

## ANIMAL GENETICS AND GENOMICS

# Genetic variability in the feeding behavior of crossbred growing cattle and associations with performance and feed efficiency

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## Abstract

The objectives of the present study were to estimate genetic parameters for several feeding behavior traits in growing cattle, as well as the genetic associations among and between feeding behavior and both performance and feed efficiency traits. An additional objective was to investigate the use of feeding behavior traits as predictors of genetic merit for feed intake. Feed intake and live-weight data on 6,088 growing cattle were used of which 4,672 had ultrasound data and 1,548 had feeding behavior data. Feeding behavior traits were defined based on individual feed events or meal events (where individual feed events were grouped into meals). Univariate and bivariate animal linear mixed models were used to estimate (co)variance components. Heritability estimates ( $\pm$  SE) for the feeding behavior traits ranged from  $0.19 \pm 0.08$  for meals per day to  $0.61 \pm 0.10$  for feeding time per day. The coefficient of genetic variation per trait varied from 5% for meals per day to 22% for the duration of each feed event. Genetically heavier cattle, those with a higher daily energy intake (MEI), or those that grew faster had a faster feeding rate, as well as a greater energy intake per feed event and per meal. Better daily feed efficiency (i.e., lower residual energy intake) was genetically associated with both a shorter feeding time per day and shorter meal time per day. In a validation population of 321 steers and heifers, the ability of estimated breeding values (EBV) for MEI to predict (adjusted) phenotypic MEI was demonstrated; EBVs for MEI were estimated using multi-trait models with different sets of predictor traits such as liveweight and/or feeding behaviors. The correlation ( $\pm$  SE) between phenotypic MEI and EBV for MEI marginally improved ( $P < 0.001$ ) from  $0.64 \pm 0.03$  to  $0.68 \pm 0.03$  when feeding behavior phenotypes from the validation population were included in a genetic evaluation that already included phenotypic mid-test metabolic live-weight from the validation population. This is one of the largest studies demonstrating that significant exploitable genetic variation exists in the feeding behavior of young crossbred growing cattle; such feeding behavior traits are also genetically correlated with several performance and feed efficiency metrics. Nonetheless, there was only a marginal benefit to the inclusion of time-related feeding behavior phenotypes in a genetic evaluation for MEI to improve the precision of the EBVs for this trait.

**Keywords:** correlation, genetic parameters, heritability, residual feed intake

## Abbreviations

CGE	completed generation equivalents
EBV	estimated breeding value
EBV <sub>MEI</sub>	estimated breeding value for daily metabolizable energy intake
ECR	energy conversion ratio
ICBF	Irish Cattle Breeding Federation
MBW	mid-test metabolic live-weight
MEI	metabolizable energy intake
REI	residual energy intake
REI <sub>U</sub>	residual energy intake adjusted for ultrasound fat depth
RFI	residual feed intake
RG	residual gain
RG <sub>U</sub>	residual gain adjusted for ultrasound fat depth
RIG	residual intake and gain
RIG <sub>U</sub>	residual intake and gain adjusted for ultrasound fat depth
TMR	total mixed ration
UFD	ultrasound fat depth

## Introduction

As interest in sensory systems for monitoring livestock species intensifies, the study of feeding behaviors and their potential application in livestock husbandry continues to grow. Several studies in swine (Quiniou et al., 2000; Young and Lawrence, 1994), poultry (Collins and Sumpter, 2007; Meunier-Salaün and Faure, 1984), cattle (Ingrand, 2000), and sheep (Behrendt et al., 2021) have investigated the dynamics of feeding behavior across time, environments, and diets; of particular interest is the role of feeding behavior in the control of voluntary feed intake in animals (Forbes, 2007). The contribution of genetic variability to inter-animal differences in feeding behavior and its potential use in the selection of farm animal species are also gaining in popularity (Labroue et al., 1997; Olson et al., 2020).

Several feeding behavior traits have also been documented to be moderately heritable in different beef populations (Chen et al., 2014; Durunna et al., 2013; Nkrumah et al., 2007; Olson et al., 2020; Robinson and Oddy, 2004). Indeed, using data from 1,481 beef steers and heifers fed a grain based diet, Robinson and Oddy (2004) reported heritability estimates ( $\pm$  SE) of  $0.36 \pm 0.05$  and  $0.44 \pm 0.07$  for the time spent feeding per day and the number of feeding events per day, respectively. Similarly, in a population of 1,394 crossbred replacement beef females fed a roughage-based diet, Olson et al. (2020) reported heritability estimates ( $\pm$  SE) of  $0.25 \pm 0.05$  and  $0.26 \pm 0.06$  for the time spent feeding per day and the number of feeding events per day, respectively. Reported genetic correlations between feeding behavior and both performance and feed efficiency metrics have also varied in magnitude and direction across different cattle populations. Genetic correlations ranging from 0.03 (Robinson and Oddy, 2004) to 0.56 (Nkrumah et al., 2007) have been reported between feed intake and feeding time per day, with respective SE of 0.13 and 0.20. Likewise, genetic correlations between residual feed intake (RFI) and the number of feeding events per day have ranged from  $-0.34$  (Nkrumah et al., 2007) to 0.43 (Robinson and Oddy, 2004), with SE ranging from 0.11 to 0.30. In general, studies investigating the extent of genetic variability in feeding behavior have been relatively small; as a result, reported genetic correlations between feeding behavior and both performance and feed efficiency traits in cattle suffer from a general lack of precision.

The objective, therefore, of the present study was to estimate genetic parameters for several feeding behavior traits, as well as the genetic associations among and between feeding behavior and both performance and feed efficiency traits in a relatively large population of growing beef cattle. In addition, of interest was the potential use of feeding behavior traits as predictors of genetic merit for feed intake.

## Materials and Methods

Animal care and use committee approval was not required in advance of conducting this study as all data were obtained from a pre-existing database managed by the Irish Cattle Breeding Federation (ICBF).

### Data

Feed intake, live-weight, and ultrasound data were available from growing cattle that were on test for feed intake at the ICBF Performance Test Centre (1992–2011, inclusive), and later the ICBF Gene Ireland Progeny Test Centre (2012 to present day) Tully, Co. Kildare, Ireland. Prior to 2012, the test center operated as a bull performance test station and details of the bull recruitment and center management practices are described in detail by Crowley et al. (2010). The test center changed function in August 2012 when young bulls, steers, and heifers entered the test center in batches to be evaluated for feed intake and efficiency and were subsequently slaughtered at the end of the test period. Some batches of animals that entered the test center from 2015 onwards also had feeding behavior data; details of animal recruitment and center management from 2012 onwards are described by Kelly et al. (2019). No data were available from the test center in the transitional period of October 2011 to July 2012, inclusive. The main breeds represented included Limousin, Charolais, Aberdeen Angus, Simmental, Belgian-Blue, Hereford, Friesian, Holstein, Saler, Shorthorn, Aubrac, Parthenaise, and Blonde d'Aquitaine.

Prior to 2012, bulls generally entered the test station in three different groups annually, hereafter referred to as batches. Bulls were offered ad libitum concentrates through a Calan Broadbent gate system (American Calan, Northwood, NH) throughout their test period. To calculate total weekly concentrate intake, concentrate refusals were recorded 1 d per week and then subtracted from the cumulative concentrate offered over the previous 7 d. Bulls were offered 1.5 kg fresh weight of grass hay daily and ad libitum access to fresh water. Bulls were weighed every 14 d between 1992 and 1995, and between 2005 and 2008, and every 21 d between 1995 and 2005, and between 2008 and 2011. All hay was assumed to have a dry matter of 85% and a metabolizable energy concentration of 8.6 MJ/ kg DM. The concentrates offered to bulls between September 1992 and September 2002 were assumed to have a dry matter of 87.5% and a metabolizable energy concentration of 12.1 MJ/ kg DM; the concentrate offered to bulls between October 2002 and September 2011 was assumed to have a dry matter of 86% and a metabolizable energy concentration of 14.5 MJ/ kg DM. Daily metabolizable energy intake (MEI) for each bull was defined as the sum of daily hay dry matter intake multiplied by hay metabolizable energy concentration plus daily concentrate dry matter intake multiplied by concentrate metabolizable energy concentration.

From 2012 onwards, young bulls, steers, and heifers entered the test center in batches where each batch was composed of one sex; 4 mo was the maximum age range of cattle within

a batch. Cattle within a batch were allocated to pens based on breed and live-weight, and subsequently underwent an acclimatization period of 21 to 30 d, followed by a test period of approximately 77 to 98 d (Kelly et al. 2019). At the end of their test period, all animals within a batch were slaughtered within a week of each other. Cattle that entered the test center from 2012 onwards were weighed on average, weekly between August 2012 and August 2013, every 21 d between September 2013 and December 2017, weekly in 2018 and 2019, and every 21 d in 2020 and 2021. Only young bulls were allocated to 10 pens that had a Calan Broadbent gate system, whereas all other pens in the center were equipped with automatic feed stations (RIC Feed-Weigh Trough, Hokofarm Group BV, Marknesse, The Netherlands). On average, there were two to three animals per automatic feed station that provided ad libitum access to feed. Throughout the test period, young bulls were given ad libitum access to concentrates alongside a daily allocation of 2 kg fresh weight of grass hay. As with bulls pre-2012, concentrate intake of young bulls fed through the Calan gates was calculated weekly by recording concentrate refusals of each bull 1 d per week and subtracting from the cumulative feed offered over the previous 7 d; this sum was subsequently divided by seven to obtain average daily concentrate intake within this time period. A total mixed ration (TMR) of approximately 45.5% concentrates, 13.6% hay, and 40.9% water on a fresh weight basis was fed to all steers and heifers. Daily feed intake from cattle fed through the automatic feed stations was calculated by summing, per day, the feed consumed in each feed event; this was then averaged across all valid test days. The concentrates offered to bulls between August 2012 and 2021 was assumed to have a dry matter of 86% and a metabolizable energy concentration of 14.1 MJ/kg DM. The TMR was assumed to have a dry matter of 51% and a metabolizable energy concentration of 12.1 MJ/kg DM. Daily metabolizable energy intake (MEI) per animal was calculated as the animal's daily total dry matter intake multiplied by the energy concentration of the diet.

All bulls tested between the years 1992 and 2011 had to be between 8 and 16 mo of age when they started their test; all young bulls, steers, and heifers tested between the years 2012 and 2021 had to be between 10 and 24 mo of age when they started their test. Only animals with at least three live-weight records after the acclimatization period were retained for further analysis. Data from a further 178 animals were removed due to abnormal growth rates, where the r-squared of a linear regression through their live weight records was < 0.90 (Kelly et al., 2019). Seventeen animals were identified as sick from a combination of their growth and feed intake patterns; data from these animals were removed from all further analyses. For cattle fed through the automatic feed stations, 5 d of feed intake records were removed due to a weight malfunction on those days, and data from the last day of test were removed where there was an incomplete feed intake record on that day (Kelly et al. 2019). Only steers and heifers on test had feeding behavior data. Furthermore, additional steps were taken to remove potentially erroneous time-related feeding behavior data, which are described in detail by Kelly et al. (2020) but are mentioned briefly here. Feed events greater than 60 min in duration and/or feed events with a dry matter intake per minute >5 kg/min were considered errors and all feed intake and feeding behavior data from an animal in the test-day that these erroneous feed events occurred were removed (Kelly et al. 2020). Subsequently, animals with fewer than 45 test-day records within the test period were removed (Kelly et al. 2020). Finally, 118 cattle without a known sire were also removed. After all edits, performance and feed

efficiency data were available on 6,088 cattle (2,942 pre-2012 bulls, 1,598 post-2011 young bulls, 937 steers, and 611 heifers), of which 4,672 animals had ultrasound data and 1,548 steers and heifers had feeding behavior data.

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

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

respectively, where  $\text{sire}_i$  and  $\text{dam}_i$  are the proportion of breed  $i$  in the sire and dam, respectively (Van Raden and Sanders, 2003). As per Twomey et al. (2016), the heterosis coefficient for each animal was divided into 12 classes (0%, 10 classes of 10% from 0% to 100%, exclusive, and 100%), and the recombination loss coefficient for each animal was divided into seven classes (0%, five classes of 10% from 0% to 50%, exclusive, and  $\geq 50\%$ ).

## Trait definitions

### Performance and feed efficiency traits

Kelly et al. (2019) previously described definitions of the performance and feed efficiency traits using a dataset that included a subset of animals in the present study. The linear regression coefficient from a simple linear regression of individual live-weight on day of test was defined as average daily gain (ADG); only live-weight records after the acclimatization period were used. Mid-test metabolic live-weight (MBW, i.e.,  $\text{live-weight}^{0.75}$ ) was represented as metabolic live-weight 35 d before the end of the test, derived from the intercept and linear regression coefficient of metabolic live-weight measures on the day of test. Ultrasound measurements of fat depth (UFD) were recorded as described by Kelly et al. (2019). Where an animal had two measures of UFD in the test center, only the last measurement before the end of test (bulls test pre-2012), or pre-slaughter (cattle tested post-2011) was retained in the current study.

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. A separate trait of REI adjusted for ultrasound fat depth ( $\text{REI}_U$ ) was calculated using the same method as for defining REI, but UFD as well as two-way interactions between UFD with both ADG and MBW were also included as fixed effects in the model. Residual gain (RG) was calculated as the residuals from a multiple linear regression of ADG on both MEI and MBW. Similarly, a separate trait of RG adjusted for UFD ( $\text{RG}_U$ ) was calculated as the residuals from a multiple linear regression of ADG on all of MEI, MBW, UFD as well as two-way interactions between UFD with both MEI and MBW. Batch was included in the model for the derivation of all residual efficiency traits. Residual intake and gain (RIG) was calculated as  $\text{RG}-\text{REI}$ , each standardized to a variance of 1 (Berry and Crowley, 2012). Similarly, residual intake and gain adjusted for UFD ( $\text{RIG}_U$ ) was calculated as  $\text{RG}_U-\text{REI}_U$ , each standardized to a variance of 1.

### Feeding behavior traits

Time series feeding behavior data from automatic feed stations were available from steers and heifers that were tested for feed intake from the year 2015 onwards. The derivation and definitions of all of the feeding behavior traits used in the present study have been described previously by Kelly et al. (2020). Each feeding behavior trait described herein was averaged across valid test days, such that a single average value per animal was generated. The traditional feeding behavior traits were

calculated from individual feed events and included 1) energy intake per feed event (MJ/feed event), 2) feed event duration (min), 3) the time between feed events (min), 4) the number of feed events per day (n/d), 5) feeding time per day (min/d), and 6) feeding rate (MJ/min).

In order to derive the meal feeding behavior traits, individual feed events were clustered into meals for each animal, as described by Kelly et al. (2020); meals were assumed to include short time intervals between feed events within meals and short intervals within meals where cattle interrupted a feed event to go to the water trough, whereas longer time intervals separated consecutive meals (Yeates et al., 2001). Following the methods 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, and a mixture of a Gaussian distribution and two Weibull distributions were fitted to the overall frequency distribution of the pooled log-transformed time intervals using PROC FMM (SAS v9.4, SAS Institute Inc., Cary, NC). A mixture of two Gaussian distributions and one Weibull distribution was also tested, but the mixture of a Gaussian distribution and two Weibull distributions was chosen as it had the lower Akaike Information Criterion. The intersection ( $\pm$  SE) of the two Weibull distributions was estimated to be  $21.70 \pm 0.11$  min, and thus, a new meal started for an animal if the time interval between two consecutive feed events exceeded 21.70 min. The meal feeding behavior traits of interest were 1) energy intake per meal (MJ/meal), 2) meal duration (min), 3) the number of feed events per meal (n/meal), 4) time between feed events within a meal (min), 5) the time between meals (min), 6) the number of meals per day (n/d), and 7) total meal time per day (min/d).

### Statistical analyses

Genetic and residual variance components, and subsequently heritability estimates, for the performance, efficiency, and feeding behavior traits were estimated using a series of univariate animal linear mixed models in ASReml (Gilmour et al., 2009). Fixed effects considered, as per Kelly et al. (2019) from a subset of the data in the present study, were batch (i.e., contemporary group effect), heterosis class, recombination loss class, age in months at the end of test, the 2-way interaction between age in months at the end of test and animal sex, and dam parity (1, 2, 3, 4,  $\geq 5$ , and missing). Animal was included as a random effect, and the average genetic relationships among animals were considered by tracing the pedigree of each animal back to founder animals, which were allocated to genetic groups based on breed. The pedigree file consisted of 75,662 animals and the median completed generation equivalents (CGE; McParland et al., 2007) was 2.80; there were 20,725 sires and 48,920 dams in the pedigree file, and the mean level of inbreeding of the 18,084 inbred animals was 1.96%. Genetic and residual covariance components among the feeding behavior traits, and between the feeding behavior traits and both the performance and feed efficiency traits, were estimated using a series of bivariate animal linear mixed models; fixed and random effects in the models were those used in the univariate analyses.

### Genetic evaluation

Several genetic evaluations were undertaken in the MiX99 software suite (MiX99 Development Team, 2015) to investigate the benefit of including the feeding behavior traits of feeding time per day, the number of feed events per day, total meal time per day, and the number of meals per day in a genetic evaluation

in order to generate estimated breeding values (EBV) for MEI. Only records from the 1,548 steers and heifers with all of feed intake, live-weight, and feeding behavior data were used in the genetic evaluation. Of these 1,548 cattle, 321 steers and heifers that finished their feed intake test between September 2020 and January 2021 were defined as the validation population, as younger animals are usually selection candidates. Eight separate genetic evaluations (i.e., scenarios) were undertaken as follows, with different traits included in the multi-trait models to generate EBVs for MEI ( $EBV_{MEI}$ ):

- Scenario 1) Univariate evaluation for MEI using MEI phenotypes from the 1,227 animals that were not validation animals;
- Scenario 2) Multi-trait evaluation with covariances fitted between MEI and MBW using phenotypic data from the 1,227 animals in Scenario 1;
- Scenario 3) Multi-trait evaluation with covariances fitted between MEI and the four feeding behavior traits using phenotypic data from the 1,227 animals in Scenario 1;
- Scenario 4) Multi-trait evaluation with covariances fitted between MEI, MBW, and the four feeding behavior traits using phenotypic data from the 1,227 animals in Scenarios 1, 2 and 3;
- Scenario 5) Scenario 2 above but with MBW phenotypes from the 321 validation animals also included;
- Scenario 6) Scenario 3 above but with feeding behavior phenotypes from the 321 validation animals also included;
- Scenario 7) Scenario 4 above but with both MBW and feeding behavior phenotypes from the 321 validation animals also included;
- Scenario 8) Scenario 1 above but with the MEI phenotypes of the 321 validation animals also included.

Phenotypic MEI records of all validation animals were masked in the evaluation except for one genetic evaluation (i.e., scenario 8). Fixed and random effects included in the model for each trait in the genetic evaluations were the same as those described in the estimation of variance components; similarly, the (co)variance components used in the genetic evaluations were those estimated in the present study. The pedigree file for the genetic evaluations included 49,372 animals and the median CGE was 2.84; the pedigree included 15,907 sires and 31,902 dams, and the mean level of inbreeding of the 11,100 inbred animals was 2.28%. Only the pedigree of the 1,548 cattle with records for all of feed intake, liveweight, and feeding behaviour was utilized in the genetic evaluations.

Within the validation population, the predictive ability of the  $EBV_{MEI}$  from each genetic evaluation scenario was determined by calculating the Pearson correlation between adjusted phenotypic MEI and the respective  $EBV_{MEI}$ . For all 1,548 steers and heifers, adjusted phenotypic MEI (i.e., yield deviations) was calculated by fitting a univariate animal linear mixed model in MiX99 and removing the fixed effect solutions; fixed and random effects included in the model were those described in the estimation of variance components. Additionally, for each scenario, adjusted phenotypic MEI was regressed on the respective scenario estimate of  $EBV_{MEI}$ , and so eight separate regressions were undertaken; this was undertaken to determine the unit change in adjusted phenotypic MEI for each unit change in  $EBV_{MEI}$ .

## Results

The mean age at the end of test for the cattle in the present study was 391 d (SD = 37 d), 486 d (SD = 52 d), 624 d (SD = 69 d), and 564 d (SD = 80 d) for bulls tested pre-2012, young bulls tested post-2011, steers, and heifers, respectively. Heritability estimates ( $\pm$  SE) were weak to moderate for the feeding behavior traits ranging from  $0.19 \pm 0.08$  for the number of meals per day to  $0.61 \pm 0.10$  for the time spent feeding per day (Table 1). Heritability estimates were greater, on average, for the traditional feeding behavior traits than for the meal feeding behavior traits. Of the feeding behavior traits, the greatest genetic variation was for the duration of each feed event (coefficient of genetic variation [ $CV_g$ ] = 22%), and the lowest was for the number of meals per day ( $CV_g$  = 5%). Heritability estimates and summary statistics for the performance and feed efficiency traits were reported previously by Kelly et al. (2019) for a subset of the cattle in the present study, but are summarized in Supplementary Table 1; the study of Kelly et al. (2019) included cattle from the period of 1992 to 2019, whereas the present study included cattle from the same test station but from the period 1992 to 2021.

### Correlations among the feeding behavior traits

The genetic and residual correlations among the traditional feeding behaviour traits are provided in Table 2. A greater time spent feeding each day was genetically associated with a lower feeding rate and a longer feed event duration. Strong negative genetic and residual correlations existed between the number of feed events per day with energy intake per feed event, feed event duration, and the time interval between feed events. Similarly, energy intake per feed event, feed event duration, and the time interval between feed events were all genetically and residually strongly correlated with each other (genetic [ $\pm$  SE] and residual correlations of  $0.81 \pm 0.05$  to  $0.93 \pm 0.03$  and  $0.87$  to  $0.90$ , respectively); this finding is mathematically expected due to the arithmetical relationship that exists between these traits.

The number of meals per day was strongly genetically and residually correlated with energy intake per meal and the time interval between meals (Table 3). Genetic correlations of  $0.56 \pm 0.12$ ,  $0.80 \pm 0.08$ , and  $-0.57 \pm 0.15$  existed between the total meal

time per day and the number of feed events per meal, meal duration, and the time interval between meals, respectively. Relative to the respective genetic correlations, weaker residual correlations of 0.35, 0.54, and  $-0.34$  existed between the total meal time per day and the number of feed events per meal, meal duration, and the time interval between meals, respectively.

The genetic and residual correlations between the traditional feeding behavior and the meal feeding behavior traits are provided in Table 4. The residual correlations were generally of the same sign as the respective genetic correlations. A greater number of feed events per day was not only genetically associated with a greater number of meals per day, but also was associated with a longer total meal time per day. The genetic correlation of  $0.95 \pm 0.02$  between the number of feed events per day and the number of feed events per meal indicates that both traits were genetically very similar. Energy intake per feed event was genetically correlated with energy intake per meal (genetic correlation of  $0.55 \pm 0.15$ ); similarly, there was a genetic correlation of  $0.61 \pm 0.16$  between the time interval between feed events and the time interval between meals.

### Correlations between feeding behavior and both performance and feed efficiency

The genetic correlations between the traditional feeding behavior traits and the performance and feed efficiency traits are in Table 5. Genetically heavier cattle, those with a higher MEI, or those that grew faster had, on average, a faster feeding rate and a greater energy intake per feed event. Genetic correlations of  $0.30 \pm 0.12$  and  $0.32 \pm 0.13$  existed between UFD and both feeding time per day and feed event duration, respectively. In general, the traditional feeding behavior traits were not genetically associated with any of the efficiency traits, although there was a genetic correlation of  $0.36 \pm 0.11$  between the time spent feeding per day and REI. Residual correlations between the traditional feeding behavior traits and the feed efficiency traits ranged from  $-0.36$  (feeding rate and RIG) to  $0.41$  (feeding rate and REI).

The genetic correlations between the meal feeding behavior traits and both performance and feed efficiency traits are provided in Table 6. Apart from energy intake per meal, genetic correlations between the meal feeding behavior traits and MEI were weak and not different from zero. A higher energy intake per meal was associated with both heavier and faster growing cattle. UFD was not genetically correlated with any of the meal feeding behavior traits. In contrast to the traditional feeding behavior traits, several meal feeding behavior traits were genetically associated with feed efficiency. Genetically more feed efficient cattle, in terms of a lower REI, on average, had a shorter meal time per day, higher energy intake per meal, and a longer time per meal. Moderately positive genetic correlations existed between  $REI_u$  and both the number of meals per day and the total meal time per day. Similarly, genetic correlations of  $-0.36 \pm 0.18$  and  $-0.34 \pm 0.15$  existed between  $RIG_u$  with both meals per day and total meal time per day, respectively. Both greater RG and  $RG_u$  were genetically associated with a higher energy intake per meal, although residually associated with a lower energy intake per meal. Both the number of feed events per meal and the time between feed events within a meal were not genetically associated with any of the performance and feed efficiency traits.

### Genetic evaluation

The accuracy of predicting phenotypic MEI in the validation population, as well as the coefficients from the regression of adjusted phenotypic MEI on  $EBV_{MEI}$ , from the different genetic

**Table 1.** Raw means, genetic SD ( $\sigma_g$ ), heritability ( $h^2$ ), and coefficient of genetic variation ( $CV_g$ ) for the feeding behavior traits of 1,548 steers and heifers

Trait	Mean	$\sigma_g$	$h^2$ (SE)	$CV_g$
Feed events per day, n	32.98	6.88	0.51 (0.097)	21
Feeding time per day, min	133.80	15.21	0.61 (0.100)	11
Feeding rate, MJ/min	1.12	0.12	0.44 (0.093)	11
Feed event duration, min	4.50	1.00	0.48 (0.094)	22
Energy intake per feed event, MJ	4.81	0.97	0.47 (0.095)	20
Time between feed events, min	43.98	8.43	0.43 (0.095)	19
Meals per day, n	8.14	0.44	0.19 (0.080)	5
Total meal time per day, min	213.40	20.28	0.49 (0.097)	10
Feed events per meal, n	4.08	0.78	0.41 (0.093)	19
Energy intake per meal, MJ	17.91	1.59	0.26 (0.083)	9
Meal duration, min	26.69	2.60	0.35 (0.089)	10
Time between meals, min	153.70	10.06	0.22 (0.083)	7
Time between feed events within a meal, min	3.47	0.53	0.40 (0.094)	15

**Table 2.** Genetic correlations (below the diagonal; SE in parentheses) and residual correlations<sup>1</sup> (above the diagonal) among the traditional feeding behavior traits

Trait	Feeding time per day	Feed events per day	Feeding rate	Energy intake per feed event	Feed event duration	Time between feed events
Feeding time per day		-0.02	-0.65	0.03	0.29	-0.11
Feed events per day	-0.02 (0.14)		0.44	-0.68	-0.75	-0.79
Feeding rate	-0.74 (0.07)	-0.05 (0.15)		-0.06	-0.47	-0.25
Energy intake per feed event	0.12 (0.14)	-0.89 (0.04)	0.18 (0.15)		0.87	0.90
Feed event duration	0.52 (0.11)	-0.83 (0.05)	-0.35 (0.14)	0.85 (0.04)		0.89
Time between feed events	-0.05 (0.15)	-0.97 (0.02)	0.12 (0.16)	0.93 (0.03)	0.81 (0.05)	

<sup>1</sup>SE of the residual correlations were all  $\leq 0.13$  and the mean residual correlation SE was 0.08.

**Table 3.** Genetic correlations (below diagonal; SE in parentheses) and residual correlations<sup>1</sup> (above diagonal) among the meal feeding behavior traits

Trait	Meals per day	Total meal time per day	Feed events per meal	Energy intake per meal	Meal duration	Time between meals	Time between feed events within a meal
Meals per day		0.23	-0.39	-0.75	-0.66	-0.95	-0.39
Total meal time per day	0.31 (0.20)		0.35	0.01	0.54	-0.34	0.10
Feed events per meal	0.23 (0.25)	0.56 (0.12)		0.58	0.60	0.36	-0.56
Energy intake per meal	-0.62 (0.15)	-0.13 (0.19)	-0.15 (0.21)		0.67	0.74	-0.24
Meal duration	-0.28 (0.21)	0.80 (0.08)	0.48 (0.13)	0.26 (0.19)		0.65	-0.03
Time between meals	-0.93 (0.03)	-0.57 (0.15)	-0.37 (0.18)	0.57 (0.16)	0.29 (0.18)		-0.12
Time between feed events within a meal	0.02 (0.23)	-0.17 (0.16)	-0.66 (0.10)	-0.27 (0.19)	-0.14 (0.16)	-0.02 (0.22)	

<sup>1</sup>SE of the residual correlations were all  $\leq 0.11$  and the mean residual correlation SE was 0.07.

evaluation scenarios is provided in Table 7. Correlations between adjusted phenotypic MEI and  $EBV_{MEI}$  where  $EBV_{MEI}$  was estimated from the phenotypes of different combinations of MEI, MBW, and feeding behavior traits (i.e., scenarios one, two, three, and four) did not differ ( $P > 0.05$ ) from each other. A greater ( $P < 0.001$ ) accuracy of prediction of phenotypic MEI was achieved when the MBW phenotypes of validation animals were included in the genetic evaluation (i.e., scenario five; correlation of  $0.64 \pm 0.03$ ) compared to when just the feeding behavior phenotypes of validation population animals were included in the evaluation (i.e., scenario six; correlation of  $0.44 \pm 0.05$ ). Nonetheless, compared to all previous scenarios (i.e., scenarios one to six), the accuracy of prediction of phenotypic MEI was slightly better ( $P < 0.001$ ) when both MBW and feeding behavior phenotypes from the validation population were included in the evaluation (i.e., scenario seven). As expected, the greatest prediction accuracy achieved was when the actual MEI phenotypes of the validation population were used to estimate  $EBV_{MEI}$  (i.e., scenario eight). The regression coefficients of phenotypic MEI on MEI were less than one ( $P < 0.05$ ) for scenarios one to four, greater than one ( $P < 0.001$ ) for scenarios five, seven, and eight, but not different from one ( $P > 0.05$ ) for scenario six. The expectation was that a one-unit increase in  $EBV_{MEI}$  would be associated with a one-unit increase in phenotypic MEI.

## Discussion

The phenotypic investigation of feeding behavior in farm animal species has been a topic of considerable scientific activity (Forbes, 2007); however, the specific study of the genetics of feeding behavior is less common in the literature, most likely due to the

necessity to collect a relatively large number of animal records to generate reliable and precise parameter estimates. Genetic variability in feeding behavior has been demonstrated to exist in farm animal species such as swine (Labroue et al., 1997; Shirali et al., 2017) and, as also demonstrated in the current study, cattle (Olson et al., 2020; Robinson and Oddy, 2004). Additionally, similar to the present study, several feeding behavior traits have been reported to be correlated with both animal performance and efficiency (Labroue et al., 1997; Robinson and Oddy, 2004). While investigations into the dynamics of feeding behavior of cattle has improved our understanding of the impact of selection for performance on animal feed intake patterns (Chen et al., 2014), such feeding behavior traits may also have an application in genetic evaluations to improve the accuracy of selection for improved animal performance and efficiency (Labroue et al., 1997); to the best of our knowledge, the latter argument has not been previously verified. In comparison to studies in swine, a paucity of cattle-based studies has documented genetic parameters for feeding behavior and their genetic correlations with performance and efficiency. Therefore, the objective of the present study was to investigate the genetic variability in several feeding behavior traits and to explore the genetic relationships among and between feeding behavior, and both performance and efficiency in young crossbred growing cattle. Furthermore, as feed intake data are expensive to collect in cattle, also of interest was the use of easier-to-measure time-related feeding behavior traits in genetic evaluations in order to improve the precision of genetic merit for feed intake. The respective phenotypic correlations among and between feeding behavior and both performance and feed efficiency have been reported previously by Kelly et al. (2020) for a subset of the cattle

**Table 4.** Genetic (SE in parentheses) and residual correlations<sup>1</sup> between the traditional and meal feeding behavior traits.

Trait	Genetic correlations						
	Meals per day	Total meal time per day	Feed events per meal	Energy intake per meal	Meal duration	Time between meals	Time between feed events within a meal
Feed events per day	0.48 (0.19)	0.61 (0.10)	0.95 (0.02)	-0.29 (0.18)	0.34 (0.15)	-0.61 (0.17)	-0.59 (0.11)
Feeding time per day	0.01 (0.20)	0.69 (0.08)	-0.03 (0.15)	0.23 (0.17)	0.69 (0.10)	-0.16 (0.18)	-0.10 (0.15)
Feeding rate	0.00 (0.22)	-0.57 (0.11)	-0.07 (0.16)	0.28 (0.17)	-0.57 (0.14)	0.11 (0.21)	0.01 (0.17)
Energy intake per feed event	-0.43 (0.20)	-0.53 (0.11)	-0.85 (0.06)	0.55 (0.15)	-0.28 (0.16)	0.55 (0.17)	0.40 (0.14)
Feed event duration	-0.36 (0.20)	-0.16 (0.15)	-0.80 (0.07)	0.33 (0.18)	0.06 (0.17)	0.40 (0.18)	0.41 (0.13)
Time between feed events	-0.44 (0.20)	-0.66 (0.09)	-0.93 (0.04)	0.30 (0.19)	-0.40 (0.15)	0.61 (0.16)	0.53 (0.12)
	Residual correlations						
Feed events per day	0.10	0.59	-0.06	0.06	0.34	-0.23	0.03
Feeding time per day	0.10	0.50	0.00	0.21	0.28	-0.12	-0.56
Feeding rate	-0.10	-0.26	0.47	0.43	-0.10	0.19	-0.30
Energy intake per feed event	-0.21	-0.45	-0.56	0.19	-0.17	0.23	0.54
Feed event duration	-0.16	-0.29	-0.65	-0.02	-0.10	0.14	0.58
Time between feed events	-0.24	-0.56	-0.64	-0.04	-0.23	0.28	0.60

<sup>1</sup>SE of the residual correlations were all  $\leq 0.11$  and the mean residual correlation SE was 0.09.

included in the current study and are therefore not discussed further.

The present study is among the first to explicitly document the genetic parameters for feeding behavior at the different levels of time (i.e., feed event, meal, and day level), as well as their genetic interrelationships, in the same cohort of cattle. Additionally, this is also the first study to demonstrate how feeding behavior phenotypes from relatives, or from the animal itself, can be used to predict phenotypic feed intake (i.e., MEI here) through a genetic evaluation. The majority of previously related studies in beef cattle have been limited in size (Benfica et al., 2020; Durunna et al., 2013; Lin et al., 2013; Nkrumah et al., 2007; Olson et al., 2020; Robinson and Oddy, 2004); a factor which contributes to large associated SE of the estimated parameters. The present study represents the largest study to date, thus contributing to the precision of genetic parameters and genetic correlation estimates associated with cattle feeding behavior in the cattle literature.

### Genetic parameters

In support of the present study, moderate heritability estimates for different feeding behavior traits in cattle have been reported elsewhere (Robinson and Oddy, 2004; Chen et al., 2014). Robinson and Oddy (2004), for example, reported heritability estimates ranging from 0.36 (feeding time per day) to 0.51 (feeding rate) in steers and heifers of temperate and tropical breeds fed a high concentrate diet. Similar heritability estimates of 0.49 for feeding time per day and 0.56 for feeding rate have been documented in Charolais steers (Chen et al., 2014). Interestingly, lower estimates of heritability have been reported in crossbred beef heifers fed a diet greater in forage proportion (Olson et al., 2020); heritability estimates of 0.25 and 0.27 have been reported

for feeding time per day and feed events per day, respectively (Olson et al., 2020). Nonetheless, the heritability estimates of different feeding behavior traits reported in the present study are largely in agreement with the cattle literature. The moderate heritability estimates for feeding behavior suggest that few records are required for the generation of relatively accurate EBVs for feeding behavior; the accuracy of EBVs from an animal's own information alone is simply the square root of the trait heritability estimate. Genetic parameters for feeding behavior defined at the meal level are generally lacking in the scientific literature of cattle, but are nonetheless similar to genetic parameters for meal feeding behavior traits estimated in Romane lambs (Marie-Etancelin et al., 2019).

The greater  $CV_g$  for the traditional feeding behavior traits compared to the meal feeding behavior traits is not surprising, given that some genetic variation is expected to be absorbed when feed events are collapsed into meals. In the current study, the feeding behavior traits had greater genetic variation (i.e., greater  $CV_g$ ) than the performance and efficiency traits, which is in agreement with the trend observed across estimates of  $CV_g$  calculated from the mean and genetic standard deviations presented in previous studies (Durunna et al., 2013; Robinson and Oddy, 2004).

### Genetic correlations

Genetic correlations between the same feeding behavior traits at the different levels of time (e.g., energy intake per feed event, per meal, and per day) are lacking from studies on cattle, although estimates have been reported in both sheep (Marie-Etancelin et al., 2019) and swine (Hall et al., 1999). Marie-Etancelin et al. (2019) reported a genetic correlation of 0.95 between feed intake per feed event and per meal, and a

Table 5. Genetic (SE in parentheses) and residual correlations<sup>1</sup> between the traditional feeding behavior traits and the performance and feed efficiency traits.

Trait <sup>2</sup>	Genetic Correlations										
	MEI	ADG	MBW	UFD	ECR	REI	REI <sub>U</sub>	RG	RG <sub>U</sub>	RIG	RIG <sub>U</sub>
Feed events per day	0.03 (0.12)	-0.08 (0.14)	-0.22 (0.13)	-0.13 (0.13)	0.05 (0.14)	0.17 (0.12)	0.18 (0.13)	-0.05 (0.15)	-0.08 (0.16)	-0.16 (0.14)	-0.20 (0.15)
Feeding time per day	0.26 (0.11)	0.16 (0.13)	-0.18 (0.12)	0.30 (0.12)	-0.17 (0.13)	0.36 (0.11)	0.19 (0.13)	0.10 (0.14)	0.00 (0.16)	-0.18 (0.13)	-0.14 (0.15)
Feeding rate	0.45 (0.10)	0.29 (0.14)	0.40 (0.11)	-0.20 (0.13)	-0.07 (0.15)	0.11 (0.12)	0.17 (0.14)	0.13 (0.16)	0.23 (0.17)	-0.03 (0.15)	-0.02 (0.16)
Energy intake per feed event	0.36 (0.12)	0.35 (0.14)	0.41 (0.12)	0.24 (0.13)	-0.21 (0.14)	0.03 (0.13)	-0.05 (0.14)	0.23 (0.15)	0.25 (0.17)	0.12 (0.15)	0.19 (0.16)
Feed event duration	0.11 (0.13)	0.13 (0.15)	0.09 (0.13)	0.32 (0.13)	-0.12 (0.14)	0.03 (0.13)	-0.13 (0.14)	0.10 (0.15)	0.06 (0.17)	0.05 (0.15)	0.16 (0.16)
Time between feed events	-0.02 (0.13)	0.07 (0.15)	0.26 (0.14)	0.16 (0.14)	-0.04 (0.15)	-0.20 (0.13)	-0.23 (0.14)	0.05 (0.16)	0.06 (0.18)	0.19 (0.15)	0.23 (0.16)
						Residual Correlations					
Feed events per day	0.42	0.12	0.21	0.26	0.15	0.37	0.39	-0.09	-0.05	-0.30	-0.30
Feeding time per day	0.22	0.22	0.36	0.00	0.09	0.07	0.17	0.06	0.14	-0.10	-0.08
Feeding rate	0.36	0.12	0.39	0.21	0.21	0.41	0.35	-0.17	-0.21	-0.36	-0.37
Energy intake per feed event	-0.02	0.03	0.14	-0.14	0.07	0.04	0.03	-0.05	-0.06	-0.08	-0.07
Feed event duration	-0.22	-0.03	-0.02	-0.26	-0.05	-0.21	-0.14	0.06	0.08	0.15	0.14
Time between feed events	-0.33	-0.14	-0.21	-0.27	-0.08	-0.23	-0.23	0.02	0.00	0.18	0.17

<sup>1</sup>SE of residual correlations were all  $\leq 0.11$  and the mean residual correlation SE was 0.08.<sup>2</sup>MEI = metabolizable energy intake; ADG = average daily gain; MBW = mid-test metabolic live-weight; UFD = ultrasound fat depth; ECR = energy conversion ratio; REI = residual energy intake; REI<sub>U</sub> = REI adjusted for UFD; RG = residual gain; RG<sub>U</sub> = RG adjusted for UFD; RIG = residual intake and gain; RIG<sub>U</sub> = RIG adjusted for UFD.Table 6. Genetic (SE in parentheses) and residual correlations<sup>1</sup> between the meal feeding behavior traits and the performance and feed efficiency traits.

Trait <sup>2</sup>	Genetic Correlations										
	MEI	ADG	MBW	UFD	ECR	REI	REI <sub>U</sub>	RG	RG <sub>U</sub>	RIG	RIG <sub>U</sub>
Meals per day	0.00 (0.19)	-0.21 (0.21)	-0.23 (0.14)	0.05 (0.18)	0.21 (0.21)	0.19 (0.18)	0.30 (0.15)	-0.25 (0.22)	-0.25 (0.18)	-0.27 (0.18)	-0.36 (0.18)
Total meal time per day	0.12 (0.13)	-0.01 (0.15)	-0.37 (0.12)	0.07 (0.13)	-0.07 (0.14)	0.39 (0.12)	0.33 (0.13)	-0.02 (0.15)	-0.18 (0.17)	-0.27 (0.13)	-0.34 (0.15)
Feed events per meal	0.00 (0.13)	-0.05 (0.15)	-0.22 (0.13)	-0.21 (0.14)	0.03 (0.15)	0.15 (0.13)	0.11 (0.14)	0.00 (0.17)	0.00 (0.17)	-0.12 (0.15)	-0.13 (0.17)
Energy intake per meal	0.78 (0.08)	0.67 (0.15)	0.46 (0.14)	0.08 (0.16)	-0.42 (0.18)	0.37 (0.12)	0.23 (0.15)	0.50 (0.19)	0.49 (0.20)	0.02 (0.18)	0.07 (0.21)
Meal duration	0.09 (0.14)	0.13 (0.16)	-0.30 (0.14)	0.04 (0.15)	-0.20 (0.16)	0.27 (0.13)	0.14 (0.16)	0.18 (0.17)	0.04 (0.19)	-0.08 (0.16)	-0.09 (0.18)
Time between meals	-0.04 (0.17)	0.20 (0.20)	0.31 (0.15)	-0.08 (0.17)	-0.14 (0.20)	-0.28 (0.17)	-0.38 (0.19)	0.24 (0.21)	0.29 (0.18)	0.33 (0.20)	0.44 (0.21)
Time between feed events within a meal	-0.18 (0.13)	-0.15 (0.16)	-0.02 (0.14)	0.01 (0.14)	0.03 (0.15)	-0.13 (0.13)	-0.04 (0.15)	-0.15 (0.17)	-0.21 (0.18)	0.02 (0.15)	-0.07 (0.17)
						Residual Correlations					
Meals per day	0.02	0.18	0.12	0.05	-0.14	-0.09	-0.13	0.19	0.20	0.15	0.18
Total meal time per day	0.24	0.20	0.24	0.19	0.06	0.09	0.13	0.08	0.17	-0.08	-0.03
Feed events per meal	0.37	0.03	0.17	0.24	0.18	0.35	0.40	-0.15	-0.15	-0.31	-0.34
Energy intake per meal	0.47	0.12	0.43	0.17	0.32	0.51	0.50	-0.24	-0.23	-0.49	-0.48
Meal duration	0.18	0.00	0.14	0.10	0.15	0.13	0.19	-0.10	-0.05	-0.18	-0.17
Time between meals	-0.06	-0.20	-0.16	-0.07	0.11	0.07	0.11	-0.18	-0.21	-0.12	-0.17
Time between feed events within a meal	-0.27	0.00	-0.14	-0.13	-0.16	-0.31	-0.36	0.18	0.20	0.32	0.36

<sup>1</sup>SE of residual correlations were all  $\leq 0.12$  and the mean residual correlation SE was 0.08.<sup>2</sup>MEI = metabolizable energy intake; ADG = average daily gain; MBW = mid-test metabolic live-weight; UFD = ultrasound fat depth; ECR = energy conversion ratio; REI = residual energy intake; REI<sub>U</sub> = REI adjusted for UFD; RG = residual gain; RG<sub>U</sub> = RG adjusted for UFD; RIG = residual intake and gain; RIG<sub>U</sub> = RIG adjusted for UFD.



**Table 7.** Pearson correlations<sup>1</sup> (r; SE in parentheses) between adjusted phenotypic daily energy intake (MEI) and the estimated breeding value for MEI (EBV<sub>MEI</sub>) for each evaluation scenario in a validation population of 321 steers and heifers. Also shown is the coefficient (b; SE in parentheses) from the regression of adjusted phenotypic MEI on the EBV<sub>MEI</sub> from each evaluation scenario

Genetic evaluation scenario <sup>2</sup>	r (SE)	b (SE) <sup>3</sup>
Scenario 1: Univariate evaluation for MEI with all phenotypes from the validation population masked	0.35 <sup>a</sup> (0.05)	0.75 <sup>a</sup> (0.11)*
Scenario 2: Multi-trait evaluation with covariances fitted between MEI and MBW and all phenotypes from the validation population masked	0.35 <sup>a</sup> (0.05)	0.75 <sup>a</sup> (0.11)*
Scenario 3: Multi-trait evaluation with covariances fitted between MEI and FB and all phenotypes from the validation population masked	0.35 <sup>a</sup> (0.05)	0.75 <sup>a</sup> (0.11)*
Scenario 4: Multi-trait evaluation with covariances fitted between MEI, MBW, and FB and all phenotypes from the validation population masked	0.35 <sup>a</sup> (0.05)	0.75 <sup>a</sup> (0.11)*
Scenario 5: Multi-trait evaluation with covariances fitted between MEI and MBW and just MEI phenotypes from the validation population masked	0.64 <sup>b</sup> (0.03)	1.25 <sup>b</sup> (0.08)**
Scenario 6: Multi-trait evaluation with covariances fitted between MEI and FB and just MEI phenotypes from the validation population masked	0.44 <sup>c</sup> (0.05)	0.94 <sup>a</sup> (0.11)
Scenario 7: Multi-trait evaluation with covariances fitted between MEI, MBW, and FB and just MEI phenotypes from the validation population masked	0.68 <sup>d</sup> (0.03)	1.34 <sup>b</sup> (0.08)***
Scenario 8: Univariate evaluation for MEI with no phenotypes from the validation population masked	0.93 <sup>e</sup> (0.01)	1.54 <sup>c</sup> (0.04)***

<sup>a-c</sup>Correlations and regression coefficients within a column with different subscripts differ ( $P < 0.05$ ).

<sup>1</sup>All correlations were both different from zero ( $P < 0.001$ ) and different from one ( $P < 0.001$ ).

<sup>2</sup>MBW = mid-test metabolic live-weight; FB = feeding behavior traits of feeding time per day, number of feed events per day, total meal time per day, and number of meals per day.

<sup>3</sup>Significance of the regression coefficient difference from one: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

genetic correlation of 0.91 between feeding time per feed event and per meal in Romane lambs. Such genetic relationships suggest that these traits are under similar genetic control in sheep; however, in the present study, feeding duration at the feed event and meal level were genetically independent of each other, although there was a moderate genetic correlation of 0.55 between energy intake per feed event and per meal. Similar to the present study, Marie-Etancelin et al. (2019) in sheep, and Hall et al. (1999) in pigs, also reported weak to moderate genetic correlations between feed intake per feed event and feed intake per day. Such weak to moderate genetic links between feed intake at the different levels of time corroborate suggestions that feed intake is regulated by homeostatic mechanisms in the short term and is influenced more by bodily reserves and nutritional requirements in the longer term (Forbes, 2007). Levels of circulating glucagon and insulin are thought to be involved in short-term feed intake regulation, whereas leptin is the likely candidate metabolite in longer-term regulation of feed intake (Forbes, 2007). Furthermore, the weak to moderate genetic correlations between short-term feeding behaviors and MEI herein support the theory that cattle seek a certain level of feed intake and may use a plastic feed intake pattern, which also varies considerably between individuals, to obtain that feed intake level (Emmans and Kyriazakis, 2001).

The genetic correlations between the traditional feeding behavior traits and performance traits estimated in the present study are within the range of those reported previously in cattle (Benfica et al., 2020; Durunna et al., 2013; Lin et al., 2013; Nkrumah et al., 2007; Olson et al., 2020; Robinson and Oddy, 2004), although considerable variation does exist in the magnitude of the same pair-wise correlations across studies. For example, documented genetic correlations between feeding time per day and feed intake per day have ranged from 0.03 (Robinson and Oddy, 2004) to 0.56 (Nkrumah et al., 2007) (genetic correlation of 0.26 in the current study); similarly, genetic correlations ranging from 0.14 (Benfica et al., 2020) to 0.81 (Chen et al., 2014) have been reported between ADG and feeding rate (genetic correlation of 0.29 in

the present study). Such large variability in genetic correlation estimates could be due to differences in the represented cattle breeds and diets across studies, as well as possibly due to genotype-by-environment interactions. For example, genetic parameters and correlations were estimated in both temperate and tropical breed steers and heifers fed a barley grain-based diet by Robinson and Oddy (2004), whereas Olson et al. (2020) estimated genetic parameters and correlations in crossbred beef heifers fed a barley silage based diet. Nonetheless, the SE of the genetic correlations reported by Olson et al. (2020) and Robinson and Oddy (2004) were quite similar to those reported in the present study; the mean SE of the same pairwise genetic correlations was 0.11 in Olson et al. (2020), 0.13 in Robinson and Oddy (2004), and 0.12 in the present study.

Exploration of the genetic relationships between feeding behavior and feed efficiency has been the focus of several studies in cattle (Durunna et al., 2011; Lin et al., 2013; Nkrumah et al., 2007). Genetically more efficient cattle, in terms of RFI, eat for a shorter time per day (Benfica et al., 2020; Chen et al., 2014; Nkrumah et al., 2007; Robinson and Oddy, 2004), a phenomenon also detected in the present study. It has, however, been suggested that the relationship between feeding behavior and feed efficiency is simply an artifact of the covariance between feeding behavior and feed intake (Cantalapiedra-Hijar et al., 2018; Kenny et al., 2018). Consequently, genetic and residual covariances between feeding behavior and feed efficiency were re-estimated in the present study, but with MEI included as a covariate in the statistical model for all feeding behavior traits. A genetic correlation of 0.28 (0.11) was still evident between feeding time per day (independent of MEI) and REI. In fact, the correlations between feed efficiency and feeding behavior before and after adjustment for MEI did not differ in the present study. Nonetheless, the genetic correlation between energy intake per meal and REI changed from 0.37 (0.12) to -0.13 (0.18) after inclusion of MEI in the bivariate model for energy intake per meal, but this is expected as MEI and energy intake per meal are strongly genetically correlated (genetic correlation of 0.78).

Therefore, results from the present study suggest that some feeding behavior traits do contribute to some of the genetic variability that exists in several feed efficiency traits.

### Usefulness of feeding behavior phenotypes in genetic evaluations for daily energy intake

Similar to the present study, several studies have reported significant genetic correlations between time-related feeding behavior traits and both feed intake and efficiency (Benfica et al., 2020; Chen et al., 2014; Lin et al., 2013; Nkrumah et al., 2007; Robinson and Oddy, 2004); this has led to feeding behavior traits being suggested as predictors of genetic merit for feed intake and efficiency (Lin et al., 2013; Nkrumah et al., 2007), but this suggestion has not been verified in cattle prior to the current study. Such an approach sounds promising as the heritability estimates of time-related feeding behavior traits were found to be generally moderate in magnitude herein and in the cattle literature (Chen et al., 2014; Durunna et al., 2013; Nkrumah et al., 2007; Robinson and Oddy, 2004); thus reasonably accurate estimates of genetic merit feed intake may be obtained if the genetic correlations between feeding behavior and feed intake are sufficiently strong. Nevertheless, in the present study, the benefit in predictive ability associated with the addition of feeding behavior phenotypes to a genetic evaluation for MEI was relatively small, compared to when just the animal's own liveweight phenotype were in the genetic evaluation. Moreover, the relatively small improvement in predictive ability from the inclusion of feeding behavior phenotypes in the evaluation may not compensate for the additional capital and running costs of investing in feed bunk sensor technologies required to measure cattle feeding behavior solely for the purposes of feed intake genetic evaluations. Nonetheless, the integration of sensor technology in livestock farming is expected to grow as the cost of sensors reduce and their durability improves (Halachmi et al. 2019). It should be also noted that the collection of feeding behavior data has other potential uses, beyond feed intake prediction, which include the monitoring of cattle health and welfare (Kayser et al., 2019; Quimby et al., 2001), as well as in the optimization of animal management (Llonch et al., 2018). Therefore, where feeding behavior data are being collected anyway on cattle for such purposes, their use in genetic evaluations for feed intake may be beneficial. The addition of genomic information to genetic evaluations is also expected to further increase the reliability of genetic evaluations for MEI (Bolormaa et al., 2013; Pryce et al., 2014), although a reference population with estimates of genetic merit for feed intake would still be required.

### Conclusions

Significant exploitable genetic variation exists in the feeding behavior of young crossbred growing cattle, and some of these behavioral traits are genetically correlated with several performance and feed efficiency measures. Nonetheless, including feeding behavior phenotypes in a genetic evaluation for MEI only marginally improved the predictive ability of EBV<sub>MEI</sub> over and above the predictive ability achieved from the inclusion of live-weight phenotypes in a genetic evaluation.

### Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

### Acknowledgments

Funding provided by the Department of Agriculture, Food and the Marine Ireland Research Stimulus Fund Ref: 17/S/235 (GreenBreed) is gratefully acknowledged.

### Conflict of interest statement

The authors declare no real or perceived conflicts of interest.

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