older from cycles I to IV; most

Table 4. Average growth parameter values, standard deviations, and minimum and maximum mature weights, estimated from crossbred cow weight records using Brody ($n = 5,156$), spline ($n = 5,041$), and quadratic ($n = 4,905$) functions

Parameter	Brody		Spline		Quadratic	
	Mean	SD	Mean	SD	Mean	SD
Avg. growth rate before knot, kg/d	—	—	0.74	0.21	—	—
Avg. knot, d	—	—	597	188	—	—
Avg. growth rate after knot, kg/d	—	—	0.12	0.06	—	—
Avg. maturing constant, d^{-1}	0.0023	0.0008	—	—	—	—
Avg. mature weight, kg	650.0	64.0	707.3	79.8	597.8	116.7
Min. mature weight, kg	462.8	—	472.5	—	212.2	—
Max. mature weight, kg	839.6	—	948.3	—	886.6	—

of the cows in cycles I–IV were sired by bulls sampled between 1969 and 1975. The mean MWT, unadjusted for body condition score, was 526 kg (SD 69.3 kg). The mean MWT adjusted for body condition score also was 526 kg (SD 69.3 kg). Our heavier estimates may be indicative of genetic trends toward heavier weights, which have been documented in other studies (Dib et al., 2009; Freetly et al., 2011; Beck et al., 2016) and in publications of EPD trends in WWT and YWT (Kuehn and Thallman, 2016b) in beef cattle.

Brody (1945) considered animals to be fully mature at 98% of their asymptotic weight. In these data, the mean proportion of weight at 6 yr, as estimated by the Brody function, was 98.1%, adhering to Brody's (1945) definition of maturity.

The MWT estimated with the spline function were heavier than those obtained with the Brody and quadratic functions. This greater weight was because the spline function lacks an asymptote; estimates of MWT would increase or decrease indefinitely after the knot if the slope for the final segment was not zero (Figure 1). In this study, that slope was positive for 90% of cows, resulting in heavier estimates of weight at 6 yr. This increase was more pronounced in cows with weight records extending only through 3 yr of age: their MWT estimates were heavier than their older counterparts (Figure 4). There was little difference, on average, between MWT estimates of cows with weight records extending into their 4th as compared to 5th yr of age; weight records through at least 4 yr of age seem necessary to obtain sensible MWT estimates from the fit of the spline function. The spline function also generated more extreme MWT estimates than the Brody function. While the spline function fit these data reasonably well, its predictive utility appears to be suboptimal.

Estimates of MWT from the quadratic function were lighter than with the Brody and spline functions, likely due to its parabolic shape. An increasing, concave-down quadratic function must decrease at an increasing rate, with weights predicted after the apex necessarily reduced. A lower tail in the distribution of MWT obtained with the quadratic function was therefore not surprising (Figures 2 and 3; Table 2). Cows with weight records only extending until younger ages had substantially lighter estimates of MWT (6 yr old) than those for cows with weight records extending until older ages; inferring MWT where data were only available at younger ages was clearly unreliable with the polynomial model. While on average MWT obtained with the spline stabilized once cows were 4 yr old, the quadratic MWT estimates were noticeably different for each age group. The MWT was also more variable (larger SD; Table 4). The tendency for polynomials to fit poorly with sparse or extreme data, and to extrapolate poorly, is well known (Parks, 1982). Among the three functions studied, the quadratic was least suitable for modeling growth or for estimating MWT at a later age.

The apex of a quadratic function, the point at which that function reaches its maximum, has been proposed as the age coinciding with maturity (Bullock et al., 1993). However, that definition for MWT has limitations. Firstly, it would be impractical for producers to collect sufficient weight data to adequately fit a quadratic polynomial for individual cows to estimate the apex. Secondly, the estimates of the apex can be biologically unreasonable. In the current data, they ranged between 2 and 91 yr of age, with such extreme ages clearly poor reflections of mature age. Predicting weight at a fixed time point (6 yr old) is more pragmatic in production settings.

The MWT ranked most similarly between Brody and quadratic functions, and ranked most dissimilarly between the spline and quadratic functions. This likely was due to the shapes of these functions. The Brody function was asymptotic. The quadratic function reached an apex

and declined thereafter. Both therefore were concave-down functions, which retrained estimates of MWT (Figure 1). Conversely, the spline function fitted represented two lines joined at a knot. Since the slope of the line following the knot was positive for most cows (Table 4), MWT estimates based on the spline function were heavier. Therefore, perhaps unsurprisingly, the MWT ranked more similarly between the Brody and quadratic functions.

The Brody function behaved best among the functions fitted. Estimates of MWT were largely insensitive to the timeframe of weight data available: they were reasonable and consistent regardless of whether a cow's weight records extended until 3, 4, or 5 yr of age (Figure 4). The shape of the curve also conformed to notions of growth through maturity (Parks, 1982). Since it is asymptotic, it was expected that the Brody function would fit the data better than the spline function; that, however, was not the case in these analyses. Based on the spline trend line (Figure 1), growth rate during the heifer development phase was greater than during the productive phase. This probably explains the better fit of the spline function relative to the Brody. Greater growth during the development phase is consistent with the fact that heifers in the early years were developed on a roughage-based diet in the feedlot, while in later years on pasture that was usually higher quality than that grazed by mature cows.

It is possible that by truncating the data at 6 yr, some cows had not yet reached their MWT. Since the fit of the Brody function seeks to define a near-asymptotic value, the quality of the fit may have been hampered. Furthermore, the fit of the spline function might have been best because it had more parameters than the Brody function (5 vs. 2). However, more parameters do not necessarily guarantee a better fit. The quadratic function also had more parameters than the Brody function yet provided the poorest fit to these data. Although the quality of the fit of the Brody function to these data was intermediate to that of the spline and quadratic functions, as expected it generated fewer extreme and generally more stable estimates of MWT. Its parameter *A*, the asymptotic weight, also had clear biological interpretation. On whole, the Brody function provided the best description of growth from weaning to maturity of the three models compared.

Maturing Constant

The maturing constant in the Brody function defines the overall shape of the function and the rate at which its asymptote is approached. The average value of 0.0023 d^{-1} (SD 0.0008 d^{-1}) was similar to those published previously. Kaps et al. (2000) reported maturing constants of 0.062 mo^{-1} (SD 0.012 mo^{-1}); converting to days yields 0.0021 d^{-1}. DeNise and Brinks (1985) reported an overall maturing constant of 0.00181 d^{-1} ± 0.00002 d^{-1} across the categories of cattle they evaluated. In linecross cows specifically, the value was 0.00185 d^{-1} ± 0.00003 d^{-1}.

Knot

The knot was the point—in this case, age—at which the spline's piecewise functions joined. On average, the knot was placed at 597 d of age, or at ~1.6 yr. While the slope after the knot was less than before the knot, it was positive for most cows. This suggests that cows continued to grow past 1.6 yr. Freetly et al. (2011) found that cows sired by Hereford, Angus, Belgian Blue, Brahman, Boran, and Tuli sires achieved puberty between 48.5 ± 0.7 and 58.2 ± 0.6 wk old (~339.5 to 407.4 d, or near 1 yr old). By that age, these cows had achieved most but not all of their mature height, and just over half of their MWT. Kaps et al. (2000) reported that cows were only 68% mature (SD 7%) even at 550 d old (about 1.5 yr). The age associated with the knot clearly did not coincide with cows reaching their mature size.

Fitting of a second interior knot was attempted, although the fit of this model failed to converge for many cows' data. It was hypothesized that the second interior knot might be placed at an older age such that the slope in the final segment was near or equal to zero, indicating that MWT had been achieved. Such would more closely reflect a typical growth pattern. However, for those fits that did converge, the second knot was usually placed closer to weaning rather than closer to maturity. Requiring that the knot to be placed closer to a mature age might have coerced the spline function to level off as with the Brody function. However, the interest here was to allow the data to dictate the position of the knot(s). At least for these data, the placement of the two internal knots was generally not reasonable and did not result in the fit of the spline function leveling off near maturity.

CONCLUSIONS

Brody, spline, and quadratic functions were fitted to weight data from crossbred GPE cows. Estimates of MWT were heavier than those

published in the 1980s and 1990s, suggesting genetic trends for increasing live weights in cattle.

The spline function seemed to fit these data well but appeared to overestimate MWT. Cows that had records to only 3 yr of age were estimated to be heavier at maturity (6 yr) than those that had records to 4 or 5 yr of age. A linear, one-knot spline function therefore may not be appropriate for estimating MWT from weight records on younger cows.

The quadratic function fit poorest and tended to underestimate MWT. This was a consequence of fitting a polynomial function that reaches an apex and then decreases at a rate that is the mirror image of its increase. Even after editing extreme MWT, the distribution of MWT obtained with the quadratic function was skewed towards lighter weights. Cows that reached 3 or 4 yr were estimated to be lighter at maturity than cows that reached 5 yr. Defining MWT at the apex did result in a better-behaved quadratic distribution, but this definition of QMWT is inconsistent with the definitions of BMWT and SMWT. Similar to the spline, the quadratic function was unsuitable for estimating MWT from earlier weight records.

The Brody function generally estimated MWT intermediate to the spline and quadratic functions. Additionally, it generated consistent MWT regardless of the timeframe weights was collected: average MWT were similar in cows that reached 3 yr and those that reached 5 yr. Of the three functions analyzed, the Brody function appeared to be most appropriate for modeling growth and for estimating weight at maturity (6 yr of age) in these crossbred cows. The mean MWT estimated from the Brody function was 650.0 kg (SD 64.0 kg).

Practically, the Brody function could be used to obtain reasonable estimates of a cow's MWT based on its weight records from younger ages. Regular weighing (at palpation in early pregnancy, during late gestation, and during lactation) from weaning to 3 yr appears to be sufficient. Since the weight of a cow substantially affects its maintenance cost, obtaining a reliable estimate of MWT early in a cow's productive life would aid a producer's evaluation of its suitability to their production environment. An outcome is a better tailoring of the cow herd to the dynamics of individual agricultural systems.

LITERATURE CITED

Beck, P. A., C. B. Stewart, M. S. Gadberry, M. Haque, and J. Biermacher. 2016. Effect of mature body weight and stocking rate on cow and calf performance, cow herd efficiency, and economics in the southeastern United States. J. Anim. Sci. 94:1689–1702. doi:10.2527/jas.2015-0049

Boligon, A. A., L. G. de Albuquerque, M. E. Z. Mercadante, and R. B. Lôbo. 2010. Study of relations among age at first calving, average weight gains and weights from weaning to maturity in Nellore cattle. R. Bras. Zootec. 39:746–751. doi:10.1590/S1516-35982010000400007

Brinks, J. S., R. T. Clark, N. M. Kieffer, and J. J. Urick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. J. Anim. Sci. 23:711–716. doi:10.2527/jas1964.233711x

Brody, S. 1945. Bioenergetics and growth; with special reference to the efficiency complex in domestic animals. New York: Reinhold Publication Corporation.

Bullock, K. D., J. K. Bertrand, and L. L. Benyshek. 1993. Genetic and environmental parameters for mature weight and other growth measures in polled hereford cattle. J. Anim. Sci. 71:1737–1741. doi:10.2527/1993.7171737x

Cushman, R. A., M. F. Allan, R. M. Thallman, and L. V. Cundiff. 2007. Characterization of biological types of cattle (cycle VII): influence of postpartum interval and estrous cycle length on fertility. J. Anim. Sci. 85:2156–2162. doi:10.2527/jas.2007-0136

DeNise, R. S., and J. S. Brinks. 1985. Genetic and environmental aspects of the growth curve parameters in beef cows. J. Anim. Sci. 61:1431–1440. doi:10.2527/jas1985.6161431x

Dib, M. G., L. D. Van Vleck, and M. L. Spangler. 2009. Genetic parameters for cow weight and height using a repeatability model in American Angus cattle. Proc. West. Sec. Am. Soc. Anim. Sci. 60:40–41.

DiCostanzo, A., J. C. Meiske, S. D. Plegge, T. M. Peters, and R. D. Goodrich. 1990. Within-herd variation in energy utilization for maintenance and gain in beef cows. J. Anim. Sci. 68:2156–2165. doi:10.2527/1990.6872156x

Federation of Animal Science Societies. 2010. Guide for the care and use of agricultural animals in research and teaching. 3rd ed. Federation of Animal Science Societies, Champagne, IL.

Ferrell, C. L., and T. G. Jenkins. 1984. Energy utilization by mature, nonpregnant, nonlactating cows of different types. J. Anim. Sci. 58:234–243. doi:10.2527/jas1984.581234x

Freetly, H. C., L. A. Kuehn, and L. V. Cundiff. 2011. Growth curves of crossbred cows sired by hereford, angus, Belgian blue, Brahman, Boran, and Tuli bulls, and the fraction of mature body weight and height at puberty. J. Anim. Sci. 89:2373–2379. doi:10.2527/jas.2011-3847

Jenkins, T. G., and C. L. Ferrell. 2006. Matching beef genetics with production environment. Proceedings of Beef Improvement Federation Annual Meeting and Symposium, Chocktaw, Mississippi; p. 41–46.

Kaps, M., W. O. Herring, and W. R. Lamberson. 1999. Genetic and environmental parameters for mature weight in Angus cattle. J. Anim. Sci. 77:569–574. doi:10.2527/1999.773569x

Kaps, M., W. O. Herring, and W. R. Lamberson. 2000. Genetic and environmental parameters for traits derived from the Brody growth curve and their relationship with weaning weight in Angus cattle. J. Anim. Sci. 78:1436–1442. doi:10.2527/2000.7861436x

Knapp, B., Jr., A. L. Baker, J. R. Quesenberry, and R. T. Clark. 1942. Growth and production factors in range cattle. Mont. Agric. Exp. Sta. Bul. 400. P. 13.

Koch, R. M., and R. T. Clark. 1955. Influence of sex, season of birth and age of dam on economic traits in

range beef cattle. J. Anim. Sci. 14:386–397. doi:10.2527/jas1955.142386x

Kuehn, L. A., and R. M. Thallman. 2016a. Mean EPDs reported by different breeds. Proceedings of Beef Improvement Federation Annual Meeting and Symposium, Manhattan, Kansas; p. 122–126.

Kuehn, L. A., and R. M. Thallman. 2016b. Across-Breed EPD tables for the year 2016 adjusted to breed differences for birth year of 2014. Proceedings of Beef Improvement Federation Annual Meeting and Symposium, Manhattan, Kansas; p. 127–154.

Meyer, K. 2005. Random regression analyses using B-splines to model growth of Australian Angus cattle. Genet. Sel. Evol. 37:473–500. doi:10.1051/gse:2005012

Meyer, D., E. Dimitriadou, K. Hornik, A. Weingessel, and F. Leisch. 2017. e1071: misc functions of the department of statistics, probability theory group (formerly: E1071), TU Wien. https://CRAN.R-project.org/package=e1071 — [accessed June 28, 2018].

Muggeo, V. M. R. 2008. Segmented: an R package to fit regression models with broken-line relationships. R News 8(1):20–25. https://cran.r-project.org/doc/Rnews/ — [accessed October 17, 2017].

Nephawe, K. A., L. V. Cundiff, M. E. Dikeman, J. D. Crouse, and L. D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: mature weight, weight adjusted for body condition score, height and body condition score of cows, and carcass traits of their steer relatives. J. Anim. Sci. 82:647–653. doi:10.2527/2004.823647x

Ott, R. L. 1993. An introduction to statistical methods and data analysis. 4th ed. Belmont, CA: Duxbury Press.

Parks, J. R. 1982. A theory of feeding and growth of animals. Berlin, Heidelberg, New York: Springer-Verlag.

R Core Team. 2017. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/ — [accessed October 17, 2017].

Rogers, L. F. 1972. Economics of replacement rates in commercial beef herds. J. Anim. Sci. 34:921–925. doi:10.2527/jas1972.346921x

Scasta, J. D., L. Henderson, and T. Smith. 2015. Drought effect on weaning weight and efficiency relative to cow size in semiarid rangeland. J. Anim. Sci. 93:5829–5839. doi:10.2527/jas.2015-9172

Schiermiester, L. N., R. M. Thallman, L. A. Kuehn, S. D. Kachman, and M. L. Spangler. 2015. Estimation of breed-specific heterosis effects for birth, weaning, and yearling weight in cattle. J. Anim. Sci. 93:46–52. doi:10.2527/jas.2014-8493

Smith, G. M., H. A. Fitzhugh, Jr., L. V. Cundiff, T. C. Cartwright, and K. E. Gregory. 1976. A genetic analysis of maturing patterns in straightbred and crossbred Hereford, Angus and Shorthorn cattle. J. Anim. Sci. 43:389–395. doi:10.2527/jas1976.432389x

St. Taylor, C. S. 1965. A relation between mature weight and time taken to mature in mammals. Anim. Sci. 7:203–220. doi:10.1017/S0003356100025629

Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2005. Characterization of biological types of cattle (cycle VII): carcass, yield, and longissimus palatability traits. J. Anim. Sci. 83:196–207. doi:10.2527/2005.831196x