

2020-07-01

Large variability in feeding behavior among crossbred growing cattle

David N. Kelly
Moorepark Animal and Grassland Research Centre

Roy D. Sleator
Department of Biological Sciences, Cork Institute of Technology, roy.sleator@cit.ie

Craig P. Murphy
Department of Biological Sciences, Cork Institute of Technology, Cork, Ireland, craig.murphy@mtu.ie

Stephen B. Conroy
Irish Cattle Breeding Federation

Michelle M. Judge
Moorepark Animal and Grassland Research Centre

See next page for additional authors

Follow this and additional works at: <https://sword.cit.ie/dptbiosciart>



Part of the [Agricultural and Resource Economics Commons](#), [Animal Studies Commons](#), [Biology Commons](#), and the [Other Animal Sciences Commons](#)

Recommended Citation

Kelly, D.N. et al., 2020. Large variability in feeding behavior among crossbred growing cattle. *Journal of Animal Science*, 98(7). Available at: <http://dx.doi.org/10.1093/jas/skaa216>.

This Article is brought to you for free and open access by the Biological Sciences at SWORD - South West Open Research Deposit. It has been accepted for inclusion in Department of Biological Sciences Publications by an authorized administrator of SWORD - South West Open Research Deposit. For more information, please contact sword@cit.ie.

Authors

David N. Kelly, Roy D. Sleator, Craig P. Murphy, Stephen B. Conroy, Michelle M. Judge, and Donagh P. Berry

ANIMAL BEHAVIOR AND COGNITION

Large variability in feeding behavior among crossbred growing cattle

David. N. Kelly,^{†,‡} Roy. D. Sleator,[‡] Craig. P. Murphy,[‡] Stephen. B. Conroy,^{||} Michelle. M Judge,[†] and Donagh. P. Berry^{†,1}

[†]Animal and Grassland Research and Innovation Centre, Teagasc, Moorepark, Fermoy, Co. Cork, Ireland, [‡]Department of Biological Sciences, Cork Institute of Technology, Bishopstown, Cork, Co. Cork, Ireland, ^{||}Irish Cattle Breeding Federation, Bandon, Co. Cork, Ireland

¹Corresponding author: donagh.berry@teagasc.ie

ORCID numbers: 0000-0003-4776-3577 (D. N. Kelly); 0000-0002-6064-2211 (C. P. Murphy).

Abstract

The purpose of this study was to define an extensive suite of feeding behavior traits in growing crossbred cattle and to investigate their phenotypic inter-relationships as well as relationships with other performance and efficiency traits. Time-series feeding behavior data, as well as feed intake and liveweight records, were available for 624 growing crossbred cattle, of which 445 were steers and 179 were heifers. Feeding behavior repeatability estimates were calculated using linear mixed models. Additionally, partial Spearman correlations were estimated among 14 feeding behavior traits, as well as between feeding behavior with both performance and feed efficiency traits, using residuals retained from linear mixed models. The marginal contribution of several feeding behavior traits to the variability in metabolizable energy intake (MEI) was also determined. Repeatability estimates of 0.57, 0.36, and 0.48 were calculated for the number of feed events per day, the total time spent feeding per day, and the feeding rate, respectively. Cattle that ate more frequently each day, ate at a faster rate and consumed less energy in each visit to the feed bunk. More efficient cattle fed less often per day and fed for a shorter duration per day; they also had a slower feeding rate and fed for longer in each visit to the feed bunk. Moreover, heavier cattle fed for a longer duration per day had a faster feeding rate, but fed less often per day; heavier animals also fed first in the pen after the fresh feed was offered. The number of feed events per day and feeding time per day together explained an additional 13.4 percentage points of the variability in MEI above that already explained by all of growth rate, liveweight, and backfat depth. The results from the present study suggest that several repeatable time-series-related feeding behavior traits, that are less resource intensive to measure, may have a role as useful predictor traits of important but relatively difficult to record traits, such as feed intake and efficiency.

Key words: correlation, dominance, feed efficiency, repeatability

Introduction

The study of animal behavior is a growing discipline in animal science (Marchant-Forde, 2015). The association between animal behavior and reproductive function, for example, is well

established in cattle, with standing-to-be-mounted behavior demonstrating a positive indication of estrus in dairy cows (Stevenson, 2001). Similarly, stereotypic behaviors, such as bar biting in sows, have been used as signals for environmental

Abbreviations

ADG	average daily gain
DMI	dry matter intake
ECR	energy conversion ratio
ICBF	Irish Cattle Breeding Federation
MBW	mid-test metabolic liveweight
MEI	metabolizable energy intake
REI	residual energy intake
REI _U	residual energy intake adjusted for ultrasound fat depth
RFI	residual feed intake
RFID	radio frequency identification
RG	residual gain
RG _U	residual gain adjusted for ultrasound fat depth
RIG	residual intake and gain
RIG _U	residual intake and gain adjusted for ultrasound fat depth
RMSE	root mean squared error
TMR	total mixed ration
UFD	ultrasound fat depth

enrichment in pig production systems (Lawrence and Terlouw, 1993). Previous studies have also have attempted to quantify the relationship between animal behavior with both feed and environmental efficiency metrics (Robinson and Oddy, 2004; Nkrumah et al., 2007). Behavioral differences in laying hens, for example, have been linked to their efficiency of food utilization in that more efficient hens spent, on average, more time resting and less time pacing than their low efficiency contemporaries (Braastad and Katle, 1989).

Several alternative measures of feeding behavior traits in cattle have been proposed (Robinson and Oddy, 2004; Nkrumah et al., 2007; Schwartzkopf-Genswein et al., 2011) but these have been largely restricted to traits reflecting the mean time spent eating per day, the mean number of feeding events per day, and the mean feed intake per minute. Schwartzkopf-Genswein et al. (2011) reported that faster-growing steers also fed at a faster rate. Robinson and Oddy (2004) documented a phenotypic correlation of 0.18 between the mean number of feeding events per day and feed efficiency, depicted by residual feed intake (RFI), as well as a correlation of 0.16 between mean time spent feeding per day and RFI in steers and heifers. Additionally, Nkrumah et al. (2007) reported that high RFI steers (i.e., deemed to be poorly efficient) ate more often and for longer per day compared with their lower RFI contemporaries. Thus, feeding behavior traits may explain some of the variability in some animal performance metrics. Given that the measurement of such behavioral traits is not particularly intensive, this approach could be applied in predicting feed intake or efficiency, the evaluation of which is otherwise quite resource-demanding. Having access to predictions of feed intake on a large population of animals can be extremely useful in breeding programs seeking to improve animal feed efficiency (Amer et al., 2001; Berry et al., 2019).

The objective of the present study was to derive feeding behavior traits in growing cattle and to gain a greater understanding of their relationship with each other, as well as with other performance and efficiency-related traits. The novelty of the present study lies in the derivation, and knowledge, of an extensive suite of feeding behavior traits, which may have downstream applications in both management and breeding strategies to monitor and improve animal performance.

Materials and Methods

The data used in the present study were obtained from a preexisting database managed by the Irish Cattle Breeding Federation (ICBF). Therefore, it was not necessary to obtain animal care and use committee approval in advance for conducting this study.

Data

Feeding-related records, as well as liveweight and ultrasound measurements, were available from growing cattle that were on test for feed intake at the ICBF Gene Ireland Progeny Test Centre (Tully, Co. Kildare, Ireland), between the years 2015 and 2019, inclusive. Details of animal recruitment as well as the diet and management of the animals have been discussed in detail elsewhere (Kelly et al., 2019). All cattle were purchased in batches by the ICBF from Irish producers between the years 2014 and 2019, inclusive. On arrival at the test station, all cattle were assigned to pens based on breed and liveweight and then underwent an acclimatization period of between 21 and 30 d, to adapt to the feeding system and environment; the subsequent test period was approximately 77 to 90 d long. While in the test station, animals were weighed every 21 d between January 2015 and December 2017, and weekly in 2018 and 2019. Thirty pens were equipped with two automatic feed stations (RIC feed-weigh trough, Hokofarm Group B.V., Marknesse, the Netherlands); each feed station was mounted on two load cells and there were four to six animals per pen. All feed stations provided ad libitum access to feed. Access to clean, fresh water was also provided ad libitum, with one water trough shared between two adjacent pens.

Each automatic feed station had a pneumatic access gate with an infrared sensor on one side that recorded the presence of an animal. An antenna directly above the access gate detected the radio frequency identification (RFID) tag (HDX EID Tag, Allflex Livestock Intelligence, Dallas, TX) in the animal's ear to identify the individual animal in the feed station. The access gate closed after the animal removed its head from the feeder and the interruption to the infrared sensor ended. A feed event commenced when an animal's RFID tag was first detected and ended after the interruption of the infrared sensor ended. This process recorded every animal's visit to the feeder and the quantity of feed eaten during each visit. The automatic feed station recorded the quantity of feed eaten in 100 g increments; therefore, a feed event was defined when ≥ 100 g of feed on a fresh-weight basis was consumed. Refusals were discarded in all feed stations daily before the feed was refreshed. A total mixed ration (TMR) of approximately 13.95% hay, 45.35% concentrates, and 40.7% water was provided to the steers and heifers once per day during the test period with a paddle mixer wagon. From Monday to Friday, the feed stations were refilled between approximately 0900 and 1700 hours, while on Saturday and Sunday, the feed stations were refilled between approximately 0830 and 1300 hours. The TMR was assumed to have a dry matter of 51% and a metabolizable energy value of 12.1 MJ/kg DM.

Data edits

Before editing, 2,302,960 individual feed event records were available from 854 animals; therefore, there were, on average, 2,697 feed events per animal. All animals had to be between the ages of 10 and 24 mo when they started their test. All cattle also had to have remained with the same pen of animals throughout

the entire test period. A total of 5 d of feed event records were removed due to feed station malfunction. Ten animals were identified as sick from a combination of their growth and feed intake patterns; data from these animals were removed from all analyses. Subsequently, 1,851,546 feed event records from 710 animals remained. Only animals with at least three liveweight records recorded after the acclimatization period were retained in the present study. Data from a further 21 animals were removed due to abnormal growth rates, where the R-squared of a linear regression through their liveweight records was <0.90 (Kelly et al., 2019). All data from 50 animals that were in pens where one or more animals were removed from the pen in previous edits were removed from all analyses.

From an examination of the duration of feeding time, a total of 996 individual feed events of greater than 60 min in duration were considered errors; 53,324 (i.e., 3.18% of all feed events after previous edits) individual feed event records from animals in the affected pens on days in which these erroneous feed events occurred were removed. Such abnormally long feed events may be due to a failure to record the exit of an animal from the automatic feed station. For the purpose of data editing, the feeding rate per feed event was defined as an animal's dry matter intake (DMI) for an individual feed event divided by the difference between the feed event start and end times. One hundred and six feed event records with a feeding rate of ≥ 5 kg/min were assumed to be errors; therefore, 13,086 (i.e., 0.81% of all feed events after previous edits) individual feed event records from animals in the affected pens on days in which these erroneous feed events occurred were removed. These errors may have been due to a sensor error or an animal raking feed out of the feed station. After the above edits, all data from animals with fewer than 45 test day records within the test period were removed. All data from any pens where one or more animals were removed from a pen in previous edits were again removed from all analyses. After all edits, 1,591,572 individual feed event records from 624 cattle (179 heifers and 445 steers) remained for analyses.

Trait definitions

Performance and efficiency traits

The definitions of the performance and efficiency traits have previously been described by Kelly et al. (2019), using a dataset, which included the animals in the present study. Daily metabolizable energy intake (MEI) was calculated by summing, per day, the feed energy consumed in each feed event and averaging across valid test days. Average daily gain (ADG) was calculated as the linear regression coefficient from a simple linear regression of individual liveweight on the day of test; only liveweight records after the acclimatization period were used. Mid-test weight was represented as liveweight 35 d before the end of the test derived from the intercept and linear regression coefficient of liveweight on days of test. The same approach was used to estimate mid-test metabolic liveweight (MBW) (i.e., $\text{liveweight}^{0.75}$) in that it was derived from the intercept and linear regression coefficient of metabolic liveweight measures on the day of test. Ultrasound measurements of fat depth (UFD) were recorded as described by Kelly et al. (2019). In the present study, only the last UFD measurement pre-slaughter was retained for each animal; 519 animals had a record for UFD.

The energy conversion ratio (ECR) was defined as MEI divided by ADG. Residual energy intake (REI) was calculated as the residuals from a multiple linear regression of MEI on both MBW and ADG; batch was included in the model as a class effect. Where ultrasound records were available, a separate trait

of REI adjusted for ultrasound fat depth (REI_U) was calculated as the residuals from a multiple linear regression of MEI on all of MBW, ADG, and UFD as well as two-way interaction between UFD with both ADG and MBW; batch was included in the model as a class effect. Residual gain (RG) was calculated as the residuals from a multiple linear regression of ADG on both MEI and MBW; batch was included in the model as a class effect. Where ultrasound records were available, a separate trait of RG adjusted for ultrasound fat depth (RG_U) was calculated as the residuals from a multiple linear regression of ADG on all of MEI, MBW, UFD as well as two-way interaction between UFD with both MEI and MBW; batch was included in the model as a class effect. Residual intake and gain (RIG) was calculated as RG minus REI, each standardized to a variance of 1 (Berry and Crowley, 2012). Similarly, residual intake and gain adjusted for ultrasound fat depth (RIG_U) was calculated as RG_U minus REI_U , each standardized to a variance of 1.

Traditional feeding behavior traits

Any individual feed event that started on one calendar day and finished on the next day was assigned to the day in which that feed event started. The following traits were calculated from individual feed events and, after repeatability estimates were generated (discussed in more detail later), each feeding behavior trait was averaged across valid test days such that a single average value per animal was generated. Feeding behavior traits calculated at the feed event level were:

- Energy intake per feed event (MJ);
- Feed event duration (min), which was the time between the start and end time of the feed event;
- Time between feed events (min), which was the time interval between the end of one feed event and the start of the next feed event.

Feeding behavior traits calculated at the day level were:

- Number of feed events per day;
- Feeding time per day (min), calculated by summing, per day, the duration of each feed event;
- Feeding rate (MJ/min), calculated as the total MEI per day divided by feeding time per day.

Meal behavior traits

For each animal, individual feed events were clustered into meals; meals were assumed to be composed of short time intervals between feed events within meals and short intervals within meals where cattle went to the water trough, while longer time intervals separated consecutive meals. As proposed by Tolkamp and Kyriazakis (1999) and Yeates et al. (2001), the time intervals, in seconds, between feed events for all steers and heifers were log-transformed, pooled together, and a mixture of a Gaussian distribution and two Weibull distributions was fitted to the frequency distribution of the pooled log-transformed time intervals using PROC FMM (SAS v9.4, SAS Institute Inc., Cary, NC, USA); the intersection of the two Weibull distributions was estimated to be 23.9 min and was considered the meal duration cutoff time. There was no difference in the meal duration cutoff times when calculated for steers and heifers separately. A new meal for an animal was defined as occurring when the time interval between two consecutive feed events exceeded the estimated duration cutoff time of 23.9 min. Any meal that started on one calendar day and finished on the next day was attributed to the day in which that meal started. The following

traits were derived from clustering feed events into meals and, after repeatability estimates were calculated (discussed later), each meal behavior trait was averaged across valid test days such that a single average value was generated per animal. Meal behavior traits calculated at the meal level were:

- Total MEI per meal (MJ);
- Meal duration (mins), which was the time between the start and end time of a meal;
- Number of feed events per meal, which was the number of feeding events that formed a meal;
- Time between feed events within a meal (min), which was the time interval between consecutive feed events within a meal;
- Time between meals (min), which was the time interval between the end of one meal and the start of the next meal.

Meal behavior traits calculated at the day level were:

- Number of meals per day;
- Total meal time per day (min), calculated by summing, per the day, the time spent in each meal and included the time within meals when an animal was both feeding and not feeding.

Dominance

Higher social dominance rank generally governs priority to resources (Syme, 1974). Therefore, the order, within a pen, in which an animal entered an automatic feed station after

the feed was refreshed, was used as a measure of intra-pen dominance. Feeding order was defined for each animal as the within pen rank order of an individual animal's first feed event after the feed stations were refilled; a lower feed rank-order value represented a more dominant animal. While two feeding stations were present in each pen, only the minimum feeding order value per animal per day (irrespective of feed station) was used as its feed rank order for that day. A graphical description of the definition of intra-pen feeding order is provided in Figure 1.

A general heterosis coefficient and recombination loss coefficient for each animal were calculated as:

$$1 - \sum_{i=1}^n \text{sire}_i \times \text{dam}_i$$

and

$$1 - \sum_{i=1}^n \frac{(\text{sire}_i^2 \times \text{dam}_i^2)}{2}$$

respectively, where sire_i and dam_i are the proportion of breed i in the sire and dam, respectively (VanRaden and Sanders, 2003). The heterosis coefficient for each animal was divided into 12 classes (0%, 10 classes each of 10 percentage units from 0% to 100%, exclusive, and 100%), and the recombination loss coefficient for each animal was divided into 7 classes (0%, 5 classes each of 10 percentage units from 0% to 50%, exclusive, and $\geq 50\%$).

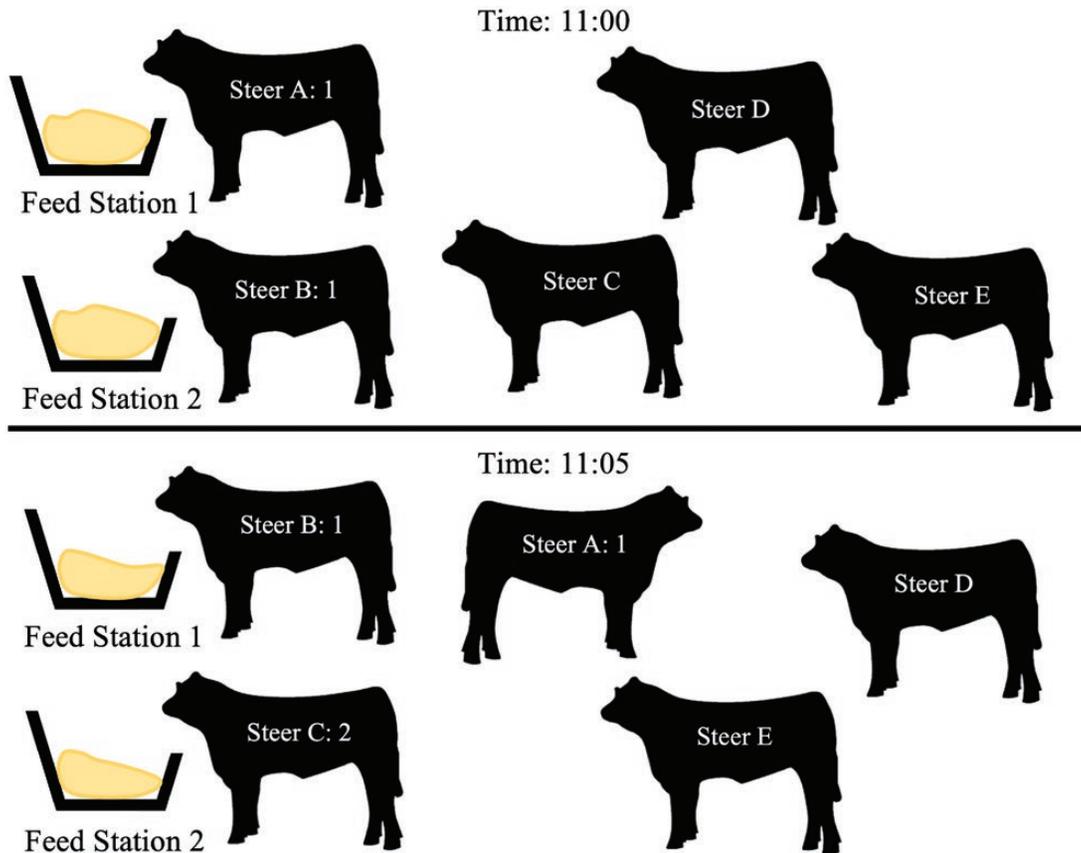


Figure 1. A graphical description of intra-pen feeding order. Steers A and B feed first at their respective feed stations after the feed is refreshed at 1100 hours and are both assigned a feed rank order of 1. After 5 min has passed, steer A finishes feeding, leaves feed station 1, and is replaced by steer B; steer B retains their feed rank order of 1. Steer C is the second animal to feed at feed station 2 and is thus assigned a feed rank order of 2 and so on.

Statistical analyses

Before averaging each feeding behavior trait over the test period, repeatability estimates for the feeding behavior traits were calculated as:

$$t = \frac{\sigma_b^2}{(\sigma_b^2 + \sigma_w^2)}$$

where t denotes repeatability, σ_b^2 denotes the between-animal variance, and σ_w^2 denotes the within-animal variance. Variance components were estimated in linear mixed models using PROC MIXED (SAS v9.4, SAS Institute Inc., Cary, NC, USA) where the fixed effects were those as described later; animal within batch was included as a random effect. Repeatability estimates were not calculated for the time interval traits. After the feeding behavior traits were averaged across the test period, the factors associated with each of the feeding behavior, performance, and efficiency traits were quantified using univariate linear mixed models also in SAS 9.4. Fixed effects considered in all models were age in months at the end of test, sex (steer or heifer), heterosis coefficient class, recombination loss coefficient class, the number of animals in a pen (4, 5, or 6), dam parity (1, 2, 3, 4, ≥ 5 , and missing), and animal breed proportion fitted as a series of linear covariates, with a separate covariate in each model for each breed. Breeds included in all analyses were Holstein-Friesian, Aberdeen-Angus, Hereford, Shorthorn, Limousin, Charolais, Simmental, Aubrac, Parthenaise, Saler, Blonde d'Aquitaine, and Belgian-Blue. Pen nested within batch was included as a random effect in all models. The residuals from the mixed models for all traits were retained and used to estimate partial Spearman's rank correlations among and between the feeding behavior, performance, and efficiency traits. In a separate analysis with MEI as the dependent variable, the traits reflecting feeding time per day, feed events per day, total mealtime per day, and meals per day were progressively added to a model already including MBW, ADG, UFD and two-way interactions between UFD with both ADG and MBW to investigate their marginal contribution to explaining the variability in MEI.

Results

Raw descriptive statistics and repeatability estimates for the feeding behavior traits are presented in Table 1. On average, the cattle in the present study ate for 142.36 min per day, with a feeding frequency of 34.41 feed events per day; the average time per feed event was 4.88 min. Of all of the traditional feeding behavior traits, energy intake per feed event had the largest inter-animal variability (coefficient of variation [CV] = 38.1%), while the number of feed events per meal had the largest CV of 36.9% of the meal behavior traits. Repeatability estimates for the traditional feeding behavior traits at the day level were larger than the repeatability estimates of the feed event-level feeding behaviors. Similarly, the day-level meal behavior repeatability estimates were greater than the repeatability estimates for the meal-level traits. Interestingly, the within-pen feeding order after the feed was refreshed was moderately repeatable indicating that cattle were somewhat consistent in the order they went to feed; feeding order repeatability estimates were also similar between heifers and steers (repeatability estimates of 0.40 and 0.37 for heifers and steers, respectively).

Correlations among and between the traditional and the meal feeding behavior traits

Based on the correlations analyses, cattle that ate more often per day ate at a faster rate and had both a lesser energy intake

Table 1. Raw means, standard deviations (SD), and repeatability estimates (t) for the traditional feeding behavior traits, feeding order, and the meal behavior traits¹

Trait	Mean	SD	t
Feed events per day	34.41	12.30	0.57
Feeding time per day, min	142.36	25.07	0.36
Feeding rate, MJ/min	1.09	0.23	0.48
Feed event duration, min	4.88	1.78	0.13
Energy intake per feed event, MJ	5.08	1.94	0.12
Feeding order			0.39
Mean time between feed events, min	42.31	15.16	
Meals per day	8.13	1.12	0.21
Total meal time per day, min	228.51	38.19	0.32
Feed events per meal	4.28	1.58	0.06
Energy intake per meal, MJ	18.50	3.94	0.03
Meal duration, min	17.87	4.16	0.05
Mean time between meals, min	151.55	23.91	
Mean time between feed events within a meal, min	3.57	1.04	

¹Means and SD were not calculated for feeding order nor were repeatability estimates calculated for the time interval traits.

per feed event and shorter duration feed events (Table 2). On the other hand, cattle that ate for longer per day ate at a slower rate and had longer feed events. Strong positive correlations existed between the feed event-level traits (i.e., energy intake per feed event and time per feed event) and the mean time interval between feed events; this would be expected, mathematically, and suggests that cattle that had shorter time intervals between feed events consumed a lesser amount of energy in each feed event and had shorter duration feed events. In general, cattle that came to the feeder earlier after the feed was refreshed ate more often per day and ate for longer each day. Animals that had more meals per day ate less per meal, had shorter meals, and had shorter time intervals between meals; they also had fewer feed events within a meal and had a longer total mealtime per day (Table 3).

The correlations between the traditional feeding behavior traits, feeding order, and the meal behavior traits are presented in Table 4. Cattle that spent longer feeding each day had, on average, meals of longer duration and also ate more per meal. Animals that ate at a faster rate had, on average, a shorter total mealtime per day and also had shorter duration meals. The correlations between feeding order and all of the meals per day, energy intake per meal, and meal duration (correlations of -0.16, 0.02, 0.03, respectively) were similar to the correlations between feeding order and all of the feed events per day, energy intake per feed event, and feed event duration (correlations of -0.13, 0.04, and 0.04, respectively).

Correlations between traditional feeding behavior traits and both performance and efficiency traits

Cattle that ate more per day fed more frequently and for longer each day; they also ate at a faster rate and ate more in each feed event (Table 5). Similarly, heavier cattle fed for longer each day had a faster feeding rate and consumed more energy per feed event; although they had fewer feed events per day, the heavier animals tended to feed first within the pen. Animals that grew faster also fed at a faster rate, ate for longer each day, and spent a longer time in each feed event. More efficient cattle (i.e., lower ECR, REI, and REI_U and greater RG, RG_U, RIG, and RIG_U) exhibited different feeding behavior patterns in comparison to their lower

Table 2. Partial Spearman correlations among the traditional feeding behavior traits and feeding order¹

Trait	Feed events per day	Feeding time per day	Feeding rate	Energy intake per feed event	Feed event duration	Mean time between feed events
Feeding time per day	0.06					
Feeding rate	0.20	-0.65				
Energy intake per feed event	-0.78	0.07	0.06			
Feed event duration	-0.80	0.38	-0.40	0.85		
Mean time between feed events	-0.92	-0.14	-0.11	0.85	0.82	
Feeding order	-0.13	-0.13	0.01	0.04	0.04	0.12

¹Spearman correlations $\leq |0.07|$ were not different ($P > 0.05$) from zero.

Table 3. Partial Spearman correlations among the meal behavior traits¹

Trait	Meals per day	Total meal time per day	Feed events per meal	Energy intake per meal	Meal duration	Mean time between meals
Total meal time per day	0.22					
Feed events per meal	-0.21	0.43				
Energy intake per meal	-0.72	-0.04	0.38			
Meal duration	-0.65	0.27	0.18	0.63		
Mean time between meals	-0.97	-0.40	0.13	0.69	0.55	
Mean time between feed events within a meal	0.15	0.00	-0.64	-0.35	-0.20	-0.15

¹Spearman correlations $\leq |0.04|$ were not different ($P > 0.05$) from zero.

efficiency counterparts. Across all of the efficiency traits, more efficient cattle fed less frequently per day; they also had a slower feeding rate and had longer duration feed events. In general, cattle that fed sooner after the feed was refreshed were heavier and fatter, grew faster, and consumed more energy per day.

Correlations between meal behavior traits and both performance and efficiency traits

In general, cattle that consumed more energy per day also had a longer total mealtime per day, had a greater energy intake per meal, and had longer duration individual meals with more feed events within a meal (Table 6). Both heavier cattle and faster-growing cattle consumed more energy per meal. The meal feeding behavior of cattle differed depending on whether the animal was deemed to be efficient or not. Across all feed efficiency traits, more efficient cattle generally had more meals per day albeit the correlations between the efficiency traits and meals per day were weak; the more efficient animals also had a shorter total mealtime per day.

Feeding behavior and the variability in MEI

The contribution of different feeding behavior traits to the variability in MEI for the 519 animals with ultrasound records is presented in Table 7. The inclusion of feed events per day explained an additional 9.2 percentage points of the variability in MEI above that explained by just MBW, ADG, and UFD; this is greater than the additional 3.3 percentage points of the variability in MEI explained by the inclusion of feeding time per day in the model that already included MBW, ADG, and UFD. The inclusion of both feed events per day and feeding time per day together explained 13.4 percentage points more of the variability in MEI above that explained by MBW, ADG, and UFD; of all models tested, it was the model with the lowest root mean

squared error (RMSE) of 9.23% of the mean MEI. In comparison, the variation in MEI explained by the model that included MBW, ADG, and UFD improved by only 5.2% with the addition of both the number of meals per day and total mealtime per day and had an RMSE that was 10.32% of the mean MEI.

Discussion

The study of animal behavior is a growing discipline within animal science, and of interest is knowledge of the factors associated with animal behavior (Marchant-Forde, 2015). The study of feeding behavior, in particular, is popular in the literature (Forbes, 2007), especially because the adoption of radio frequency technology has made the monitoring of the feed intake and feeding behavioral patterns of individual animals far easier and less expensive to undertake (Durunna et al., 2011). Nevertheless, the associations between a multitude of different feeding behavior traits at each of the feed event level, meal level, and day level have not been extensively investigated in the same group of growing beef cattle. Therefore, the objective of the present study was to derive several feeding behavior traits in growing crossbred cattle to gain a better understanding of their inter-relationships as well as their relationships with common performance and efficiency traits.

Of the studies that have explicitly reported phenotypic correlations between feeding behavior traits and both performance and efficiency traits in a relatively large cohort of cattle (Robinson and Oddy, 2004; Nkrumah et al., 2007; Lancaster et al., 2009; Kelly et al., 2010; Schwartzkopf-Genswein et al., 2011; Lin et al., 2013), the present study is one of the largest. Furthermore, there is a paucity of studies (Kelly et al., 2010) that have reported the repeatability estimates for feeding behavior traits in cattle using mixed models methodology, and few studies

Table 4. Partial Spearman correlations between the meal behavior traits and both the traditional feeding behavior traits and feeding order¹

Trait	Meals per day	Total meal time per day	Feed events per meal	Energy intake per meal	Meal duration	Mean time between meals	Mean time between feed events within a meal
Feed events per day	0.20	0.56	0.88	0.07	-0.09	-0.29	-0.57
Feeding time per day	0.02	0.58	0.04	0.16	0.70	-0.12	-0.13
Feeding rate	-0.05	-0.36	0.24	0.36	-0.43	0.12	-0.17
Energy intake per feed event	-0.26	-0.48	-0.65	0.30	0.24	0.34	0.35
Feed event duration	-0.23	-0.26	-0.69	0.11	0.44	0.26	0.40
Mean time between feed events	-0.22	-0.61	-0.81	-0.03	0.05	0.32	0.56
Feeding order	-0.16	-0.03	-0.04	0.02	0.03	0.14	0.22

¹Spearman correlations $\leq |0.07|$ were not different ($P > 0.05$) from zero.

Table 5. Partial Spearman correlations between the traditional feeding behavior traits and feeding order with a selection of performance and efficiency traits¹

Trait	MEI	ADG	MBW	UFD	ECR	REI	REI _U	RG	RG _U	RIG	RIG _U
Feed events per day	0.29	0.00	-0.05	0.13	0.21	0.38	0.40	-0.08	-0.13	-0.29	-0.32
Feeding time per day	0.27	0.16	0.11	0.19	0.01	0.21	0.18	0.09	0.10	-0.09	-0.06
Feeding rate	0.46	0.12	0.26	-0.02	0.20	0.37	0.41	-0.07	-0.10	-0.27	-0.32
Energy intake per feed event	0.18	0.15	0.26	-0.04	-0.05	0.03	0.02	0.09	0.12	0.04	0.06
Feed event duration	-0.06	0.07	0.11	-0.03	-0.13	-0.16	-0.19	0.10	0.14	0.16	0.19
Mean time between feed events	-0.24	-0.02	0.04	-0.14	-0.17	-0.32	-0.33	0.06	0.11	0.24	0.27
Feeding order	-0.14	-0.11	-0.20	-0.16	0.03	-0.04	-0.01	-0.07	-0.08	-0.02	-0.04

¹Spearman correlations $\leq |0.08|$ were not different ($P > 0.05$) from zero.

(Durunna et al., 2011; McGee et al., 2014; Herd et al., 2019) have calculated the contribution of different feeding behavior traits to the variation in either DMI or MEI. There is also a paucity of studies (McGee et al., 2014) reporting correlations at both the feed event level and meal level with performance and efficiency traits in the same cohort of cattle; moreover, information on correlations between feeding behavior and both RG and RIG are apparently nonexistent.

Repeatability of feeding behavior and feeding order

Calculating the repeatability of a trait is important when determining whether that trait can provide worthwhile information in the monitoring of animal behavior and whether the behavior follows a consistent pattern over time. Repeatability estimates also set the upper threshold for heritability estimates; knowledge of the heritability of a trait can help inform a breeding scheme design, such as the value of an animal's own record(s) or the number of progeny records required to achieve a high accuracy of selection. Repeatability estimates from the present study for the day-level traits suggest that cattle have a moderately consistent feeding behavior pattern from day-to-day; in contrast, feeding behavior appears to be less repeatable at both the feed event and meal level. Based on 50 Limousin × Friesian heifers on an 84-d-long test for feed efficiency, the repeatability estimates, calculated using a mixed model, for feeding time per day, number of feed events per day, and feeding rate (estimates of 0.37, 0.60, and 0.56, respectively) reported by Kelly et al. (2010) were larger than the repeatability estimates for the same traits calculated in the present study. Unlike the present study, Kelly et al. (2010) did not include any fixed effects in their mixed model when calculating their feeding behavior

repeatability estimates. In addition, Kelly et al. (2010) reported a repeatability of 0.62 for feed intake per feed event, which is much greater than the respective repeatability of 0.12 calculated herein; this is most likely due to the fact that Kelly et al. (2010) actually calculated average feed intake per feed event per day (i.e., DMI per day divided by feed events per day) instead of the actual energy intake for each individual feed event used in the present study. In the present study, with no fixed effects included in the mixed model, a repeatability of 0.58 was calculated for feed intake per feed event when defined as described by Kelly et al. (2010); averaging a trait across a day will remove a large proportion of the within-day variance associated with that trait, which will increase that repeatability estimate.

Using time-series data and repeatability to determine a social hierarchy in farm-animal species has been previously investigated (Berry and McCarthy, 2012). For example, Berry and McCarthy (2012) documented that the order in which dairy cows entered the milking parlor for milking, determined using electronic milk recording meters, was moderately repeatable (within and across lactation repeatability estimates of 0.51 and 0.47, respectively). Interestingly, few studies have investigated the relationship between dominance, defined using a rank-order trait, and both feeding behavior and efficiency in beef cattle. As feeding order was moderately repeatable, this suggests that a social hierarchy was established within the pen and remained relatively consistent across the test period. Cattle with a lower feed rank order (i.e., fed soon after the feed was refreshed) were considered more socially dominant in the present study; these more dominant animals fed more frequently per day and for longer each day, which is in agreement with previous research by Llonch et al. (2018) in loose-housed beef steers in which

Table 6. Partial Spearman correlations between the meal behavior traits with performance and efficiency traits¹

Trait	MEI	ADG	MBW	UFD	ECR	REI	REI _U	RG	RG _U	RIG	RIG _U
Meals per day	-0.07	0.05	-0.01	0.05	-0.06	-0.08	-0.09	0.06	0.07	0.09	0.10
Total meal time per day	0.17	0.06	-0.01	0.21	0.08	0.22	0.21	-0.01	-0.01	-0.13	-0.14
Feed events per meal	0.31	-0.02	-0.05	0.11	0.23	0.40	0.43	-0.10	-0.15	-0.31	-0.36
Energy intake per meal	0.66	0.20	0.31	0.13	0.22	0.54	0.55	-0.02	-0.04	-0.35	-0.37
Meal duration	0.24	0.09	0.07	0.12	0.05	0.22	0.19	0.03	0.04	-0.12	-0.10
Mean time between meals	0.04	-0.05	0.02	-0.07	0.05	0.03	0.05	-0.06	-0.06	-0.05	-0.07
Mean time between feed events within a meal	-0.32	-0.05	-0.04	-0.12	-0.19	-0.37	-0.38	0.07	0.09	0.28	0.30

¹Spearman correlations $\leq |0.08|$ were not different ($P > 0.05$) from zero.

Table 7. Multiple coefficients of determination (R^2) and RMSE for models with MEI as the dependent variable and feeding behavior traits as independent variables

MEI model	R^2	RMSE (MJ/d)
Base model [ADG + MBW + UFD + (UFD × ADG) + (UFD × MBW)]	0.533	16.14
Base model + feed events/d	0.624	14.50
Base model + feeding time/d	0.566	15.60
Base model + total meal time/d	0.570	15.56
Base model + meals/d	0.544	16.02
Base model + feed events/d + feeding time/d	0.667	13.70
Base model + total meal time/d + meals/d	0.585	15.32

visual observation was used to determine the dominance. Bennett and Holmes (1987) also used visual observation of competitive interactions to define feeding order in yearling steers. In the study of Bennett and Holmes (1987), dominant cattle also had a lower rank-order value (i.e., fed soon after the fresh feed was offered and won a greater proportion of competitive interactions at the feed bunk); heavier cattle were considered more dominant, which is consistent with the results from the present study. Nevertheless, the feed intake test procedures employed at the ICBF are designed to limit the effects of social dominance between animals (Beef Improvement Federation, 2010) by penning animals of the same breed and of similar liveweight together, with four to six animals per pen; this may have contributed to the weak correlations between feeding order and both performance and efficiency reported in the present study. Stronger relationships between feeding order and both performance and efficiency may be more evident if animals are penned in larger groups or if feed bunk space is limited. Nevertheless, similar to the current study, albeit using a different definition of dominance, Haskell et al. (2019) reported that there was no association between dominance and either feed conversion ratio or RFI in crossbred Charolais ($n = 41$) and Luining ($n = 39$) steers when penned at 20 animals per pen and where pens were balanced for breed, age, and liveweight at the start of the test.

Feeding behavior, performance, and feed efficiency

The present study is the first to report phenotypic correlations between traditional feeding behavior traits and meal behavior traits in the same large cohort of cattle. Although total feeding time per day is encompassed within total mealtime per day, the moderate correlation that exists between these two traits is perhaps due to the time within meals where the animal is not

feeding, which is included in the total mealtime per day trait. More efficient cattle (i.e., lower REI) ate less often per day and ate for a shorter duration per day in the present study, which is in agreement with the cattle literature (Robinson and Oddy, 2004; Nkrumah et al., 2007; Kelly et al., 2010; Lin et al., 2013). Less efficient cattle seem to binge feed in each feed event, while also feeding more frequently daily, whereas more efficient cattle tend to eat at a slower rate, while also eating a lesser total amount of feed daily. Richardson and Herd (2004) demonstrated that higher efficiency (i.e., lower RFI) was associated with greater feed digestibility in Angus steers, and the results from the present study imply that more efficient animals may have a slower rate of food passage through the digestive tract, thus allowing relatively more time for feed digestion. It also appears that feed efficiency is also related to energy expenditure associated with feeding activity. In their review of the physiological basis of RFI, Herd and Arthur (2009) reported that a relatively large proportion of the variation in RFI could be due to the energy cost of different levels of physical activity between animals, and this also appears to be the case in the present study. The greater feeding activity of poorly efficient cattle may be related to their greater actual physical activity, especially in the feedlot conditions of the present study. Similar relationships between feed efficiency and both feeding and physical activity have been quantified in other species. For example, previous research in battery hens (Braastad and Katle, 1989) has demonstrated that hens of a low-efficiency (i.e., high RFI) selection line spent more time per day pecking at feed, walking, and pacing and displayed more aggressive behaviors than hens from a high-efficiency (i.e., low RFI) selection line. Additionally, more feed-efficient pigs (i.e., low RFI) were found to feed less frequently per day and for a shorter duration per day (de Haer et al., 1993).

Estimating feed intake using feeding behavior

Studies to date in growing cattle indicate that the number of feed events per day explained an additional 5.7 to 6.0 percentage points of the variability in DMI over and above that already explained by MBW, ADG, and backfat depth (Durunna et al., 2011; Herd et al., 2019); this is less than the 9.2 percentage point improvement observed in the present study for MEI. Additionally, in steers fed a high energy finishing diet, Durunna et al. (2011) reported an increase in R^2 from 54% to 64% when both feeding time per day and number of feed events per day were included in a model with DMI as the dependent variable; this is similar to the calculated increase from 53% to 67% for the R^2 of the MEI model in the present study. To the best of our knowledge, McGee et al. (2014) is the only other study in cattle to report the marginal contribution of meal

behavior traits to the variability in DMI. Across two cohorts of Wagyu bulls, the variation explained in DMI increased by 2.0 to 10.0 percentage points when the number of meals per day was added to a model that already including MBW, ADG, and rib fat thickness (McGee et al., 2014). This increase in R^2 is larger than the 1.1 percentage point increase in variability in MEI explained by the addition of the number of meals per day in the present study.

A strong correlation may have been expected between feeding time per day and MEI in the present study, but the observed weak correlation may have been due to the relationship between feeding time per day and feeding rate. To test this, the feeding rate was included as a covariate in the mixed model with feeding time per day as the dependent variable. The Spearman correlation between feeding time per day and MEI increased from 0.27 to 0.79 when feeding time per day was corrected for differences in feeding rate, which confirms that the variation in feeding rate between animals may be responsible for the observed weak correlation between feeding time per day and MEI. Additionally, the explained variability in MEI increased from 56.6% to 92.5% when the feeding rate was added to a model that already included MBW, ADG, UFD, and feeding time per day. The model R^2 increased to 99.5% when a two-way interaction between feeding time per day and feeding rate was also included, so the model explained almost all of the variation in MEI, perhaps partly due to the fact that energy intake is itself included in the derivation of feeding rate. Nevertheless, the correlation between MEI and feeding time per day reported herein was not different ($P > 0.05$) from the correlations of either DMI or feed intake with feeding time per day reported previously in the cattle literature (Robinson and Oddy, 2004; Nkrumah et al., 2007; Kelly et al., 2010; Schwartzkopf-Genswein et al., 2011; Lin et al., 2013). Although the strength of the correlations between the feeding behavior traits and MEI varied from weak to moderate, several feeding behavior traits that were not explicitly derived from feed intake still explained a significant proportion of variation in MEI and, therefore, may have roles as useful predictor traits of feed intake where feed intake itself is not being measured, though not as the sole predictor variable. Furthermore, our results suggest that the more repeatable traditional feeding behavior traits are better predictor traits of energy intake than the meal behavior traits.

Benefits of measuring and utilizing feeding behavior

Time-related feeding behavior could be simply measured at the feed bunk using a receiver at the feed face and an RFID tag (or a similar system) in the animal's ear. Compared with measuring feed intake directly, measuring feeding behavior provides relatively inexpensive feeding activity data that may have downstream applications in breeding and management strategies to monitor and improve animal performance. Knowledge of the relationships between feeding behavior and performance can provide useful information to the producer seeking to approximate individual animal feed intake for feed rationing and financial budgeting purposes. For example, from the regression of MEI on the relevant fixed effects and either feeding time per day or the number of feed events per day in the present study, a 10 min increase in daily feeding time was associated with a 2.47 MJ (SE = 0.35 MJ) increase in MEI, and each extra feed event per day was associated with a 0.55 MJ (SE = 0.067 MJ) increase in MEI.

Similar to the present study, the dominance of animals could be established using time-series feeding behavior data, collected on-farm, which may directly benefit on-farm management decisions. For example, penning dominant and

subordinate cattle together could reduce aggressive social interactions and thereby reduce the risk of injury to individual cattle and to the herdsman (Bouissou, 1980). Conversely, although the dominance-subordinate relationship between two animals is generally stable over time (Bouissou, 1980), the introduction of unfamiliar animals to each other may lead to a new social hierarchy and thus change which animals are dominant or subordinate. Additionally, a sensor at the feed bunk in combination with an RFID ear tag has the added benefit of providing the ability to monitor feeding patterns and identify temporal deviations from same. Indeed, the potential benefits of measuring such feeding behavior extend beyond just estimating the feed intake but can be applied to monitoring the health and welfare of animals also. For example, the analysis of temporal deviations in feeding behavior has been demonstrated to facilitate the early detection of morbidity in weaned steers (Quimby et al., 2001) and to enable the early detection of bovine respiratory disease complex in Angus bulls (Kayser et al., 2019). Moreover, data on feeding behavior patterns could be beneficial in confinement systems where a large group of cattle are housed together; for example, the on-farm analysis of feeding behavior as part of precision farm management could help identify those animals that are perhaps being bullied at the feed bunk by their contemporaries and enable early intervention by the herdsman before animal performance or welfare is compromised. Using feeding behavior to identify such health-related issues and unfavorable social interactions could be more widely adopted within the industry as sensor technology improves and becomes less expensive for the end user to implement.

Conclusions

Considerable phenotypic variation in feeding behavior between animals was detected, and it is clear that complex interactions exist among different feeding behavior traits as well as between feeding behavior patterns and both performance and efficiency traits, regardless of whether feeding behavior is quantified at the day level, meal level, or visit level. Knowledge of the relationships between repeatable feeding behavior traits and both performance and efficiency in growing cattle can provide information on the usefulness of feeding behavior traits to predict other traits that are more resource intensive to measure, such as feed intake and feed efficiency. Access to predictions of feed intake on a large population of animals can be extremely useful in breeding objectives that aim to improve the efficiency of feed utilization (Amer et al., 2001; Berry et al., 2019).

Acknowledgments

Funding from the Department of Agriculture, Food and the Marine Ireland Research Stimulus Fund Ref: 17/S/235 (GreenBreed) is gratefully acknowledged as well as a research grant from Science Foundation Ireland and the Department of Agriculture, Food and Marine on behalf of the Government of Ireland under the Grant 16/RC/3835 (VistaMilk).

Conflict of interest statement

The authors declare no conflict of interest.

Literature Cited

- Amer, P., G. Simm, M. Keane, M. Diskin, and B. Wickham. 2001. Breeding objectives for beef cattle in Ireland. *Livest. Prod. Sci.* 67:223–239. doi:10.1016/S0301-6226(00)00201-3
- Beef Improvement Federation. 2010. *Guidelines for Uniform Beef Improvement Programs*. 9th ed. Raleigh (NC): North Carolina State University.
- Bennett, I. L., and C. R. Holmes. 1987. Formation of a feeding order in a group of cattle and its relationship with grazing behaviour, heat-tolerance and production. *Appl. Anim. Behav. Sci.* 17:9–18. doi:10.1016/0168-1591(87)90003-7
- Berry, D. P., P. R. Amer, R. D. Evans, T. Byrne, A. R. Cromie, and F. Hely. 2019. A breeding index to rank beef bulls for use on dairy females to maximize profit. *J. Dairy Sci.* 102:10056–10072. doi:10.3168/jds.2019-16912
- Berry, D. P., and J. J. Crowley. 2012. Residual intake and body weight gain: a new measure of efficiency in growing cattle. *J. Anim. Sci.* 90:109–115. doi:10.2527/jas.2011-4245
- Berry, D. P., and J. McCarthy. 2012. Genetic and non-genetic factors associated with milking order in lactating dairy cows. *Appl. Anim. Behav. Sci.* 136:15–19. doi:10.1016/j.applanim.2011.11.012
- Bouissou, M. F. 1980. Social relationships in domestic cattle under modern management techniques. *Ital. J. Zool.* 47:343–353. doi:10.1080/11250008009438691
- Braastad, B. O., and J. Katle. 1989. Behavioural differences between laying hen populations selected for high and low efficiency of food utilisation. *Br. Poult. Sci.* 30:533–544. doi:10.1080/00071668908417177
- Durunna, O. N., Z. Wang, J. A. Basarab, E. K. Okine, and S. S. Moore. 2011. Phenotypic and genetic relationships among feeding behavior traits, feed intake, and residual feed intake in steers fed grower and finisher diets. *J. Anim. Sci.* 89:3401–3409. doi:10.2527/jas.2011-3867
- Forbes, J. M., 2007. *Voluntary food intake and diet selection in farm animals*. 2nd ed. Wallingford (UK): CABI International.
- de Haer, L. C. M., P. Luiting, and H. L. M. Aarts. 1993. Relations among individual (residual) feed intake, growth performance and feed intake pattern of growing pigs in group housing. *Livest. Prod. Sci.* 36:233–253. doi:10.1016/0301-6226(93)90056-N
- Haskell, M. J., J. A. Rooke, R. Roehe, S. P. Turner, J. J. Hyslop, A. Waterhouse, and C. A. Duthie. 2019. Relationships between feeding behaviour, activity, dominance and feed efficiency in finishing beef steers. *Appl. Anim. Behav. Sci.* 210:9–15. doi:10.1016/j.applanim.2018.10.012
- Herd, R. M., and P. F. Arthur. 2009. Physiological basis for residual feed intake. *J. Anim. Sci.* 87(14 Suppl):E64–E71. doi:10.2527/jas.2008-1345
- Herd, R. M., J. I. Velazco, H. Smith, P. F. Arthur, B. Hine, H. Oddy, R. C. Dobos, and R. S. Hegarty. 2019. Genetic variation in residual feed intake is associated with body composition, behavior, rumen, heat production, hematology, and immune competence traits in Angus cattle. *J. Anim. Sci.* 97:2202–2219. doi:10.1093/jas/skz077
- Kayser, W. C., G. E. Carstens, K. E. Washburn, T. H. Welsh, S. D. Lawhon, S. M. Reddy, W. E. Pinchak, E. Chevaux, and A. L. Skidmore. 2019. Effects of combined viral-bacterial challenge with or without supplementation of *Saccharomyces cerevisiae boulardii* strain CNCM I-1079 on immune upregulation and DMI in beef heifers. *J. Anim. Sci.* 97:1171–1184. doi:10.1093/jas/sky483
- Kelly, A. K., M. McGee, D. H. Crews Jr, T. Sweeney, T. M. Boland, and D. A. Kenny. 2010. Repeatability of feed efficiency, carcass ultrasound, feeding behavior, and blood metabolic variables in finishing heifers divergently selected for residual feed intake. *J. Anim. Sci.* 88:3214–3225. doi:10.2527/jas.2009-2700
- Kelly, D. N., C. Murphy, R. D. Sleator, M. M. Judge, S. B. Conroy, and D. P. Berry. 2019. Feed efficiency and carcass metrics in growing cattle. *J. Anim. Sci.* 97:4405–4417. doi:10.1093/jas/skz316
- Lancaster, P. A., G. E. Carstens, F. R. B. Ribeiro, L. O. Tedeschi, and J. D. H. Crews. 2009. Characterization of feed efficiency traits and relationships with feeding behavior and ultrasound carcass traits in growing bulls. *J. Anim. Sci.* 87:1528–1539. doi:10.2527/jas.2008-1352
- Lawrence, A. B., and E. M. Terlouw. 1993. A review of behavioral factors involved in the development and continued performance of stereotypic behaviors in pigs. *J. Anim. Sci.* 71:2815–2825. doi:10.2527/1993.71102815x
- Lin, Z., I. Macleod, and J. E. Pryce. 2013. Short Communication: Estimation of genetic parameters for residual feed intake and feeding behavior traits in dairy heifers. *J. Dairy Sci.* 96:2654–2656. doi:10.3168/jds.2012-6134
- Llonch, P., M. Somarriba, C. A. Duthie, S. Troy, R. Roehe, J. Rooke, M. J. Haskell, and S. P. Turner. 2018. Temperament and dominance relate to feeding behaviour and activity in beef cattle: implications for performance and methane emissions. *Animal* 12:2639–2648. doi:10.1017/S1751731118000617
- Marchant-Forde, J. N. 2015. The science of animal behavior and welfare: challenges, opportunities, and global perspective. *Front. Vet. Sci.* 2:16. doi:10.3389/fvets.2015.00016
- McGee, M., J. A. Ramirez, G. E. Carstens, W. J. Price, J. B. Hall, and R. A. Hill. 2014. Relationships of feeding behaviors with efficiency in RFI-divergent Japanese Black cattle. *J. Anim. Sci.* 92:3580–3590. doi:10.2527/jas.2013-7360
- Nkrumah, J. D., J. D. H. Crews, J. A. Basarab, M. A. Price, E. K. Okine, Z. Wang, C. Li, and S. S. Moore. 2007. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. *J. Anim. Sci.* 85:2382–2390. doi:10.2527/jas.2006-657
- Quimby, W. F., B. F. Sowell, J. G. P. Bowman, M. E. Branine, M. E. Hubbert, and H. W. Sherwood. 2001. Application of feeding behaviour to predict morbidity of newly received calves in a commercial feedlot. *Can. J. Anim. Sci.* 81:315–320. doi:10.4141/A00-098
- Richardson, E. C., and R. M. Herd. 2004. Biological basis for variation in residual feed intake in beef cattle. 2. Synthesis of results following divergent selection. *Aust. J. Exp. Agric.* 44:431–440. doi:10.1071/EA02221
- Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. *Livest. Prod. Sci.* 90: 255–270. doi:10.1016/j.livprodsci.2004.06.011
- Schwartzkopf-Genswein, K. S., D. D. Hickman, M. A. Shah, C. R. Krehbiel, B. M. Genswein, R. Silasi, D. G. Gibb, D. H. Crews, and T. A. McAllister. 2011. Relationship between feeding behavior and performance of feedlot steers fed barley-based diets. *J. Anim. Sci.* 89:1180–1192. doi:10.2527/jas.2010-3007
- Stevenson, J. S. 2001. A review of oestrous behaviour and detection in dairy cows. *BSAP Occas. Publ.* 26: 43–62. doi:10.1017/S0263967X00033589
- Syme, G. J. 1974. Competitive orders as measures of social dominance. *Anim. Behav.* 22: 931–940. doi:10.1016/0003-3472(74)90016-5
- Tolkamp, B. J., and I. Kyriazakis. 1999. To split behaviour into bouts, log-transform the intervals. *Anim. Behav.* 57:807–817. doi:10.1006/anbe.1998.1022
- VanRaden, P. M., and A. H. Sanders. 2003. Economic merit of crossbred and purebred US dairy cattle. *J. Dairy Sci.* 86:1036–1044. doi:10.3168/jds.S0022-0302(03)73687-X
- Yeates, M. P., B. J. Tolkamp, D. J. Allcroft, and I. Kyriazakis. 2001. The use of mixed distribution models to determine bout criteria for analysis of animal behaviour. *J. Theor. Biol.* 213:413–425. doi:10.1006/jtbi.2001.2425