APPLICATION OF CHEMOMETRICS TO PREDICT INTAKE AND FEED EFFICIENCY USING FEEDING BEHAVIOR PATTERNS IN GROWING CATTLE

A Dissertation

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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August 2019

Major Subject: Animal Science

ABSTRACT

Residual feed intake (RFI) is an ideal trait for use in selection programs to improve feed efficiency in beef cattle, as it quantifies between-animal variation in DMI that is independent of body size and productivity, to better reflect inherent differences in biologically relevant processes associated with feed efficiency. RFI is an expensive phenotype to measure and thus there is need to identify biomarkers to more cost effectively predict genetic merit for RFI. Objectives of this study were to characterize feeding behavior patterns of cattle with divergent RFI phenotypes and to evaluate the accuracy of using feeding behavior traits to predict individual-animal RFI and DMI. Performance, DMI, and feeding behavior data were collected from 498 Angus-based composite steers (Study 1), 408 heifers (Study 2) and 321 steers (Study 3) comprised of Brangus, Braford, Simbrah, and Angus breeds, and 1,787 Holstein heifers (Study 4). DMI and feeding behavior traits were measured using a GrowSafe System, and RFI calculated within trial. Nineteen feeding behavior traits were evaluated: Frequency and duration of bunk visit (BV) and meal events, head-down duration (HDD), average meal length, maximum non-feeding interval, corresponding day-to-day variation (SD) of these traits, and ratios of HDD per BV duration, HDD per meal duration, and BV events per meal event. Consistently, low-RFI animals consumed 16 to 24% less DMI, had less day-to-day variation in DMI, fewer and shorter BV events, and less HDD than high-RFI animals. Associations between RFI and meal traits were less consistent across studies, as individual-animal meal criterion values were higher for low-RFI Angus-composite steers and Holstein heifers, but were not different for mixed-breed steers and heifers, compared to high-RFI animals. However, meal duration was lower for low-RFI animals compared to high-RFI animals across studies. Across studies, low-RFI animals had less day-to-day variation in feeding behavior patterns than high-RFI animals. Between-animal differences in feeding behavior patterns accounted for 35 to 47% of the variation in RFI, and 17 to 29% of the variation in DMI independent of mid-test $BW^{0.75}$ and ADG. Ongoing development of biosensor-based technologies to quantify feeding behavior patterns will provide opportunities to more accurately predict DMI in support of precision-nutrition strategies, and to more cost effectively select more feed-efficient cattle.

DEDICATION

I would like to dedicate this dissertation to my family. To my loving husband who has supported me unconditionally over the past six years. Although we could have never imagined taking on the role as houseparents of some amazing kids, much less while also supporting me through my PhD program, you have been the rock to this family and provided a great example to our boys and daughter of what a father and husband should be. To my “boys”, you will never know how grateful I am that God placed you in my life, or how much I love and care for you. You made sure my life was never dull and provided ample entertainment and frustration along this journey. To my loving father who first introduced me to the agriculture industry, and provided me with many opportunities that have influenced where I am today, and to my Granpy who supported my dreams. Though they are no longer with us physically, they continue to watch over me from heaven. To my mother who has provided unconditional love and support and has pushed me my entire life to go above and beyond to reach my goals. To my grandparents who have been there for me through the good and bad times. They have been amazing role models and have helped me to pursue my dreams.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Gordon Carstens, as well as my committee members, Dr. Doug Tolleson, Dr. Luis Tedeschi, and Dr. Bill Pinchak, for their continued support and guidance throughout the course of this research. You are all responsible for increasing my knowledge and providing me with unique experiences that will remain with me throughout my career.

I would also like to thank my coworkers and friends that have helped me with my research even when things got messy. Also, for their continued entertainment that was always available to cheer me up after a long day.

Finally, I would like to thank my husband Cameron. You are always there to listen to my daily highs and lows, and have been so forgiving on those not so good days. I am so lucky to have such an amazing person in my life that I can always turn to for love and support.

CONTRIBUTORS AND FUNDING SOURCES

This work was supervised by a dissertation committee consisting of Professor Gordon Carstens [advisor] and Luis Tedeschi of the Department of Animal Science and Professors Douglas Tolleson and William Pinchak of the Department of Ecosystems Science and Management.

Graduate study was supported by an assistantship from the Animal Science Department at Texas A&M and by STgenetics. The funding from STgenetics was made possible through the help of Jose Moreno, Joseph Deeb and Claas Heuer.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Introduction

Growing per capita incomes and increasing population growth will continue to drive the demand for animal protein sources. With the global human population projected to reach over 9 billion by the year 2050, the agricultural industries will be challenged to increase productivity in the face of rising input costs associated with competition for land, energy, and water supplies. Furthermore, emerging societal concerns about climate change continue to challenge the industry to reduce its' environmental impact. Consequently, the beef cattle industry is faced with the challenge to develop and implement new technologies that will increase the economic and environmental sustainability of production systems.

Residual feed intake

Feed is the largest variable input cost for dairy and beef cattle operations, thus the economic success of these operations depends on the efficient use of feed to meet the nutrient requirements of the cattle. Research has demonstrated that substantial genetic differences exist in RFI, such that efficient animals (low RFI) consume less feed and produce less methane per unit of product produced compared to their non-efficient high-RFI counterparts (Nkrumah et al., 2007; Lancaster et al., 2009b; Hafla et al., 2012; Basarab et al., 2013; Kayser and Hill, 2013; Bonilha et al., 2017; Baldassini et al., 2018).

Residual feed intake (RFI) is a moderately heritable trait (Schenkel et al., 2004; Williams et al., 2011) that is ideal for use in selection programs to improve feed efficiency as it accounts for the variation between individual animals' feed efficiency, independent of growth and production. Efficient or low-RFI cattle have reduced feed intake (Nkrumah et al., 2006; Lancaster et al., 2009b; Hafla et al., 2013) and decreased methane emissions (Hegarty et al., 2007; Basarab et al., 2013) compared to their inefficient or high-RFI counterparts with no impact on growth and performance.

Unfortunately, widespread industry adoption of these technologies to improve feed efficiency has been limited due to the relatively high costs of accurately quantifying individual-animal feed intake in beef cattle. Research in this area has profound implications not only to enable producers with technology to more cost effectively select for more efficient animals, but also to enable improve accuracy of predicting feed intake to support precision-nutrition strategies to more cost effectively meet the nutritional requirements of animals.

Individual-animal intake determinations

For confined animals, accurate and reliable measures of individual animal intake can be achieved through individual pen feeding or the use of specialized feeding systems in which individual animal intake can be measured in group pens by electronic feed bunks (Johnson, 2014). While there are various specialized feeding systems currently available for use, such as Calan-gate feeders or the GrowSafe^{TM} system, they are not commonly applicable in production settings due to their high relative cost and/or complex designs. Regardless of their application in production settings, these specialized feeding systems have aided in the development and validation of techniques to estimate DMI of both grazing and confined cattle. Such techniques involve measurements of herbage mass disappearance or the use of prediction models, internal and external markers, and fecal near infrared reflectance spectroscopy (Macoon et al., 2003; Undi et al., 2008; Johnson et al., 2017). Johnson (2014) summarized numerous studies involving these techniques and found that each are relatively effective in predicting DMI for groups of animals, but have limited ability to precisely estimate DMI of individual animals. Therefore, research is still warranted to develop a technique to accurately estimate individual animal intake or feed efficiency.

Individual-animal intake is driven by a complex series of mechanisms that are highly variable within and among animals (Grovum et al., 1998). The complexity of these mechanisms has hindered estimation techniques as it is difficult to predict how these mechanisms will interact with different diet and animal conditions. However, there is evidence to suggest that feed intake is controlled by physical factors such as ruminal fill and digesta passage when ruminants are consuming a less digestible, low-energy diet, and by the energy demands of the animal or metabolic factors when consuming a highly digestible, high-energy diet (NASEM, 2016). Based on these concepts, predictive equations have been developed to predict DMI with considerations for both the composition of the diet and the energy requirements of the animal. Anele et al. (2014) evaluated 4 equations to predict DMI in individual-animals using BW and NE concentrations of the diet and reported a range in r^2 of 0.13 to 0.25. These results indicate the need for additional factors to be considered in predictive equations to better estimate the energy demands of the animal. Accordingly, factors such as gender, age, physiological state, level of production, climate, and frame size have been evaluated, but equations still produced poor results, even for predicting group intake across studies (Rim et al., 2008; Parsons et al., 2012).

While their simplicity and ease of application make predictive equations advantageous for estimating intake of animals, current equations have limited ability to measure between-animal variation. Therefore, additional variables will need to be considered for use in predictive models to account for more of the individual-animal variation in net feed efficiency.

Monitoring the feeding behavior patterns of livestock

Precision livestock farming has been identified as the key to providing an economically efficient and environmentally sustainable future for the livestock industry given the immense between-animal variation that exist amongst animals. Precision livestock farming involves the use of sensor technologies to capture individual-animal physiological, behavioral, and productivity data to support optimal management of livestock animals. Real-time collection of sensor-based technologies can be used to improve accuracy of predicting expected productivity, feed intake, or feed efficiency amongst individual-animals. Implementation of precision livestock farming practices will enhance producers’ ability to detect and manage health and productivity, meet the nutritional requirements of their animals and mitigate environmental impact of production systems. Continued development of precision sensor technologies, and predictive algorithms that are capable of easily and accurately measuring individual-animal phenotypes in commercial settings are critical to the success of precision livestock farming in the future.

An area of emerging interest involves the monitoring of individual-animal feeding behavior patterns as they are highly associated with feed intake (Lancaster et al., 2009b; Kelly et al., 2010a; Kayser and Hill, 2013) and feed efficiency (Nkrumah et al., 2006; Lancaster et al., 2009b; Hafla et al., 2013) of individual-animals. Additionally, deviations in feeding behavior patterns have been shows to be predictive of health status in livestock (Quimby et al., 2001; Kayser et al., 2018). Thus, technology advances to capture individual-animal feeding patterns has implications for improving the prediction of feed intake, feed efficiency, and sickness of individual-animals, all of which drastically affect the profitability of livestock operations.

Generally, feeding behavior traits are based on the frequency and duration of individual-animal bunk visits (BV), with a BV event commencing when the animal approaches a feed bunk and ending when the animal leaves. When BV events are recorded, BV frequency and duration (min/d) can be computed as the number of visits an animal made to the feed bunk, and the summation of time the animal spent at the feed bunk recorded during a 24-hour period, respectively. While BV frequency and duration can be used to evaluate feeding behavior data, these variables may not always provide the most biologically relevant information in regards to an animals’ feeding behavior or subsequent intake. Specifically, although some variation in BV frequency may be related to innate differences between individual-animals, daily observations indicate that social hierarchy ranks may result in an animal being displaced from a bunk “involuntarily” (Tolkamp et al., 1999). This can especially be observed during peak intake periods following a feed delivery and will therefore, vary from trial to trial where competition and feed availability may differ. Accordingly, an animals’ BV event can be influenced by the individual animal as well as by the social hierarchy rank or competition for bunk space. Additionally, feed bunk construction has been shown to influence individual-animals’ BV events, with fewer BV events being recorded following the installation of yokes (Tolkamp et al., 1999). The authors suggest that the observed reduction in BV events resulted from both a reduction in the frequency of displacements, and the slight increase in difficulty of entering and leaving a bunk. Accordingly, it may be difficult to compare associations between feeding behavior patterns and various traits such as intake, efficiency, or sickness across trials using only BV event data as visits are ended as a result of what appears to be a random process (Tolkamp et al., 1999).

To avoid some of the issues described above, clusters of BV events separated by short intervals can be grouped together to form a meal. Meals have been identified as the most biologically relevant trait to examine feeding behavior patterns as they are less subject to social hierarchy, bunk competition, or environmental changes (Bailey, 2011). Accordingly, meals may be more representative of individual-animal differences in satiety mechanisms than BV events. However, the relevance of meal traits for identifying individual-animal differences depends on the estimation of an appropriate meal criterion for each animal, which is the longest non-feeding interval considered to be part of a meal (Yeates et al., 2001). Tolkamp and Kyriazakis (1999) evaluated multiple techniques for estimating meal criterion in dairy cattle and concluded that a bimodal distribution model provided the most biologically relevant meal criterion as $\log_{10}$- transformed nonfeeding intervals were clearly separated into within and between meal populations. Bailey et al. (2012) then investigated various combinations of probability density functions and determined that for beef cattle, nonfeeding interval data was best fit using the Gaussian-Weibull bimodal distribution model. Accordingly, meal criterion can be estimated by fitting a 2-pool, bimodal probability density function to the $\log_{10}$-transformed non-feeding intervals of each animal using the Meal Criterion Calculation Software (MCC; http://nutritionmodels.tamu.edu), with meal criterion being the intersection of the 2 probability density functions. Meal criterion can then be used to cluster BV events into meals, with meal frequency, length, and duration being defined as the number of meal events, average meal event length, and sum of length of meal events recorded each day, respectively (Miller, 2016). These feeding behavior parameters can be used to uncover mechanisms regulating feed intake and feed efficiency in cattle, and may therefore, have applications for use in feed intake or efficiency prediction models (Yeates et al., 2001; Bailey et al., 2012).

Previously, individual-animal feeding behavior patterns were monitored using direct observations of time-lapse video recordings. Each of these techniques provide accurate determinations of individual-animal feeding behavior, however, they are labor intensive, and therefore not applicable for use in commercial livestock operations. More recently, advancements in electronic radio frequency identification (RFID) and geolocation systems have enabled the development of new technologies that work to provide information regarding the presence or absence of an animal at a feed bunk or water trough. Currently, the majority of commercially available systems involve some variation of RFID technology in combination with sensors to capture an animals' feeding behavior patterns (Parsons, 2018). Although many systems differ slightly in their design, several have been validated to accurately quantify the frequency and duration of BV events and to measure individual animal intake using closed (Insentec, Hokofarm Group, Marknesse, Netherlands; SmartFeed Pro, C-lock Inc., Rapid City, SD, USA) or open (GrowSafe Systems, Airdrie, Alberta, Canada; SmartFeed, C-lock Inc., Rapid City, SD, USA; Intergado Ltd., Contagem, Minas Gerais, Brazil) gated feed bunks. While these systems are advantageous given their abilities to determine feed intake and behavior, they have limited application in commercial settings given their infrastructure and cost limitations (Parsons, 2018; Richeson et al., 2018). Accordingly, feeding and water behavioral monitoring systems have been developed to complement existing feed yard infrastructures, providing more applicable methods for determining feeding behavior patterns of animals in commercial dairy and feedlot settings. These systems utilize either receiver cables mounted above an open feed bunk line in combination with UHF RFID tags (AniTrace, Santa Clara, CA) or ultra-wide band transmitters attached to the ear tags of animals which transmit to readers positioned around the pen and at the front of an open feed bunk line (CattleTraq Inc., Westworth Village, TX). Although these systems do not provide quantify feed intake of animals, they do have application in measuring individual-animal feeding behavior in commercial settings.

In addition to RFID-based technologies, behavioral monitoring devices have been developed to quantify feeding behavior that use 3-axis accelerometers, strategically placed on the animals’ ear (CowManager SensOor, Agis, Harmelen, Netherlands), neck (Hobo Pendant G logger, Onset Computer Corp., Pocasset, MA), or leg (Track A Cow, ENGS, Rosh Pina, Israel). These devices are advantageous for monitoring individual-animal feeding behavior as they require little or no changes to the infrastructure of commercial facilities. However, many accelerometer devices record feeding behavior exclusively as the time spent feeding, and do not evaluate other feeding behavior traits such as BV duration or frequency. In a study by Mattachini et al. (2016), HOBO Pendant G logger devices were found to accurately quantify feeding time ($R^2 = 0.90$), but were limited in their ability to quantify the number of visits an animal made to the feed bunk ($R^2 = 0.31$). These results agree with those obtained for feeding times using the CowManager SensOors or Track A Cow Systems (Borchers et al., 2016), but indicate that accelerometer devices may be inferior to the previously described systems for quantifying individual-animal feeding behavior patterns. Regardless, accelerometer devices provide yet another tool that can be used to increase the precision in which the industry manages livestock.

Overall, recent advancements in RFID technology and improvements in three-axis accelerometers have enabled the development of technologies to quantify individual-animal feeding behavior patterns. These individual-animal measurements can be used to further advance precision farming practices, however, further research is necessary to validate these systems in commercial settings and evaluate which feeding behavior traits are most relevant for inclusion into future prediction models.

Bio-markers for feed intake or efficiency

Residual feed intake is a feed efficiency trait that quantifies the between-animal variation in DMI independent of differences in mid-test $BW^{0.75}$ and ADG. Therefore, traits that are highly associated with RFI may be good candidates for use as biomarkers for the prediction of RFI in a more cost-effective manner. Research has found that a significant proportion of the between-animal variation in RFI can be explained by differences in protein turnover, tissue metabolism, stress, digestibility, heat increment, fermentation, physical activity, body composition, and feeding patterns (Richardson and Herd, 2004).

Differences in body composition have been shown to account for about 5% of the variation in observed RFI (Richardson and Herd, 2004). Numerous studies have demonstrated that low-RFI (efficient) cattle deposit less fat than their high-RFI (non-efficient) counterparts (Arthur et al., 2001; Nkrumah et al., 2004; Schenkel et al., 2004; Lancaster et al., 2009a). Thus, low-RFI animal are more efficient due to the fact that the deposition of fat is more energetically costly than that of lean tissue (Alende et al., 2016). However, some studies have found no correlation between RFI and fat proportion (Cruz et al., 2010; Fitzsimons et al., 2014; Perkins et al., 2014). For longissimus muscle (LM) area, studies have found weak positive and negative correlations between RFI

(Nkrumah et al., 2004; Schenkel et al., 2004; Basarab et al., 2013). Thus, the use of ultrasound to measure body composition has limited utility to predict RFI in beef cattle.

Feeding behavior traits have been shown to differ between low- and high-RFI cattle, such that low-RFI animals have fewer bunk visits per day (Nkrumah et al., 2006; Alende et al., 2016), lower daily feeding durations (Nkrumah et al., 2006; Gomes et al., 2013), and consume feed intake at slower rates (Lancaster et al., 2009b; Kelly et al., 2010a) compared to high-RFI animals. Daily bunk visit frequency accounted for 20% of the variation in DMI of growing beef heifers (Kelly et al., 2010a) and daily bunk visit frequency and duration accounted for 44% (de Haer et al., 1993) and 35% (Lancaster et al., 2009b) of the variation in DMI in pigs and growing bulls, respectively. Accordingly, low-RFI animals may have reduced daily energy expenditures associated with reduced time spent eating and daily physical activity, contributing to their improved feed efficiency (Lancaster et al., 2009b; Kelly et al., 2010a; Gomes et al., 2013). This is likely, given that energy expenditure associated with eating is strongly related to time spent eating, and total energy expenditure is positively correlated with time spent standing (Susenbeth et al., 1998), both of which are lower in low-RFI cattle (Herd et al., 2004; Lancaster et al., 2009b). Additionally, Gibb et al. (1998) and Kelly et al. (2010b) found that feeding behavior traits were moderately repeatable, indicating that they would useful traits to predict between-animal variation in feed efficiency.

In addition to daily feeding behavior traits such as those described above, day-to-day variation of feeding behavior patterns have been found to be associated with both feed intake and efficiency in beef cattle (Parsons, 2018). In this study, low-RFI steers exhibited significantly less ($P < 0.01$) day-to-day variation in feeding behavior patterns and DMI compared to high-RFI steers. Specifically, feed efficient steers had a 9.7% reduction in day-to-day variation of intake, and a 23.5 and 13.8% reduction in day-to-day variation of BV frequency and duration, respectively. The results from this study present novel findings indicating a direct association between daily consumption patterns and feed efficiency. Although limited data has been reported to support this phenomenon, increased daily intake fluctuations in feed intake are thought to predispose cattle to metabolic disorders such as acidosis, which would reduce productivity. However, despite this common belief, negative effects of feed intake variation on acidosis and cattle performance have not been consistently observed. In a study by Cooper et al. (1999), increases in daily fluctuations in feed intake were not associated with increase acidosis or decrease performance in finishing steers fed at ad libitum intakes of a high-grain diet. However, Galyean et al. (1992) found that increased daily fluctuations in feed intake was negatively association with gain and feed efficiency in steers that were limit-fed a high-grain diet. Schwartzkopf-Genswein et al. (2011) fed steers a barley-based diet and actually reported an increased ADG and trend toward higher G:F for animals with greater variation in their daily eating patterns.

In the study by Parsons (2018), no differences were found in the growth or performance of steers despite high-RFI animals exhibiting increased variation in their daily intake patterns compared to their low-RFI counterparts. While this study did not evaluate the incidence of acidosis in these animals, subacute acidosis usually results in increased intake variation along with a decrease in DMI, as cattle generally reduce their intake when pH drops below 5.6 (Cooper et al., 1997). One could speculate that the increased intake variation observed for high-RFI animals in this study was not a function of increased subacute acidosis as high-RFI animals had higher DMI than low-RFI animals. However, during the grain adaptation period, Cooper et al. (1997) observed a tendency towards higher intakes and increased area below a pH of 5.6 in cattle consuming a control diet compared to a diet containing monensin. Therefore, DMI may not be a reliable indicator of acidosis. Overall, the lack of pH data inhibits further determinations in this case.

When Cooper et al. (1997) evaluated the effect of daily intake fluctuations on ruminal pH and DMI, they observed an increase in the magnitude of change and in the variation of daily values for ruminal pH levels of animals consuming the control diet, while no differences were observed for animals consuming a diet containing monensin; DMI was not affected by diet or intake fluctuation. Thus, low-RFI animals may have exhibited a reduction in daily variation in feed intake as a function of improved metabolic efficiencies similar to those observed for cattle supplemented with monensin. Further research is needed to evaluate the mechanisms by which daily variation in feeding patterns relates with metabolic efficiencies or metabolic disorders. Currently, it is unclear as to whether increases in daily intake variation causes increased metabolic disorders and reduced digestive efficiencies, or if metabolic disorders trigger increased variations in daily feeding patterns.

Overall, Parsons (2018) concluded that improved feed efficiency is associated with reduced daily variation in feeding patterns, however, they did not able establish whether or not this was related to reduced metabolic disorders or increased digestive efficiency. Results from their study indicated that daily variations in feeding patterns were more associated with feed efficiency than performance, implying that such variations may impact digestibility and overall energetic expenditures, however, literature is not currently available to support this hypothesis.

Partial least squares regression to predict DMI and RFI

Since feeding behavior traits have been shown to account for substantial portions of the individual-animal variation in RFI, their use as biomarkers for the prediction of RFI or DMI is warranted. However, it is important to recognize that the use of multiple linear regression (MLR) models to predict DMI or feed efficiency using feeding behavior traits may not be robust, as MLR does not account for the multi-collinear nature of feeding behavior traits. Alternatively, partial least squares regression (PLSR) may be a more appropriate method for calibrating and validating prediction models for DMI and feed efficiency using feeding behavior traits in combination with body composition measurements and other previously evaluated traits (i.e. body weight, gender, age, physiological state, level of production, climate, and frame size).

Partial least squares regression was introduced by Wold (1966) as an alternative approach to ordinary least squares regression when ill-conditioned linear regression models arise from there being many predictor variables and relatively few samples or from highly correlated covariates (Chun and Keles, 2010). Such situations are becoming more common as biotechnology advancements have led to an increased need for modelling of high dimensional data (Chun and Keles, 2010).

Partial least squares regression creates relationships between the dependent (Y) and independent (X) variables by constructing new explanatory variables, often called latent variables or components (Garthwaite, 1994). Components are constructed using centered and scaled dependent (U_1) and independent (V_j) variables, with the first component (T_1) being a linear combination of V_j, useful in predicting U_1. The next component (T_2) is then the linear combination of the residuals from the regression of V_j on T_1, which would be useful in predicting the residuals from the regression of U_1 on T_1. Each iterative component ($T_3, \ldots, T_p$) is then determined from the residuals of regressions on the preceding component (Garthwaite, 1994). The constructed components are then used as independent variables in an ordinary linear least squares regression analysis to predict the dependent variable.

The use of components in the standard linear regression eliminates the ill-conditions that arise from many, highly correlated independent variables being used, as the components are usually far fewer in number than the independent variables, and are uncorrelated amongst each other (Garthwaite, 1994). Accordingly, the PLSR method may be used on data sets that have many, highly correlated independent variables, regardless of sample size. It is important to note however, that while each component contributes to the variation observed in the dependent variable, measured data is never noise-free (Geladi and Kowalski, 1986). Thus, some form of cross-validation should be used to determine the number of appropriate components to include in the regression model (Wold, 1966; Geladi and Kowalski, 1986; Garthwaite, 1994). Typically, this is accomplished by evaluating the minimum root mean prediction residual sum of squares (PRESS) of each successive component, but there are other methods available (Gomes et al., 2013). Considerations may also need to be made for determining the appropriate number of original independent variables to be used in the PLSR model. Although this is a controversial topic in the literature, some researchers recommend using variable of importance (VIP) scores to eliminate original independent variables that may not contribute significantly to the dependent variable (Wold, 1966; Geladi and Kowalski, 1986). However, removal of original independent variables from the model often removes important information that might not be relevant to the current data set, but may diminish the robustness of the model for predicting future datasets (Eriksson et al., 2006). Therefore, the removal of independent variables should be considered with caution on a case by case basis.

Overall, PLSR would be the most appropriate method for developing equations to predict DMI or RFI using feeding behavior traits, as feeding behavior traits are highly correlated amongst each other. While only a few studies to date has developed such equations, PLSR has been used to predict DMI and RFI in cattle based on fecal near infrared reflectance spectroscopy (hunington et al., 2010; Johnson et al., 2017). Additionally, PLSR was found to be an adequate technique for identifying relationships between feeding behavior and RFI in dairy cattle (Fischer et al., 2018), social status and boldness in zebra fish (Dahlbom et al., 2011) and caffeine consumption and impulsive behavior in humans (Grant and Chamberlain, 2018). In each of these behavioral studies, PLSR was found to be adequate in identifying and selecting behaviors that were predictive of the desired dependent variable, despite correlations amongst behavior traits.

Lepron et al. (2007) evaluated the relationship between residual energy intake (REI) and behavior in growing pigs from three genetic lines. Their study looked at the animals' aggression during mixing, activity, feeding behavior, and social interactions while in their resident pen, and ease of handling during weighing. The relationship between these behavior traits and REI were analyzed using PLSR. Results from PLSR showed that postures, locomotion, eating, aggressive and stress-related behaviors explained 35.9% of the variation in REI. However, small values of loadings in this study indicate that the measured behaviors are not strongly related to REI, contrary to the authors' original hypothesis. Similarly, Fischer et al. (2018) used PLSR analysis to identify biological determinants of feed efficiency in lactating Holstein cows. However, in this study, the final PLSR model was developed using 27 original variables associated with milk yield expenditure, maintenance, digestibility, body reserves change, rumen temperature, activity, feeding behavior, and unidentified activity traits. The model accounted for 58.9% of the variation in REI with activity, feeding behavior, and unidentified activity explaining 26.5, 21.3, and 10.6% of the variation in REI, respectively.

Overall, PLSR analysis has been shown to be an appropriate method for evaluating the relationship between behavior and feed efficiency. Therefore, PLSR could be used to develop predictive models for RFI and DMI using feeding behavior traits.

However, industry acceptance of such models relies on the presence of an applicable method for quantifying individual-animal feeding behavior patterns in commercial operations.

Summary

Research to support favorable selection of livestock for feed efficiency has been limited by the absence of cost-effective methods to accurately quantify individual-animal feed intake or feed efficiency. While accurate and reliable measurements of individual-animal feed intake can be achieved through the use of specialized electronic feed-intake measurement systems, these methods have not been widely adopted in production settings due to their high cost and complex design. Alternatively, the use of biosensors to more cost effectively quantify feeding behavior traits that are associated with individual-animal variation in RFI has considerable potential to be more widely adopted by the beef industry. Feeding behavior traits would then provide opportunity to improve the accuracy in which the industry estimates DMI of individual animals, as they account for a proportion of the individual-animal variation in net feed efficiency. Feeding behavior patterns can then be included into PLSR prediction models to improve the accuracy in which the industry estimates DMI of individual animals, as they account for a proportion of the individual-animal variation in net feed efficiency and DMI. Accordingly, implications for further research regarding the use of PLSR models to predict DMI and RFI using feeding behavior traits exist.

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CHAPTER II

APPLICATION OF PARTIAL LEAST SQUARES REGRESSION TO QUANTIFY THE RELATIONSHIP BETWEEN RESIDUAL FEED INTKAE AND FEEDING BEHAVIOR TRAITS IN BEEF CATTLE

Introduction

The efficient use of feed to meet the nutrient requirements of animals is necessary for the economic sustainability of the beef industry as feed accounts for the largest variable input cost of production. Previous research has identified residual feed intake (**RFI**) as an ideal trait for quantifying individual-animals feed efficiency as efficient animals have reduced intake (Nkrumah et al., 2007; Lancaster et al., 2009b; Hafla et al., 2012; Kayser and Hill, 2013; Bonilha et al., 2017; Baldassini et al., 2018) and decreased methane emissions (Hegarty et al., 2007; Basarab et al., 2013) compared to their inefficient counterparts, independent of growth and production. Furthermore, RFI can be used in selection programs for favorable feed efficiency as it is a moderately heritable trait (Schenkel et al., 2004; Williams et al., 2011). Unfortunately, RFI is an expensive phenotype trait to measure, and not applicable in most commercial large-scale operations. Consequently, numerous research efforts have focused on the discovery of genomic markers (Pryce et al., 2012; Berry et al., 2014; Pryce et al., 2014; VandeHaar et al., 2016) and phenotypic biomarkers for the prediction of RFI in beef cattle.

Research has found that a significant proportion of the between-animal variation in RFI can be explained by protein turnover, tissue metabolism, stress, digestibility, heat increment, fermentation, physical activity, body composition, and feeding patterns (Richardson and Herd, 2004). Of these mechanisms, distinctive differences in feeding behavior patterns have been consistently observed in cattle with divergent RFI phenotypes, such that low-RFI animals have fewer bunk visits per day (Nkrumah et al., 2006; Alende et al., 2016), lower daily feeding durations (Nkrumah et al., 2006; Gomes et al., 2013) and consume DM at slower rates (Lancaster et al., 2009b; Kelly et al., 2010a) compared to high-RFI animals. While previous studies have primarily focused on the frequency and duration of bunk visit (BV) or meal events (Cantalapiedra-Hijar et al., 2018), research suggests a link between day-to-day fluctuations in feed intake and gain to feed ratios of livestock (Galyean et al., 1992; Stock et al., 1995). Accordingly, implications exist in evaluating both the daily feeding patterns and the day-to-day variations of such patterns in cattle as they may serve as useful bio-markers for RFI, especially given that feeding behavior traits were found to be highly repeatable (Gibb et al., 1998; Kelly et al., 2010b), and moderately heritable (Nkrumah et al., 2007). Furthermore, recent advancements in electronic RFID systems for monitoring feeding behavior in cattle may provide opportunity for accurate determinations of individual-animal feeding behavior in both research and commercial settings, further indicating feeding behavior traits as potential bio-markers for feed efficiency. However, inconsistencies have been reported in regards to which specific feeding behavior traits differ across low- and high- RFI animals, warranting further investigation into the associations between individual feeding behavior traits and RFI.

Historically, multiple linear regression (**MLR**) methods have been used to quantify the associations between feeding behavior traits and RFI, with feeding behavior traits accounting for 13 to 44% of the variation in RFI (Lancaster et al., 2009b; Kayser and Hill, 2013; Miller, 2016). However, MLR does not account for collinearity amongst independent variables, such as observed between feeding behavior traits. Thus, MLR models may not be the most effective technique for identifying associations between highly-correlated feeding behavior traits and RFI. Alternatively, partial least squares regression (**PLSR**) can be used when ill-conditioned linear regression models arise from there being many, highly-correlated independent variables (Chun and Keles, 2010).

Partial least squares regression procedures have been used to identify relationships between feeding behavior and RFI in dairy cattle (Fischer et al., 2018), social status and boldness in zebra fish (Dahlbom et al., 2011) and caffeine consumption and impulsive behavior in humans (Grant and Chamberlain, 2018). In each of these behavioral studies, PLSR analysis was found to be adequate in identifying and selecting behaviors that were predictive of the desired dependent variable, despite moderate to high correlations present amongst behavior traits. Furthermore, Fischer et al. (2018) used PLSR analysis to identify biological determinants of feed efficiency in lactating Holstein cows and found that activity, feeding behavior, and unidentified activity explaining 27, 21, and 11% of the variation in residual energy intake, respectively.

The objective of this study was to evaluate the use of PLSR models to quantify the between-animal variation in RFI accounted for by performance, feeding behavior, and ultrasound traits of composite Angus steers consuming a high-grain feedlot diet.

Material and methods

All animal care and use procedures were in accordance with the guidelines for use of Animals in Agricultural Teaching and Research as approved by the Texas A&M University Institutional Animal Care and Use Committee.

Experimental animals and design

Data collected from 3 trials utilizing 498 composite Angus steers were used for this study (n = 169 trial 1, n = 165 trial 2, n = 164 trial 3). For each trial, steers (initial BW = 309.8 ± 57.7 kg; initial age = 289.1 ± 15.9 d) were blocked by BW, randomly assigned to 1 of 2 pens equipped with 10 electronic feed bunks (GrowSafe Systems LTD., Airdrie, AB, Canada) and adapted to a high-grain feedlot diet (Table 2.1) for 28 d. Following the adaptation period, feed intake, performance, and feeding behavior traits were measured for 70, 70, and 77 d, respectively.

Data collection

For each trial, BW was measured at 14-d intervals and hip height and ultrasound measurements of 12th rib-fat (**BF**) depth, LM area, and intramuscular fat percentage (**IMF**) were collected on days 0 and 70. Ultrasound measurements were collected by a certified technician using an Aloka 500-V instrument with a 17-cm, 3.5-MHz transducer

(Corometrics Medical Systems Inc., Wallingford, CT). Collected images were sent to the Centralized Ultrasound Processing laboratory (Ames, IA) for analysis.

Diet samples were collected weekly, composited by weight at the end of each trial, and sent to Cumberland Valley Analytical Services Inc. (Hagerstown, MD) for chemical analysis.

Computation of traits

Individual animal feed intake was computed using a subroutine of the GrowSafe 4000E software (Process feed intakes) as described by Parsons et al. (2019). For each trial, data was deleted for a pen when the assigned feed disappearance (**AFD**) of an individual bunk in a pen was below 90% or the average AFD of the pen was less than 95%. When data was deleted due to system failure, daily intake values were estimated by linear regression of DMI on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC).

Linear regression of serial BW data on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC) was used to determine mid-test $BW^{0.75}$ and ADG. Residual feed intake was computed as the difference between actual and expected DMI from the linear regression of DMI on mid-test $BW^{0.75}$ and ADG as described by Koch et al. (1963). Trial was included as a fixed effect in this model, with mid-test $BW^{0.75}$ and ADG accounting for 43% of the variation in DMI. Similarly, residual gain (**RG**) was computed within trial as the residual from the linear regression of ADG on mean DMI and mid-test $BW^{0.75}$ (Koch et al., 1963). Within trial, steers were ranked by RFI and classified into one of three RFI phenotypic groups; low (< 0.5 SD), medium (± 0.5 SD) or high (> 0.5 SD).

Feeding behavior traits were computed based on the frequency and duration of bunk visit (**BV**) and meal events as described by Parsons et al. (2019). Bunk visit events commenced when an animals' electronic identification (**EID**) tag was detected by a feed bunk and ended when the duration of the time between the last 2 consecutive EID readings exceeded 100-s, the EID tag was detected in another feed bunk, or the EID of another animal was detected at the same feed bunk (Mendes et al., 2011). Bunk visit frequency and duration were defined as the number and the sum of duration of BV events recorded during a 24-h period, regardless of whether feed was consumed, respectively. The interval between BV events was defined as the non-feeding interval (**NFI**), with maximum NFI being defined as the longest NFI during a 24-h period. Head down (**HD**) duration was computed as the sum of EID tag readings detected each day, multiplied by the scan rate of the GrowSafe system, which was 1.0 reading per second (Jackson et al., 2016). Time to bunk (**TTB**) was computed as the interval between feed delivery and each animal's first BV event each day.

Meals were defined as the clusters of BV events that are differentiated from the next meal by a nonfeeding interval that is longer compared with the nonfeeding intervals within a meal (Bailey et al., 2012). The longest nonfeeding interval considered to be a part of a meal is defined as the meal criterion. Meal criterion was estimated by fitting a 2-pool, Gaussian-Weibull bimodal probability density function to the $\log_{10}$-transformed interval lengths between BV events for each animal using the Meal Criterion Calculation

Software (MCC; ver. 1.7.6836.33854; http://nutritionmodels.tamu.edu). Meal criterion was defined as the intersection of the Gaussian-Weibull probability density functions (Bailey et al., 2012). Meal criterion was used to cluster bunk visit events into meals, with meal frequency, length, and duration being defined as the number of meal events, average meal event length, and sum of length of meal events recorded each day, respectively (Miller, 2016).

Day-to-day variation of feeding behavior traits were calculated as the SD of the residuals of actual vs. predicted values based on linear regression of feeding behavior traits on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC). Day-to-day variation was calculated for BV frequency and duration, HD duration, maximum NFI, TTB, meal frequency, meal duration, and meal length. Additionally, 3 ratio traits were computed; BV frequency per meal event, HD duration per meal event, and HD duration per BV event.

Overall, 19 feeding behavior traits were evaluated, including frequency and duration of BV and meal events, HD duration, meal length, maximum non-feeding interval, TTB, corresponding day-to-day variation (SD) of these traits, and ratios of HD duration per BV duration, HD duration per meal duration, and BV events per meal event.

Statistical Analysis

To evaluate the effect of RFI classification on performance, feed efficiency, ultrasound, and feeding behavior traits, a mixed model (JMP; SAS Inst. Inc., Cary, NC) was used that included the fixed effect of RFI classification, and the random effect of trial. Tukey-Kramer test was used to evaluate differences among treatment means. To generate phenotypic correlation coefficients, performance, feed efficiency, and feeding behavior traits were adjusted for the random effect of trial, then used in the multivariate platform of JMP (SAS Inst. Inc., Cary, NC) to obtain phenotypic correlations.

Partial least squares regression was used to quantify the variation in RFI and DMI explained by performance, feeding behavior and ultra sound traits in JMP (SAS Inst. Inc., Cary, NC). For each model, the optimal number of components were determined by minimizing the root mean squared error of prediction (RMSEP) using the *k*-fold cross-validation procedure. This cross-validation technique involves the partitioning of observations into *k* subsets, which will be used iteratively as validation sets for models developed using the remaining observations. All potential independent variables were included in the PLSR models, with variable of importance in projection (**VIP**) scores used to identify independent variables that were most influential in explaining individual-animal variation in RFI or DMI.

For model development, feeding behavior traits were divided up into two categories: daily feeding behavior traits (**Daily-FB**), which included BV, meal, and intensity traits, and day-to-day variation traits **(Var-FB**), which included the day-to-day variation of BV, meal traits, and intensity traits. Ultrasound traits included in the models were initial and final ultrasound measurements of back fat depth, intramuscular fat, and LM area. Three models were developed for RFI: 1) included Daily-FB traits as independent variables; 2) included Daily-FB and Var-FB traits as independent variables; and 3) included Daily-FB, Var-FB, and ultrasound traits as independent variables.

Additional models were developed to predict DMI based on performance, feeding behavior, and ultrasound traits. The first of these models was used as the base model from which to compare the R^2 and root mean square error (**RMSE**) of the remaining models, and included ADG and mid-test $BW^{0.75}$ as independent variables (**Base model**). Three additional models were developed for DMI: 1) Base model plus Daily-FB traits; 2) Base model plus Daily-FB and Var-FB traits; and 3) Base model plus Daily-FB, Var-FB, and ultrasound traits.

For each of the PLSR models, the coefficient of determination for cross-validation ($\mathbf{R^2_{cv}}$), RMSE, Spearman's rank correlations, and VIP scores were used to evaluate the relationships between the independent and dependent variables.

Results and discussion

Effects of RFI on performance, efficiency, and ultrasound traits

Effects of RFI on performance, efficiency, and ultrasound traits in steers are presented in Table 2.2. As expected, low-RFI animals consumed 16.4% less feed and had 17.1% higher G:F than their high-RFI counterparts, with no differences in initial BW, ADG, or initial hip height. These results agree with other studies that reported 10 to 20% reductions in feed consumption of low-RFI cattle compared to their high-RFI counterparts (Basarab et al., 2003; Lancaster et al., 2009b; Bourgon et al., 2017; Baldassini et al., 2018).

Final intramuscular fat ($P = 0.05$) and initial and final BF depth ($P < 0.05$) were reduced in low-RFI steers compared to their high-RFI counterparts, which is consistent with previous studies that reported that body fatness was positively correlated with RFI (Richardson, 2000; Arthur et al., 2003; Basarab et al., 2003; Lancaster et al., 2009b; Shaffer et al., 2011). However, some studies have found no correlation between RFI and fat proportion (Cruz et al., 2010; Fitzsimons et al., 2014; Perkins et al., 2014). In this study, ultrasound measurements of initial IMF and initial and final LM area were not different ($P > 0.10$) across divergent RFI phenotypes, which is in agreement with previous studies (Nkrumah et al., 2004; Schenkel et al., 2004).

Effects of RFI on feeding behavior patterns

The effects of RFI classification on feeding behavior traits in composite Angus steers are presented in Table 2.3. Low-RFI animals had 18% fewer ($P < 0.001$) BV events and spent 27% less ($P < 0.001$) time at the bunk each day compared to high-RFI animals. Similar results were reported by Durunna et al. (2011), as low-RFI steers had fewer BV events and reduced BV feeding durations each day while consuming a grower and a finisher diet. Further, Golden et al. (2008) evaluated feeding behavior patterns of steers with divergent RFI phenotypes and found an 18 to 40% increase in the BV frequency of high-RFI steers consuming feedlot diets. In addition to BV frequency and duration, distinctive differences were also observed in the BV eating rates of steers, as low-RFI animals consumed feed 6% faster (g/min) than high-RFI animals in the current study. In contrast, several studies have reported no differences in the BV eating rate of steers consuming finisher diets (Golden et al., 2008; Durunna et al., 2011).

The rate of ingestion and duration of feeding are associated with the energetic cost of eating in cattle (Adam et al., 1984). During ingestion, heat production associated with eating and ruminating account for up to one-third of the total ME provided by low-quality roughages in cattle, with the rate of ingestion and duration of feeding accounting for the greatest proportion of heat produced during ingestion (Susenbeth et al., 1998). Differences in heat increment associated with observed variations in feeding behavior patterns may therefore, represent a mechanisms that contributes to between-animal differences in RFI. Specifically, lower daily feeding durations of low-RFI cattle would reduce the heat increment associated with ingestion of food, favorably impacting their feed efficiency compared to high-RFI animals. Further, low-RFI animals may have reduced energetic expenditures associated with physical activity as reduced daily feeding durations and BV events may imply that low-RFI animals spend less time standing or walking compared to their high-RFI counterparts. Although physical activity was not recorded in the current study, physical activity has been found to be positively correlated with RFI in ruminant (Herd et al., 2004) and non-ruminant animals (Luiting et al., 1991; Bunger et al., 1998). The associations between BV frequency and RFI may also be related to energetic expenditures, given that time spent standing is correlated with total energy expenditure in beef cattle (Susenbeth et al., 1998).

Individual-animal meal criterion were used in this study to cluster BV events into meal events to determine daily frequency and duration of meal event, as well as the mean length and size of meal events. Meal traits were evaluated in addition to BV traits as meal events have been identified as a more biologically relevant trait to examine feeding behavior patterns as they are less subject to social hierarchy, bunk competition, or environmental changes (Bailey, 2011). Thus, meal events may be more representative of individual-animal differences in appetite or satiety mechanisms than BV events (Tolkamp et al., 1999). Individual-animal meal criterion were longer ($P < 0.05$) for low-RFI steers than high-RFI steers. Thus, low-RFI steers had 11% fewer ($P < 0.05$) meal events each day that were 9% shorter ($P < 0.05$) in length compared to high-RFI steers. Additionally, low-RFI animals had lower ($P < 0.05$) daily meal durations and consumed 12% less ($P < 0.05$) feed during each meal compared to their high-RFI counterparts. Differences ($P > 0.05$) were not observed between the meal eating rate of low- and high-RFI steers, although low-RFI steers did consume feed at a slower ($P < 0.05$) rate than medium-RFI steers. In previous studies, BV events were clustered into meal events using an average meal criterion of 5 min for all animals (Nkrumah et al., 2007; Lancaster et al., 2009; Basarab et al., 2011; Kayser and Hill, 2013). Although the use of a static meal criterion value may be more useful for evaluating differences in appetite and satiety mechanisms than BV events, the use of individually-derived meal criterion is advantageous as it more fully captures individual animal differences.

Despite differences in methods used to define meal events, previous studies have also observed a reduction in the frequency and duration of meal events in low-RFI vs. high-RFI bulls (Lancaster et al., 2009b) and steers (Nkrumah et al., 2007) consuming feedlot diets. However, in growing heifers consuming a barley silage diet, no differences were observed in the meal duration between animals with divergent RFI phenotypes, despite low-RFI heifers having fewer meal events each day (Basarab et al., 2011).

Furthermore, in growing Angus and Hereford bulls consuming a grower diet, no differences were observed in meal frequency of animals with divergent RFI phenotypes (Kayser and Hill, 2013). Given the proposed associations between meal traits and appetite and satiety mechanisms, it is likely that differences in feedback control mechanisms may have affected the associations between meal frequency and duration and RFI. In these studies, between-animal variations in meal traits may have been limited when feedback controls or appetite were regulated by physical factors, such as gut fill or distension, which limit intake of high roughage diets (Forbes, 2003). Alternatively, when animals were consuming high-grain diets, greater differences were observed in meal patterns amongst animals with divergent RFI. These findings suggest that between-animal variation in chemostatic mechanisms may play a more important role than physical mechanisms related to gut fill in affecting efficiency of feed utilization.

Type of diet does not appear to affect the associations between meal size and RFI, as low-RFI steers in the current study consumed less feed per meal compared to high-RFI steers, which agrees with results reported by Kayser and Hill (2013) for cattle consuming grower diets. For meal eating rate, no differences ($P > 0.10$) were found between steers with divergent RFI phenotypes in the current study. These findings agree with results reported by Lancaster et al. (2009b) for Angus bulls, but disagree with those reported by Kayser and Hill (2013) as they found slower meal eating rates in high-RFI bulls compared to the low-RFI bulls in their study.

Compared to high-RFI steers, low-RFI steers took 5.5 min longer (*P* < 0.01) to approach the feed bunk following feed delivery. Few studies have evaluated the associations between TTB and feed efficiency, but in situations where animals must compete for feed, latency of an animal to a feed bunk has been identified as a social dominance trait. In studies that have used electronic feed bunks to measure individual-animal intake, TTB may provide information regarding an animals' social hierarchy rank, which affects an animal's access to feed and subsequent feeding behavior patterns (McPhee et al., 1964; Haskell et al., 2019). Haskell et al. (2019) found that more dominant finishing cattle had increased DMI and ADG compared to less dominant cattle, however, no correlations were observed between dominance and RFI. In the current study, although dominance was not directly evaluated, negative correlations were observed between TTB and DMI, ADG, and RFI (r = -0.17, -0.18, and -0.16, respectively; *P* < 0.05). Although dominance was not directly evaluated in this study, the reduced TTB of high-RFI compared to low-RFI steers appears to have influenced DMI, indicating that high-RFI steers had priority access to feed. If low-RFI steers had lower social dominance ranks compared to high-RFI steers, they may have avoided approaching the feed bunk when dominant animals were present, explaining their reduced TTB. However, while reduced levels of intake could favorably impact feed efficiency (Staples et al., 1984), reduced DMI of less dominant animals does not alone explain variation in RFI as Haskell et al. (2019) found a negative association between dominance and DMI, but not RFI. Instead, associations between TTB and RFI may be related to differences in the energetic cost of physical activity, as a negative correlation (r = -0.57; P < 0.05) was observed between TTB and BV frequency. Although animals had access to feed at all times, increased displacement of cattle from feeders has been observed following periods of peak intake, such as would be expected following feed delivery (Tolkamp et al., 1999; Haskell et al., 2019).

Therefore, associations between TTB and RFI may result from high-RFI animals having reduced TTB or increased social hierarchy ranks compared to low-RFI animals, and subsequent increased physical activity associated with displacing other animals or being displaced from a feed bunk. However, in the study by Haskell et al. (2019), BV frequency was not affected by dominance, potentially a function of reduced competition (2.5 vs. ~8 animals per feed bin), which may explain the lack of an observed association between dominance and RFI. However, further research is necessary to elucidate the mechanism contributing to variations in TTB.

In evaluating intensity traits associated with feeding behavior patterns, low-RFI animals had 33% lower ($P < 0.05$) HD durations, and reduced ($P < 0.05$) ratios of HD duration per BV duration, HD duration per meal duration, and BV duration per meal event compared to high-RFI steers. Similar reductions in HD durations have been observed in previous studies, with low-RFI animals having 15 to 40% lower HD durations compared to their high-RFI counterparts (Nkrumah et al., 2007; Lancaster et al., 2009b; Durunna et al., 2011; Kayser and Hill, 2013). Further, Kayser and Hill (2013) reported a 32% reduction in HD duration per meal, which agrees with the findings in the current study. The correlation between HD duration and RFI (r = 0.56; $P < 0.05$) was very similar to that observed between BV duration and RFI (r = 0.55; $P < 0.05$), indicating that both feeding behavior traits may account for variation in daily energetic expenditures associated with time spent eating.

Effects of RFI on day-to-day variation of DMI and feeding behavior patterns

Compared to low-RFI steers, high-RFI animals exhibited more ($P < 0.05$) day-to-day variation in DMI. These results are the first to report that day-to-day variation in DMI is affected by RFI. It is unclear whether the increased day-to-day variation of DMI observed for high-RFI cattle compared to low-RFI cattle is an inherent behavior that impacts digestive efficiency, or if the variation is driven by differences in the digestive efficiency or rumen environment between animals with divergent RFI. Stock et al. (1995) reported that day-to-day variation in DMI was negatively correlated with G:F ratio in cattle consuming 100% concentrate diets, but not in cattle consuming 92.5% concentrate diets. In contrast, daily variation in DMI was positively correlated to G:F in cattle fed grower and finisher diets (Schwartzkopf-Genswein et al., 2011). When finishing cattle were exposed to deliberate fluctuations in daily intake of up to 1.8 kg/d, no differences were found in the performance between individual-animals compared to cattle receiving a consistent ad-libitum diet (Cooper et al., 1999). In pen-based studies, Soto-Navarro et al. (2000) observed a 6% reduction in G:F of cattle exposed to daily fluctuations in feed intake during the finishing period when cattle were fed ad-libitum.

Generally, impaired performance of cattle subjected to daily intake fluctuations has been attributed to an increased occurrence of subclinical acidosis in cattle (Galyean et al., 1992; Stock et al., 1995; Soto-Navarro et al., 2000). This theory has remained prevalent as nutritionist and feedlot managers commonly attribute metabolic disturbances such as subclinical acidosis to increased daily intake variation (Gibb and McAllister, 1999; Soto-Navarro et al., 2000; Pritchard and Bruns, 2003; Schwartzkopf-Genswein et al., 2003). However, as discussed above, negative effects of daily feed intake fluctuations have not always been observed (Cooper et al., 1999; Schwartzkopf-Genswein et al., 2011). Further, the lack of ruminal pH data available in previous studies makes it difficult to evaluate whether the increased day-to-day variation in DMI is attributed to increased metabolic disorders in cattle (Gibb and McAllister, 1999) or whether increased day-today variation in DMI may predispose cattle to metabolic disorders (Galyean et al., 1992).

Given that cattle generally reduce their intake when pH drops below 5.6 (Cooper et al., 1997), it is unlikely that the increased day-to-day variation of DMI observed for high-RFI animals in the current study attributed to an increased incidence of subacute acidosis, or that an increased incidence of subacute acidosis caused an increase in day-to-day variation of DMI, as high-RFI animals consumed more DMI than low-RFI animals in this study. However, Cooper et al. (1997) observed a tendency towards higher intakes and increased area below a pH of 5.6 in cattle consuming a control diet compared to a diet containing monensin. Nonetheless, in a recent study, low-RFI cattle actually spent more time ($P < 0.05$) in an acidotic state (ruminal pH < 5.6), and had consistently lower ruminal pH compared to high-RFI cattle (Lam et al., 2018). Although this study did not evaluate the day-to-day variation in DMI of these cattle, the findings do not support the idea that high-RFI animals have increased day-to-day variation in

DMI and subsequent reduced efficiencies based on increased incidences of subclinical acidosis.

Alternatively, reduced day-to-day variation observed for low-RFI animals in the current study may have impacted digestibility. Following the introduction of monensin into the diet, Cooper et al. (1997) attributed an observed reduction in daily intake variation and increased feed efficiency to improved digestibility along with favorable changes in feeding behavior. Monensin is an ionophore that has been shown to improve F:G, as a result of reduced DMI, reduced methane production, and reduced fecal energy losses (Wedegaertner and Johnson, 1983). In Angus steers, monensin reduced feed intake and eating rate (Baile et al., 1979), and additional studies have indicated a stabilization in day-to-day variation of feed intake following monensin supplementation (Soto-Navarro et al., 2000; Erickson et al., 2003; Millen et al., 2015). Thus, one can speculate that the reduction in daily feed intake variation observed in low-RFI steers may have been associated with improved digestibility.

Reduced day-to-day variation observed in low-RFI animals may also be a result of altered appetite signaling mechanisms. This hypothesis stems from research that has identified differences in the expression of several hypothalamic and adipose-specific genes known to regulate appetite, and subsequent feeding behavior (Perkins et al., 2014). Specifically, the expression of orexigenic genes neuropeptite-Y and relaxin-3 were decreased, while the expression of anorexigenic gene and pro-opiomelanocortin were elevated in the arcuate nucleus of low-RFI compared to high-RFI steers. While this study did not evaluate the associations of these genes with day-to-day variation in DMI or feeding behavior patterns, they may also be responsible for the observed variations in daily feeding patterns amongst animals with divergent RFI. While yet proven, it is reasonable to speculate that such alterations to appetite controlling mechanisms would favorably impact digestibility and rumen fermentation given their associations with RFI. However, results have been inconsistent in regards to the associations between digestibility and RFI (Cantalapiedra-Hijar et al., 2018). Further research is warranted to better understand the impact of appetite controlling mechanisms on day-to-day variations of feed intake and feeding behavior, and their impact on digestive disorders in cattle.

In addition to increased day-to-day variation of DMI, high-RFI steers exhibited increased ($P < 0.05$) day-to-day variation in feeding behavior traits including BV frequency and duration, HD duration, and meal frequency and duration. Time to bunk was the only feeding behavior trait in which low-RFI animals actually exhibited more ($P = 0.04$) day-to-day variation compared to their inefficient counterparts (53.1 vs. 48.2 min, respectively). Differences in day-to-day variation of max non-feeding interval or meal length were not observed among cattle with divergent RFI phenotypes. Overall, efficient animals in this study had reduced day-to-day variation of feeding behavior patterns. These results are supported by Haskell et al. (2019) who found a positive association between RFI and day-to-day variation in feeding durations of Luing steers, although no differences were found for Charolais-crossbred steers that had divergent RFI. Interestingly, Charolais-crossbred steers had higher dominance ranks compared to Luing steers, which may indicate a relationship between dominance and day-to-day variation of feeding behavior, suggesting that more dominant animals are less consistent in their daily feeding patterns. Based on intensity traits evaluated in the current study, high-RFI steers appeared to be more dominant than low-RFI steers, further indicating a potential relationship between dominance and day-to-day variation of feeding behavior patterns. However, despite results from the current study, associations between feed efficiency and day-to-day variation of feed intake and feeding behavior patterns have yet to be fully explored. Further research is needed to reveal the mechanisms contributing to individual-animal variations in daily feeding patterns.

Results from this study demonstrate that distinctive differences exist in the feeding behavior patterns between cattle with divergent phenotypes for RFI. More specifically, low-RFI animals visited the bunk fewer times each day, had lower daily feeding durations, and less day-to-day variance in feeding behavior patterns.

Partial least squares regression to quantify associations between feeding behavior and RFI

Pearson correlations between feeding behavior traits in this study are presented in Table 2.4. As expected, numerous feeding behavior traits were highly correlated amongst each other. Due to the high degree of collinearity among these feeding behavior traits, models for this study were developed using PLSR, as MLR does no account for collinearity amongst independent variables

Cross-validation results of PLSR models are presented in Table 2.5. Partial least squares regression of RFI on Daily-FB traits resulted in RMSE and R^2_{cv} values of 0.39 and 0.42, respectively. Inclusion of Var-FB traits into the model increased R^2_{cv} from

0.42 to 0.47, accounting for an additional 5% of the variation in individual-animal RFI. Based on these results, both feeding behavior patterns and the day-to-day variation of such feeding behavior patterns are useful in accounting for variation in individual-animal RFI.

When ultrasound traits were included in the RFI model with Daily-FB and Var-FB traits as independent-variables, the model accounted for an additional 5% (0.47 vs. 0.52) of the variation in individual-animal RFI with no impact on RMSE (0.39 vs. 0.40, respectively). Fischer et al. (2018) used Medria Axel loggers (Medria) to measure feeding behavior patterns in dairy cows using 25 feeding behavior variables which described each of the 24 h in a day and the total daily duration. In their study, feeding behavior traits accounted for 21.3% of the variation in residual energy intake, which is lower than in the current study. However, given the difference in methods used to quantify feeding behavior traits, it is difficult to compare the results across these studies.

The Spearman’s rank correlation between observed and predicted RFI was 0.65 for the regression of RFI on Daily-FB traits alone, 0.68 when Daily-FB and Var-FB traits were included in the model, and 0.72 when initial and final BF, LM area, and IMF were added to the PLSR model. Variable of importance in projection scores were used to access an individual traits influence on the dependent variable and are presented in Table 2.6. Of the feeding behavior traits, HD duration and BV duration had the highest VIP scores, indicating that these traits significantly influenced individual-animal variation in RFI. These results agree with current literature as numerous studies have found significant correlations between HD and BV durations and RFI (Nkrumah et al., 2007;

Lancaster et al., 2009a; Durunna et al., 2011; Kayser and Hill, 2013). In total, 10 of the 19 feeding behavior traits included in the final PLSR model for RFI had VIP scores greater than 0.80. Traits with VIP scores greater than 0.80 are considered influential based on criterion proposed by Wold (1966), indicating that each of these traits contributed to the variation observed in RFI. When ultrasound traits were added to the model, both final BF depth and IMF had VIP scores greater than 0.80. Fat thickness has repeatedly been shown to correlate with RFI (Lancaster et al., 2009b; Shaffer et al., 2011; Hafla et al., 2013), so these results only further indicate the existence of associations between fatness and RFI.

Partial least squares regression of DMI on ADG and mid-test $BW^{0.75}$ resulted in RMSE and R^2_{cv} values of 0.81 and 0.42 (Table 2.5), which were similar to results obtained by multiple linear regression (RMSE = 0.81; $R^2 = 0.42$). The variation in DMI accounted for by ADG and mid-test $BW^{0.75}$ in this study was less than in previous studies (Arthur et al., 2003; Lancaster et al., 2009b; Hafla et al., 2013) that reported R^2 ranging from 0.61 to 0.80. However, when Daily-FB traits were added to the base model, R^2_{cv} increased from 0.42 to 0.64, respectively. Further, when Var-FB traits were added to the base model with Daily-FB traits, R^2_{cv} increased an additional 3% (0.64 vs. 0.67). Overall, feeding behavior traits accounted for an additional 25% (0.42 vs. 0.67) of the variation in DMI, unaccounted for by ADG and mid-test $BW^{0.75}$. These results are similar to standard regression values reported by Kayser and Hill (2013) as they found an 18% and 35% increase in model R^2 for Angus and Hereford bulls when HD duration was added to the base model (MBW and ADG) for RFI, respectively. Additional studies that used MLR models found daily BV events to account for 20% (Kelly et al., 2010a) and daily BV frequency and duration to account for 44% (de Haer et al., 1993) and 35% (Lancaster et al., 2009b) of the variation in DMI of growing heifers, pigs and growing bulls, respectively.

When ultrasound traits were included in the PLSR model for DMI, R^2_{cv} increased from 0.67 to 0.70. These results are similar to other studies (Arthur et al., 2003; Basarab et al., 2003; Lancaster et al., 2009b) that have reported that differences in carcass-fat traits accounted for an additional 3 to 4% of the variation in DMI using MLR models.

The traits with the highest VIP scores for all PLSR models deriving expected DMI were mid-test $BW^{0.75}$ and ADG. Consistent with results from the PLSR models for RFI, BV and HD durations were the most influential feeding behavior traits and final BF was the most influential ultrasound trait in accounting for between-animal variation in DMI.

Based on the distinctive differences observed in feeding behavior patterns of animals with divergent RFI phenotypes, feeding behavior traits may be useful biomarkers in identifying feed efficient animals. Previous research has evaluated correlations between feeding behavior traits and RFI with a significant amount of data indicating the existence of strong associations between feeding behavior patterns and RFI (Nkrumah et al., 2007; Lancaster et al., 2009b; Kelly et al., 2010a; Kayser and Hill, 2013). Furthermore, researchers have used MLR models to quantify the associations between feeding behavior traits and RFI, with feeding behavior traits accounting for 13 to 44% units additional variation in RFI (Lancaster et al., 2009b; Kayser and Hill, 2013;

Miller, 2016). However, caution must be taken when using MLR as it does not account for collinearity that may exist amongst independent variables. Based on the Pearson correlation values reported for this study (Table 2.4), it is evident that many feeding behavior traits are weakly to highly correlated amongst each other. Thus, PLSR is a more appropriate method as it uses independent and dependent variables to construct new latent variables that are uncorrelated to each other, and fewer in number than the independent variables (Garthwaite, 1994).

Overall, feeding behavior patterns of cattle in the current study accounted for 47% of the variation in RFI, and 25% of the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. Differences in energetic cost of eating, chewing, and ruminating, as well as physical activity associated with feeding behavior patterns may have been associated with the observed variation in RFI. Specifically, high-RFI animals may have had increased energetic costs due to increased BV frequency and duration. This idea is supported as energy expenditures associated with eating have been shown to be strongly related to time spent eating (Susenbeth et al., 1998). Additionally, Susenbeth et al. (1998) found a positive correlation between time spent standing and total energy expenditure. Although activity data was not measured in this study, increased BV frequency and duration of high-RFI animals may be related to increased activity as positive correlations between physical activity and RFI have been reported in ruminant (Herd et al., 2004) and non-ruminant animals (Luiting et al., 1991; Bunger et al., 1998). However, Hafla et al. (2013) found no significant differences in physical activity of pregnant females despite differences in BV duration across animals with divergent RFI.

The observed associations between feeding behavior patterns and DMI in the current study are reasonable as feeding behavior is determined by the integration of central and peripheral signals in brain feeding centers, associated with hunger or satiety signals (Allen, 2014). However, meal traits are generally believed to be more representative of individual-animal satiety mechanisms than BV traits (Bailey, 2011), although they were less influential in accounting for individual-animal variation in DMI in the current study.

In the PLSR models, day-to-day variation of BV frequency and duration, meal duration, and HD duration were considered to be influential for the RFI model (VIP > 0.80), while only the day-to-day variation of HD duration was found to be influential for the DMI model. Although the associations between daily variation of feeding behavior and RFI or DMI are not well understood, day-to-day variation appears to be associated with RFI and DMI. However, as previously discussed, further research is needed to evaluate the effects of daily feeding variations on diet digestibility, rumen parameters, hormonal signaling, and appetite regulation to better understand how these variations affect RFI or DMI.

Conclusion

This study provides further evidence that strong associations exist between feeding behavior patterns and feed efficiency classification in cattle. Specifically, efficient animals visited the bunk fewer times each day, spent less time consuming feed, and had reduced day-to-day variation in DMI and feeding behavior patterns. These distinct differences accounted for 47% of the variation in RFI and explained 25% of the variation in DMI, unaccounted for by mid-test $BW^{0.75}$ and ADG. Daily feeding behavior patterns and the day-to-day variation of such patterns may serve as useful bio-markers for identifying feed efficient animals, and for improving current prediction models for DMI, especially given recent advancements in electronic RFID systems capable of monitoring individual-animal feeding behavior patterns in cattle.

Further research is warranted in understanding the mechanisms involved with associations between feeding behavior and RFI, and in the development of prediction models for the identification of feed efficient animals or for the prediction of DMI using feeding behavior traits of cattle. Additionally, research is needed to better understand the impact of day-to-day variations in DMI and feeding behavior patterns on feed intake and efficiency, and to evaluate such patterns in situations where animals are not provided ad-libitum access to feed as commercial feedlots typically manage for a period of empty feed bunks, which may impact variations in DMI and feeding behavior patterns.

In conclusion, results from this study provide a framework for future research involving the use of feeding behavior traits as biomarkers for feed intake and efficiency. Future prediction models should evaluate both the inclusion of daily feeding behavior patterns and the day-to-day variation of feeding behavior patterns to account for individual-animal variations.

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Table 2. 1. Ingredient and chemical composition of experimental diets.

Item	Trial 1	Trial 2	Trial 3
Ingredient composition, % as-fed			
Dry rolled corn	72.7	73.7	74.3
Brome hay	5.5	6.0	5.4
Cottonseed meal	8.0	6.0	7.8
Cottonseed hulls	5.5	6.0	5.4
Molasses	5.0	5.0	6.0
Mineral premix[1]	2.5	2.5	2.5
Urea	0.8	0.8	0.7
Chemical analysis, % DM			
DM, %	88	90.2	88
CP, %	11	12.6	14.9
NDF, %	17.9	20.3	20.8
NEm, Mcal/kg	1.59	1.74	1.70
NEg, Mcal/kg	1.06	1.16	1.08

[1] Mineral premix contained minimum 15.5% Ca, 2800 ppm Zn, 1200 ppm Mn, 12 ppm Se, 14 ppm Co, 30 ppm I, 45.4 KIU/kg Vit-A, 2.3 KIU/kg Vit-D, 726 IU/kg Vit-E, 1200 Monensin, and 400 ppm Tylan.

Table 2. 2. Effects of residual feed intake (RFI) on performance and growth, feed efficiency, and ultrasound traits in growing steers (3 trials; 498 animals) consuming a high-grain diet.

Item	Mean	SD	Low	Medium	High	SE	*P*-value
No. animals			147	199	152		
Performance and growth traits:							
Initial age, d	289	16	290	290	290	9	0.908
Initial BW, kg	310	57	308	310	310	35	0.827
Final BW, kg	430	52	428	430	429	28	0.864
ADG, kg/d	1.71	0.26	1.72	1.72	1.70	0.11	0.570
Initial hip height, cm	122	5	122	122	121	3	0.136
DMI, kg/d	10.1	1.1	9.2^{a}	10.2^{b}	11.0^{c}	0.2	<0.001
DMI SD, kg/d	2.29	0.42	2.22^{a}	2.33^{ab}	2.31^{b}	0.08	0.033
Feed efficiency traits:							
RFI, kg/d	0.003	0.795	-0.911^{a}	0.009^{b}	0.880^{c}	0.030	<0.001
RG, g/d	1.20	175.38	59.09^{a}	9.76^{b}	-68.29^{c}	11.53	<0.001
G:F, kg/kg	0.170	0.028	0.187^{a}	0.170^{b}	0.155^{c}	0.014	<0.001
Ultrasound traits:							
Initial back fat depth, cm	0.393	0.190	0.370^{a}	0.394^{ab}	0.407^{b}	0.109	0.013
Final back fat depth, cm	0.717	0.236	0.648^{a}	0.734^{b}	0.758^{b}	0.085	<0.001
Initial intramuscular fat, %	2.85	0.61	2.91	2.82	2.82	0.26	0.198
Final intramuscular fat, %	3.15	0.70	3.05	3.18	3.21	0.23	0.054
Initial LM area, cm^2	20.4	2.8	20.4	20.6	20.2	1.3	0.348
Final LM area, cm^2	26.0	3.0	26.2	25.9	25.8	1.0	0.415

$^{a, b, c}$ Means within row with different superscripts differ ($P < 0.05$).

Table 2. 3. Effects of residual feed intake (RFI) on feeding behavior traits in growing steers (3 trials; 498 animals) consuming a high-grain diet.

Item	Mean	SD	Low	Medium	High	SE	*P*-value
No. animals			147	199	152		
Bunk visit traits:							
BV frequency, events/d	49.1	12.9	43.9^{a}	49.1^{b}	53.7^{c}	6.1	<0.001
BV duration, min/d	63.3	13.2	56.2^{a}	62.3^{b}	71.5^{c}	2.8	<0.001
Max non-feeding interval, min	720	82	723	726	709	20	0.103
BV eating rate, g/min	166	33	170^{a}	168^{a}	159^{b}	9	0.002
Meal traits:							
Meal criterion, min	12.8	7.8	14.1^{a}	11.9^{b}	12.7^{a}	2.1	0.019
Meal frequency, events/d	6.06	2.48	5.59^{a}	6.22^{b}	6.28^{b}	0.72	0.013
Meal duration, min/d	124	25	117^{a}	121^{a}	134^{b}	5	<0.001
Meal length, min/event	25.5	10.7	25.0^{ab}	24.6^{a}	27.4^{b}	2.9	0.018
Meal size, g/event	1.89	0.63	1.80^{a}	1.85^{a}	2.04^{b}	0.19	0.001
Meal eating rate, g/min	85.0	18.6	81.2^{a}	87.2^{b}	85.7^{ab}	4.6	0.006
Intensity traits:							
HD duration, min/d	45.2	14.2	36.9^{a}	44.1^{b}	54.8^{c}	0.9	<0.001
Time to bunk, min	36.3	17.5	39.5^{a}	35.8^{b}	34.0^{b}	7.7	0.002
HD duration per BV duration	0.705	0.121	0.649^{a}	0.702^{b}	0.762^{c}	0.030	<0.001
HD duration per meal duration	0.372	0.113	0.321^{a}	0.371^{b}	0.420^{c}	0.013	<0.001
BV events per meal event	8.80	2.86	8.30^{a}	8.63^{a}	9.48^{b}	0.48	<0.001
Day-to-day variation traits†:							
BV frequency SD, events/d	16.2	4.1	14.6^{a}	16.3^{b}	17.5^{c}	1.5	<0.001
BV duration SD, min/d	19.0	4.0	17.8^{a}	18.8^{b}	20.5^{c}	1.0	<0.001
Max non-feeding interval SD, min	182	27	184	182	182	9	0.752
Meal frequency SD, events/d	2.02	1.06	1.81^{a}	2.12^{b}	2.08^{b}	0.28	0.009
Meal duration SD, min/d	32.7	8.5	32.2^{a}	31.6^{a}	34.7^{b}	1.0	0.003
Meal length SD, min/event	8.68	3.83	8.49	8.51	9.12	0.80	0.222
HD duration SD, min/d	14.2	4.2	12.4^{a}	13.9^{b}	16.3^{c}	0.6	<0.001
Time to bunk SD, min	50.5	19.6	53.1^{a}	50.7^{ab}	48.2^{b}	7.1	0.040

† Day-to-day variation traits = day-to-day standard deviation for each trait.

$^{a, b, c}$ Means within row with different superscripts differ ($P < 0.05$).

Table 2. 4. Pearson correlations between feeding behavior traits in growing steers.

Item	BV duration	HD duration	Time to bunk	Max non-feeding interval	Meal frequency	Meal duration	Meal length	BV frequency SD^{1}	BV duration SD^{1}	HD duration SD^{1}	Time to bunk SD^{1}	Max non-feeding interval SD^{1}	Meal frequency SD^{1}	Meal duration SD^{1}	Meal length SD
Bunk visit (**BV**) frequency	0.01	0.19*	-0.57*	-0.34*	0.46*	0.22*	-0.20*	0.85*	0.44*	0.34*	-0.48*	-0.25*	0.42*	0.12*	-0.13*
BV duration		0.87*	0.13*	-0.20*	-0.04	0.46*	0.26*	0.07	0.52*	0.67*	0.06	0.16*	-0.06	0.27*	0.17*
Head down (**HD**) duration			0.01	-0.19*	0.07	0.37*	0.16*	0.25*	0.53*	0.80*	-0.02	0.07	0.07	0.24*	0.11*
Time to bunk				0.23*	-0.40*	-0.17*	0.23*	-0.38*	-0.09	-0.01	0.85*	0.47*	-0.30*	-0.01	0.18*
Max non-feeding interval					-0.28*	-0.13*	0.25*	-0.19*	-0.28*	-0.19*	0.21*	-0.02	-0.12*	-0.05	0.32*
Meal frequency						-0.40*	-0.78*	0.42*	0.12*	0.10*	-0.34*	-0.19*	0.94*	-0.41*	-0.65*
Meal duration							0.76*	0.17*	0.29*	0.28*	-0.15*	0.03	-0.42*	0.81*	0.69*
Meal length								-0.17*	0.06	0.09*	0.21*	0.17*	-0.72*	0.72*	0.91*
BV frequency SD^{1}									0.47*	0.43*	-0.28*	-0.10*	0.45*	0.25*	-0.08
BV duration SD^{1}										0.86*	-0.05	0.18*	0.11*	0.37*	0.07
HD duration SD^{1}											0.01	0.17*	0.12*	0.33*	0.08
Time to bunk SD^{1}												0.48*	-0.22*	0.03	0.19*
Max non-feeding interval SD^{1}													-0.12*	0.17*	0.14*
Meal frequency SD^{1}														-0.38*	-0.55*
Meal duration SD^{1}															0.71*

[1] SD = Day-to-day variation.

Table 2. 5. Summary statistics for cross-validation of partial least squares regression (PLSR) for residual feed intake (RFI) or dry matter intake (DMI) in growing steers (3 trials; 498 animals).

		Cross-validation		
Dependent and independent variables for PLSR models	N	RMSE	R^2_{cv}	Spearman's
Residual feed intake models				
RFI = Bunk visit, meal, and intensity (Daily-FB) traits	498	0.39	0.42	0.65*
RFI = Daily-FB and day-to-day variation of FB (Var-FB) traits	498	0.40	0.47	0.68*
RFI = Daly-FB, Var-FB, and ultrasound (US) traits	498	0.40	0.52	0.72*
Dry matter intake models				
DMI = ADG and mid-test $BW^{0.75}$ (Base model)	498	0.81	0.42	0.65*
DMI = Base model + Daily-FB traits	498	0.63	0.64	0.80*
DMI = Base model + Daily-FB and Var-FB traits	498	0.61	0.67	0.82*
DMI = Base model + Daily-FB, Var-FB, and US traits	498	0.58	0.70	0.84*

R^2_{cv} = coefficient of determination for cross-validation; RMSE = Root mean square error; Spearman's = Spearman's rank correlation between observed and predicted values.

Table 2. 6. Variable of importance in projections (VIP) scores for each independent-variable included in the final partial least squares regression (PLSR) models used to quantify the variation in residual feed intake (RFI) and dry matter intake (DMI).

	VIP Scores‡	
Trait	RFI	DMI
Bunk visit traits:		
BV frequency, events/d	**1.11**	**0.839**
BV duration, min/d	**1.78**	**1.41**
Max non-feeding interval, min	0.696	0.494
Meal traits:		
Meal frequency, events/d	0.552	0.601
Meal duration, min/d	**0.893**	**0.863**
Meal length, min/event	0.520	0.608
Intensity traits:		
HD duration, min/d	**1.85**	**1.40**
Time to bunk, min	0.690	0.752
HD duration per BV duration	**1.43**	**1.09**
HD duration per meal duration	**1.37**	**0.983**
BV events per meal event	0.669	0.629
Day-to-day variation traits†:		
BV frequency SD, events/d	**1.09**	0.634
BV duration SD, min/d	**1.26**	0.798
Max non-feeding interval SD, min	0.591	0.755
Meal frequency SD, events/d	0.510	0.572
Meal duration SD, min/d	**0.819**	0.719
Meal length SD, min/event	0.465	0.490
HD duration SD, min/d	**1.49**	**1.01**
Time to bunk SD, min	0.647	0.677
Ultrasound traits:		
Initial back fat depth, cm	0.722	0.758
Final back fat depth, cm	**1.10**	**1.24**
Initial intramuscular fat, %	**0.821**	0.384
Final intramuscular fat, %	0.583	0.678
Initial LM area, cm^2	0.655	**0.826**
Final LM area, cm^2	0.617	**1.07**
Performance traits:		
ADG, kg/d	---	**1.71**
Mid-test BW, $kg^{0.75}$	---	**2.20**

† Day-to-day variation traits = day-to-day standard deviation for each trait.

‡ Variable of importance in projection scores for each independent variable included in the final models for RFI and DMI.

CHAPTER III

CHARACTERIZATION OF FEEDING BEHAVIOR PATTERNS IN FINISHING CATTLE WITH DIVERGENT RESIDUAL FEED INTAKE

Introduction

The economic success of livestock operations depends on the efficient use of feed to meet the nutrient requirements of animals, as feed is the largest variable input cost in production. Accordingly, a great deal of research has investigated methods to identify and select animals for improved feed efficiency. Through this research, residual feed intake (RFI) has been identified as an ideal trait for use in selection programs as it is moderately heritable (Schenkel et al., 2004) and accounts for the variation in individual animals' feed efficiency, independent of growth and production. Efficient or low-RFI cattle have reduced feed intake (Nkrumah et al., 2004; Lancaster et al., 2009b; Hafla et al., 2013; Baldassini et al., 2018; Lam et al., 2018) and decreased methane emissions (Hegarty et al., 2007; Basarab et al., 2013) compared to their inefficient or high-RFI counterparts with no impact on growth and performance. Accordingly, a great deal of research has investigated mechanisms contributing to the variation observed in feed efficiency to identify genetic and phenotypic bio-markers for the identification of feed efficient animals.

Current literature has identified relationships between protein turnover, tissue metabolism, stress, digestibility, heat increment, fermentation, physical activity, body composition, and feeding patterns (Richardson and Herd, 2004; Nkrumah et al., 2007; Lancaster et al., 2009b; Kayser and Hill, 2013; Cantalapiedra-Hijar et al., 2018) and RFI in animals. Historically, accurate determinations of feeding behavior traits were not applicable in commercial settings, limiting their use as bio-markers for RFI. However, recent advancements in electronic RFID technology has provided opportunity for the development of accurate and large-scale systems capable of capturing variation observed in feeding behavior patterns of cattle with divergent RFI phenotypes. In general, low-RFI animals have been shown to have fewer bunk visits per day (Nkrumah et al., 2006; Nkrumah et al., 2007; Golden et al., 2008; Fitzsimons et al., 2014; Ramirez, 2014; Alende et al., 2016) and lower daily feeding durations (Nkrumah et al., 2006; Gomes et al., 2013; Hafla et al., 2013; Parsons et al., 2019) compared to high-RFI animals. These differences likely indicate a reduced daily energy expenditure of low-RFI animals, as total energy expenditure is positively associated with the energetic cost of eating and time spent standing (Susenbeth et al., 1998), both of which are lower in low-RFI cattle (Herd et al., 2004; Lancaster et al., 2009b).

More recently, a study also identified differences in the daily variation of feeding patterns amongst animals with divergent feed efficiency, such that low-RFI animals have reduced day-to-day variation in intake and feeding behavior patterns compared to high-RFI animals (Parsons et al., 2019). Although there is little in the literature regarding this phenomenon, the authors speculate that improved digestive efficiencies or reduced metabolic disturbances may contribute to the more consistent feeding patterns observed for low-RFI animals. Nonetheless, feeding behavior patterns and the day-to-day variation of such patterns may serve as useful bio-markers in identifying feed efficient animals, especially given that feeding behavior traits were found to be moderately repeatable (Gibb et al., 1998; Kelly et al., 2010b), and heritable (Nkrumah et al., 2007).

In previous studies, feeding behavior traits accounted for 13 to 44% of the variation observed in feed efficiency of cattle using multiple linear regression (Lancaster et al., 2009b; Kayser and Hill, 2013; Miller, 2016). Although these results reveal associations between feeding behavior traits and feed efficiency, multiple linear regression may not be the most effective technique for identifying associations as it does not account for the collinearity present amongst feeding behavior traits. Instead, partial least squares regression techniques should be used as it provides an alternative approach to least squares regression when ill-conditioned linear regression models arise from there being many, highly correlated independent variables (Chun and Keles, 2010).

Overall, feeding behavior traits have been shown to account for significant portions of the individual-animal variation in net feed efficiency. However, research is still needed to evaluate the associations between various feeding behavior traits and their day-to-day variation and RFI, and to evaluate the use of feeding behavior traits as bio-markers in combination with other applicable traits such as mid-test $BW^{0.75}$, ADG, or body composition measurements.

The objectives of this paper were to characterize feeding behavior patterns in steers and heifers with divergent RFI and to quantify the between-animal variation in feed efficiency accounted for by performance, feeding behavior, and ultrasound traits of these animals.

Material and methods

All animal care and use procedures were in accordance with the guidelines for use of Animals in Agricultural Teaching and Research as approved by the Texas A&M University Institutional Animal Care and Use Committee.

Experimental animals and design

Data were collected from 3 consecutive year trials utilizing 408 Brangus (n = 120), Braford (n = 115), Simbrah (n = 110), and Angus (n = 63) heifers (n = 169 year 1; n = 115 year 2; n = 124 in year 3) and 2 consecutive year trials utilizing 326 Brangus (n = 112), Simbrah (n = 95), Angus (n = 71), and Braford (n = 48) steers (n = 168 year 1; n = 158 year 2) from the Deseret Ranch in St. Cloud, FL. For each trial, heifers (initial BW = 280.8 ± 35.9 kg; initial age = 340.1 ± 35.1 d) or steers (initial BW = 290.9 ± 45.9 kg; initial age = 333.5 ± 19.1 d) were randomly assigned to 1 of 2 pens equipped with 10 electronic feed bunks, or 1 of 4 pens equipped with 4 electronic feed bunks (GrowSafe Systems LTD., Airdrie, AB, Canada). Animals were adapted to a high-grain feedlot diet consisting of approximately 73.7% dry rolled corn, 6% chopped hay, 6% cottonseed meal, 6% cottonseed hulls, 5% molasses, 2.5% premix, and 0.8% urea (ME = 3.0 Mcal/kg DM; CP = 12.6% DM) for 28 d. Following adaptation, *ad libitum* feed intake, performance, and feeding behavior traits were measured for 70 d.

Data collection

For each trial, BW was measured at 14-d intervals and hip height (HH) and ultrasound measurements of 12th rib-fat (BF) depth, LM area, and intramuscular fat percentage (IMF) were collected on d 0 and 70. Ultrasound measurements were collected by a certified technician using an Aloka 500-V instrument with a 17-cm, 3.5-MHz transducer (Corometrics Medical Systems Inc., Wallingford, CT). Collected images were sent to the Centralized Ultrasound Processing laboratory (Ames, IA) for analysis.

Diet samples were collected weekly, composited by weight at the end of each trial, and sent to Cumberland Valley Analytical Services Inc. (Hagerstown, MD) for chemical analysis.

Computation of traits

Individual animal feed intake was computed using a subroutine of the GrowSafe 4000E software (Process feed intakes) as described by Parsons et al. (2019). For each trial, data was deleted for a pen when the assigned feed disappearance (AFD) of an individual bunk in a pen was below 90% or the average AFD of the pen was less than 95%. When data was deleted due to system failure, daily intake values were determined by linear regression of DMI on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC).

Linear regression of serial BW data on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC) was used to determine mid-test metabolic $BW^{0.75}$ and ADG. Residual feed intake was computed across trials as the difference between actual and expected DMI from the linear regression of mean DMI on mid-test $BW^{0.75}$ and ADG as described by Koch et al. (1963). Trial was included as a fixed effect in this model, with mid-test $BW^{0.75}$ and ADG accounting for 63% of the variation in DMI. Similarly, residual gain (RG) was computed as the residual from the linear regression of ADG on mean DMI and mid-test $BW^{0.75}$ (Koch et al., 1963). Steers and heifers were ranked by RFI and classified into one of three RFI phenotypic groups; low (< 0.5 SD), medium (± 0.5 SD) or high (> 0.5 SD).

Feeding behavior traits were computed based on the frequency and duration of individual animal bunk visits (BV) and meal events as described by Parsons et al. (2019). Bunk visit events commenced when an animals' electronic identification (EID) tag was detected by a feed bunk and ended when the duration of the time between the last 2 consecutive EID readings exceeded 100-s, the EID tag was detected in another feed bunk, or the EID of another animal was detected at the same feed bunk (Mendes et al., 2011). Bunk visit frequency and duration were then defined as the number and the sum of duration of BV events recorded during a 24-hour period, regardless of whether feed was consumed, respectively. The interval between BV events was defined as the non-feeding interval (NFI), with maximum NFI being defined as the longest NFI during a 24-hour period. Head down (HD) duration was computed as the sum of EID tag readings detected each day, multiplied by the scan rate of the GrowSafe system, which was 1.0 reading per second (Jackson et al., 2016).

Meals were defined as the clusters of BV events that are differentiated from the next meal by a nonfeeding interval that is longer compared with the nonfeeding intervals within a meal (Bailey et al., 2012). The longest nonfeeding interval considered to be a part of a meal is defined as the meal criterion. Meal criterion was estimated by fitting a 2-pool, Gaussion-Weibull bimodal probability density function to the $\log_{10}$-transformed interval lengths between BV events for each animal using the Meal Criterion Calculation Software (MCC; ver. 1.7.6836.33854; http://nutritionmodels.tamu.edu). Meal criterion was defined as the intersection of the Gaussion-Weibull probability density functions (Bailey et al., 2012). Meal criterion was used to cluster bunk visit events into meals, with meal frequency, length, and duration being defined as the number of meal events, average meal event length, and sum of length of meal events recorded each day, respectively (Miller, 2016).

Day-to-day variation of feeding behavior traits were calculated as the SD of the residuals of actual vs. predicted values based on linear regression of feeding behavior traits on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC). Day-to-day variation was calculated for BV frequency and duration, HD duration, maximum NFI, meal frequency, meal duration, and meal length. Additionally, 3 ratio traits were computed; BV frequency per meal event, HD duration per meal event, and HD duration per BV event.

Seventeen feeding behavior traits were evaluated in this study including frequency and duration of BV and meal events, HD duration, meal length, maximum non-feeding interval, corresponding day-to-day variation (SD) of these traits, and ratios of HD duration per BV duration, HD duration per meal duration, and BV events per meal event.

Statistical Analysis

To evaluate the effect of RFI classification on performance, feed efficiency, ultrasound, and feeding behavior traits, a mixed model (JMP; SAS Inst. Inc., Cary, NC) was used by gender, that included the random effect of trial and fixed effects of RFI classification, breed, and the interaction of RFI class and breed. Tukey-Kramer test was used to evaluate the differences among treatment means.

To evaluate the repeatability of performance, feed efficiency, and feeding behavior traits, individual-animal means were computed within the first 28 d and the last 42 d of each trial. For each trait, individual-animal means were adjusted for the random effect of trial. Repeatability was then estimated on adjusted means using Pearson correlation coefficient estimates between individual traits measured during the first 28 d and the last 42 d of each trial.

Partial least squares regression (PLSR) was used to quantify the variation in RFI and DMI explained by performance, feeding behavior and ultrasound traits in JMP (SAS Inst. Inc., Cary, NC). For each model, the optimal number of components were determined by minimizing the root mean squared error of prediction (RMSEP) using the k-fold cross-validation procedure. This cross-validation technique involves the partitioning of observations into *k* subsets, which are then used iteratively as validation sets for models developed using the remaining observations. All potential independent variables were included in the PLSR models, with variable of importance in projection (VIP) scores being used to identify the biological traits that were most influential in explaining the variation in RFI.

Preliminary PLSR models were developed by breed and gender to examine whether or not the PLSR models identified similar influential traits for each group of cattle. Variable of importance in projection scores were used to compare and contrast the impact of various feeding behavior traits on RFI.

Following the preliminary analysis, PLSR models were developed across breeds and gender to quantify the associations between feeding behavior and ultrasound traits with RFI. For model development, feeding behavior traits were divided up into two categories: daily feeding behavior traits (Daily-FB), which included BV, meal, and intensity traits, and day-to-day variation traits (Var-FB), which included the day-to-day variation of BV, meal traits, and intensity traits. Initial and final ultrasound measurements were used to compute the gain in ultrasound measurements, with gain and final ultrasound measurements of back fat, intramuscular fat, and LM area being used as independent variables in PLSR models that included ultrasound traits. Three models were developed for RFI: 1) included Daily-FB traits as independent variables; 2) included Daily-FB and Var-FB traits as independent variables; and 3) included Daily-FB, Var-FB, and ultrasound traits as independent variables.

Additional models were developed to predict DMI based on performance, feeding behavior, and ultrasound traits. The first of these models was used as the base model from which to compare the R^2 and root mean square error (RMSE) of the remaining models, and included ADG and mid-test $BW^{0.75}$ as independent variables (Base model). Three additional models were developed for DMI: 1) Base model plus Daily-FB traits; 2) Base model plus Daily-FB and Var-FB traits; and 3) Base model plus Daily-FB, Var-FB, and ultrasound traits.

To evaluate the model performance using data collected during the first 28 d of each trial, PLSR models were also developed for RFI and DMI as described above using feeding behavior traits measured during the first 28 d of each trial. For these models, Daily-FB and Var-FB measured during the first 28 d, initial measurements of back fat depth, IMF, and LM area, and ADG and mid-test $BW^{0.75}$ determined using BW measurements from day 0, 14, and 28 were included as independent variables.

For each of the PLSR models, cross-validation R^2, RMSE, Spearman’s rank correlations, and variable of importance in projection (VIP) scores were used to evaluate the relationships between the independent and dependent variables.

Results and Discussion

Intake, performance, ultrasound, and feed efficiency

The effects of RFI on performance, efficiency, and ultrasound traits in heifers are presented in Table 3.1. Overall, low-RFI heifers consumed 20% less feed and had 18% higher G:F than their high-RFI counterparts. As expected, no differences were observed in initial BW or ADG due to RFI class. However, there was a RFI × breed interaction for initial BW and ADG. High-RFI Brangus heifers were heavier than low-RFI Brangus heifers at the start of the trial, and medium-RFI Simbrah heifers grew slower then low-RFI Simbrah heifers, while differences in initial BW and ADG due to RFI class were not observed in the other breeds, as expected. Further, significant breed × RFI interactions were observed for DMI in heifers, because DMI for medium-RFI Angus and Simbrah heifers did not differ from high-RFI (Angus) and low-RFI (Simbrah) heifers (Figure 3.1). As the primary objective of this study was to examine differences in performance, feed efficiency, carcass ultrasound, and feeding behavior traits in steers and heifers with divergent RFI, minimal discussion of the breed effects will be presented in this manuscript.

Effects of RFI on performance, efficiency, and ultrasound traits in steers are presented in Table 3.2. Overall, low-RFI steers consumed 18% less feed and had 22% higher G:F than their high-RFI counterparts, with no differences in initial BW or ADG. As with the heifers, there was a significant RFI × breed interaction ($P < 0.01$) for ADG, as low-RFI Brangus steers had higher ADG compared to the medium- and high-RFI Brangus steers, but RFI class did not affect ADG in the other 3 breeds (Figure 3.1).

Residual feed intake averaged 0.00 ± 0.92 kg/d for heifers and 0.03 ± 0.88 kg/d for steers. As expected, RG was higher ($P < 0.001$) for efficient heifers (0.165 kg/d) and steers (0.097 kg/d) compared to their inefficient counterparts (-0.097 and -0.125 kg/d, respectively).

Final back fat depth and gain in backfat depth were reduced ($P > 0.05$) in low-RFI heifers compared to high-RFI heifers. Several previous studies have also reported associations between backfat depth and RFI, with low-RFI animals exhibiting leaner carcasses compared to high-RFI animals (Lancaster et al., 2009b; Shaffer et al., 2011; Hafla et al., 2013). Given that fat is more energetically costly to deposit than lean tissue (Alende et al., 2016), it is logical that low-RFI animals may have increased efficiencies of nutrient use as a result of their leaner carcasses. However, some studies have found no correlation between RFI and fat proportion (Cruz et al., 2010; Fitzsimons et al., 2014; Perkins et al., 2014), which agrees with results observed for steers in the current study as no differences were observed in gain or final back fat depth between steers with divergent RFI. Gain and final measurements of intramuscular fat and LM area were not different ($P > 0.10$) between heifers or steers with divergent RFI in the current study, which agrees with previously reported data (Nkrumah et al., 2004; Schenkel et al., 2004). However, significant RFI × breed interactions ($P < 0.01$) were observed for gain and final measurements of intramuscular fat in heifers as both were higher in medium-RFI Angus heifers compared to high-RFI Angus heifers. Accordingly, medium-RFI Angus heifers deposited more intramuscular fat during the trial, which may explain why no differences were observed for DMI between medium- and high-RFI animals in the current study.

Feeding behavior patterns

The effects of RFI classification on feeding behavior traits in finishing heifers and steers are presented in Tables 3.3 and 3.4, respectively. Low-RFI heifers and steers had 13 and 21% fewer ($P < 0.001$) BV events and spent 30 and 23% less ($P < 0.001$) time at the bunk each day compared to high-RFI animals, respectively. Previous studies have reported similar results for daily BV frequency in crossbred steers consuming a grower or finisher diet (Durunna et al., 2011) and in Angus steers consuming a finisher diets (Golden et al., 2008). Additionally, low-RFI steers had reduced daily BV durations compared to high-RFI steers during the growing and finishing phase of production (Durunna et al., 2011). In the current study, BV eating rates were 19% higher ($P < 0.05$)

for low-RFI heifers and tended (*P* = 0.10) to be 8% higher for low-RFI steers compared to their high-RFI counterparts. These results are similar to those reported in the previous chapter, but differ from values reported previously in the literature as no differences were reported for feedlot steers (Golden et al., 2008; Durunna et al., 2011).

Distinctive differences observed in the daily feeding durations and BV eating rates of animals with divergent RFI phenotypes may impact the heat increment associated with eating, as the rate of ingestion and duration of feeding have been reported as key factors influencing heat production during the ingestion of food (Adam et al., 1984; Susenbeth et al., 1998). Accordingly, low-RFI animals may have a reduced heat increment and subsequent reduction in their energetic expenditures associated with eating, as a result of having lower daily feeding durations and increased BV eating rates compared to high-RFI animals. Further, variations in BV events may reveal differences in the daily physical activity level of animals, such that low-RFI animals may spend less time standing or walking compared to high-RFI animals as they have lower daily feeding durations and visit the bunk fewer times each day. Although physical activity was not measured in the current study, physical activity was found to positively correlate with RFI in ruminant (Herd et al., 2004) and non-ruminant (Luiting et al., 1991; Bunger et al., 1998) animals. Since time spent standing is correlated with total energy expenditure, this may represent another mechanism by which low-RFI animals have improved feed efficiency (Susenbeth et al., 1998).

Meal traits were evaluated in addition to BV traits as meal events have been identified as a more biologically relevant trait to examine feeding behavior patterns of cattle as they are less subject to social hierarchy, bunk competition, or environmental changes (Bailey et al., 2012). Therefore, meal events may be more representative of individual-animal differences in appetite or satiety mechanisms compared to BV events (Tolkamp et al., 1999). Previous studies that examined meal patterns in cattle with divergent RFI used a static 5- or 10-min meal criterion for all animals. Although few studies have evaluated the associations between individual-animal meal criterion values and RFI, the relevance of meal traits for identifying individual-animal differences depends on the estimation of an appropriate meal criterion for each animal (Yeates et al., 2001). While a standard 5- or 10-min meal criterion may provide an improved indication of an animals' appetite and satiety mechanism compared to BV events, as cattle have an opportunity to continue their meal event if "involuntarily" displaced from a feed bunk, the relevance of meal traits calculated in such a manor may not be as biologically relevant as those determined for individual animals (Yeates et al., 2001). Therefore, in this study, individual-animal meal criterion values were used to cluster BV events into meal events to determine frequency and length of meal events.

Individual-animal meal criterion was not different ($P > 0.05$) for steers or heifers with divergent RFI phenotypes in the current study. Therefore, no differences ($P > 0.05$) were observed in the meal frequency of low- and high-RFI animals. These findings disagree with previously published data generated using a standard 5 min meal criterion for cattle consuming a finisher diet (Nkrumah et al., 2007; Lancaster et al., 2009b) and a barley silage diet (Basarab et al., 2011), but agree with those reported for bulls consuming a grower diet (Kayser and Hill, 2013). When individual-animal meal criterion values were determined in the previous chapter, significant ($P < 0.05$) differences were found in the meal criterion and meal frequency of animals with divergent RFI phenotypes, which also disagrees with the results in the current study.

Similar to the findings in the previous chapter, low-RFI heifers and steers in the current study had ($P < 0.05$) lower daily meal durations and reduced meal size compared to their high-RFI counterparts. In agreement with these results, previous studies involving feedlot bulls (Lancaster et al., 2009b) and steers (Nkrumah et al., 2007) consuming finisher diets also reported lower daily meal durations for low-RFI animals compared to their high-RFI counterparts based on a 5 min meal criterion. Further, Kayser and Hill (2013) observed similar reductions in meal size of bulls consuming grower diets as low-RFI bulls consumed less feed during each meal compared to high-RFI bulls. However, no differences were observed between the meal durations of heifers with divergent RFI when fed a barley silage diet (Basarab et al., 2011). In regards to meal eating rate, no differences were found between heifers and steers with divergent RFI phenotypes in the current study. These results agree with those reported by Lancaster et al. (2009b) for Angus bulls, but disagree with those reported by Kayser and Hill (2013) as they reported slower meal eating rates in high-RFI bulls compared to low-RFI bulls.

In the previous chapter, a review of literature indicated that the associations between meal frequency and duration may be affected by the type of diet consumed, as differences were observed consistently for these traits in cattle consuming high-grain (Nkrumah et al., 2007; Lancaster et al., 2009b), but not high-roughage diets (Basarab et al., 2013; Kayser and Hill, 2013). Given that meal traits, being less influenced by social hierarchy, bunk competition, and environmental factors, may represent individual-animal differences in appetite or satiety signaling mechanisms (Bailey, 2011), it is likely that diet could affect such associations. However, differences in meal frequency were not observed for cattle consuming a high-grain diet in the current study, which is in contrary to this concept. Regardless differences in hormonal concentrations and expression of several hypothalamic and adipose-specific genes known to regulate appetite, and subsequent feeding behavior have been observed amongst cattle with divergent RFI phenotypes (Perkins et al., 2014; Cantalapiedra-Hijar et al., 2018). It is likely that in the current study, variations in appetite and satiety signaling mechanisms may have been responsible for the reduced daily meal duration and meal size, as well as the reduced DMI of low-RFI animals compared to high-RFI animals. Overall, associations between BV events and RFI appear to be more indicative of variations in the daily energetic expenditure of animals, while associations between meal events and RFI may reveal differences in appetite or satiety mechanisms. However, further research is needed to advance current understanding of mechanisms contributing to the variation in BV and meal events and their associations with RFI.

Compared to high-RFI animals, low-RFI animals had 37% lower HD durations. These results agree with those reported in the previous chapter for Angus steers, and with previous studies (Nkrumah et al., 2007; Lancaster et al., 2009b; Durunna et al., 2011; Kayser and Hill, 2013). Further, low-RFI animals had a 24% reduction in the ratio of HD duration per meal duration which agrees with the 32 and 33% reductions reported by Kayser and Hill (2013) for Hereford and Angus bulls, respectively. These results suggest that high-RFI steers and heifers were more assertive in their feeding behavior patterns compared to their low-RFI counterparts. Although current literature is not available, increased assertiveness of animals may impact daily energetic expenditures as more assertive animals may have increased physical activity associated with displacing other animals or being displaced from a feed bunk. In the previous chapter this was proposed as high-RFI animals approached the bunk sooner after the feed delivery and had increased BV frequency compared to low-RFI animals. These findings together support the observations that cattle are displaced from the feed bunk more frequently during periods of peak intake, such as would be expected following the feed delivery (Tolkamp et al., 1999; Haskell et al., 2019). However, TTB was not evaluated in the current study, so this theory cannot be confirmed. Instead the observed increase in HD duration of high-RFI animals compared to low-RFI animals may simply indicate an increased energetic expenditure associated with eating of high-RFI animals, similar to that proposed in regards to BV duration.

Day-to-day variation of DMI and feeding behavior patterns

High-RFI animals exhibited significantly more ($P < 0.05$) day-to-day variation in DMI than their low-RFI counterparts. Although few studies have examined the associations between day-to-day variation in DMI and RFI, these results agree with those reported in the previous chapter. Further, previous studies have reported reduced G:F of animals exhibiting greater day-to-day variation in their daily intake (Stock et al., 1995), and for cattle exposed to deliberate fluctuation in daily intake (Galyean et al., 1992; Soto-Navarro et al., 2000). Although associations between feed efficiency and daily feed intake fluctuations have not always been observed (Cooper et al., 1999; Schwartzkopf-Genswein et al., 2011), previous studies generally attribute reduced feed efficiency to increased metabolic disturbances such as subclinical acidosis (Gibb and McAllister, 1999; Soto-Navarro et al., 2000; Pritchard and Bruns, 2003; Schwartzkopf-Genswein et al., 2003). However, ruminal pH data is limited in previous studies, so it is unclear whether increased day-to-day variation in DMI may attribute to metabolic disorders in cattle (Gibb and McAllister, 1999) or if it can predispose cattle to metabolic disorders (Galyean et al., 1992).

It is unlikely that high-RFI animals had increased incidences of subacute acidosis in the current study, as high-RFI animals maintained higher levels of DMI compared to low-RFI animals. Generally, when pH drops below 5.6, cattle reduce their intakes (Cooper et al., 1997). However, ruminal pH levels were not measured so no determinations could be made. Alternatively, between-animal differences in the day-to-day variation of DMI may be associated with differences in digestibility (Cooper et al., 1997) of animals with divergent RFI phenotypes. Specifically, associations between day-to-day variation and digestibility seem likely as reduced daily intake variation and increased feed efficiency following the introduction of Monensin into the diet was attributed to improved digestibility in a study by Cooper et al. (1997). Additional studies have also reported more consistent intakes (Soto-Navarro et al., 2000; Erickson et al., 2003; Millen et al., 2015), and improved digestibility (Wedegaertner and Johnson, 1983) following Monensin supplementation. However, the associations between digestibility and day-to-day variation in DMI have not been revealed. Compared to high-RFI animals, it is unclear whether low-RFI animals have similar improvements in their digestibility as a result of having reduced day-to-day variation in DMI, or if variations in appetite or satiety mechanisms favorably impact digestibility, with more consistent feeding patterns being a result of improved digestibility.

In addition to having increased day-to-day variation in DMI, high-RFI heifers and steers also exhibited greater ($P < 0.05$) day-to-day variations of BV frequency and duration, HD duration, and meal duration compared to low-RFI animals. No differences were observed in the day-to-day variation of meal frequency ($P > 0.10$) for steers and heifers. Further, while day-to-day variation of max non-feeding interval tended to be greater ($P = 0.09$) in low-RFI heifers compared to high-RFI heifers, no differences ($P = 0.96$) were observed amongst steers with divergent feed efficiency. These results agree with the findings from the previous chapter, as low-RFI animals exhibited more consistent feeding patterns compared to high-RFI animals. Although few studies have evaluated the day-to-day variation of feeding behavior traits and their associations with RFI, Haskell et al. (2019) observed a positive association between the day-to-day variation of feeding patterns and RFI in Luing steers, but not in Charolais-crossbred steers. Their results indicate a potential relationship between dominance and day-to-day variation, as Luing steers had lower dominance ranks compared to Charolais-crossbred steers in their study. Given that high-RFI animals appeared to be more assertive in their feeding behavior patterns, and were found to have less consistent feeding patterns compared to low-RFI animals in the current study, a similar association between dominance and day-to-day variation may have been present. However, dominance was not evaluated in the current study, so no determinations can be made.

Overall, low-RFI heifers and steers visited the bunk fewer times each day, spent less time at the bunk, and had less day-to-day variation in their feeding behavior patterns compared to their high-RFI counterparts. These results support findings of previous literature where distinctive differences were observed in the feeding behavior patterns of cattle with divergent RFI. Accordingly, feeding behavior traits, and the day-to-day variation of such traits may be useful in accounting for variation in individual-animal RFI, however, further research is needed to better understand the contributing mechanisms.

Influence of breed and gender on the associations between feeding behavior traits and RFI

Four breed types (Angus, Brangus, Brahman, and Simbrah) were represented in each of the 5 trials included in this study. Thus, it was important to evaluate whether or not breed affected the associations between feeding behavior traits and RFI. There were no significant ($P > 0.05$) breed x RFI class interactions observed for any of the feeding behavior traits for heifers and steers, with the exception that the breed × RFI interaction for BV frequency tended to be significant for steers. To further examine the effect of breed on the associations between feeding behavior traits and RFI, PLSR models were developed by breed and gender to examine the relative influence each trait had on explaining the variation in RFI. Each of these RFI models included all 17 feeding behavior traits as independent variables. The VIP scores for these PLS models are presented in Table 3.5. For both steers and heifers, VIP scores of feeding behavior traits were relatively comparable across all breeds. Feeding behavior traits with the largest range in VIP scores across breeds and gender included max non-feeding interval, which ranged from 0.04 for Braford steers to 0.95 for Angus steers, and the day-to-day variation of max non-feeding interval, which ranged from 0.21 for Angus steers to 1.25 for Angus heifers. These findings were not surprising as these 2 traits typically were not significantly affected by RFI classification in steers or heifers. Based on the results from this PLSR analysis, we concluded that PLSR models did not need to account for breed effects as the VIP scores of the most influential feeding behavior traits according to PLSR were greater than 0.80 across breeds.

Similarly, PLSR models were developed across breeds by gender to determine whether or not PLSR models should be developed by gender for this study. Although the effect of gender on feeding behavior traits could not be directly examined as both genders were not represented in each study, PLSR models were developed individually by gender and across genders to evaluate influential feeding behavior traits across models. The VIP scores for each of these PLSR models are presented in Table 3.6. With the exception of max non-feeding interval, each model identified the same feeding behavior traits as being influential in explaining the variation in RFI (VIP > 0.80). Thus, it was concluded that PLSR models did not need to account for gender effects.

Partial least squares regression to quantify associations between feeding behavior and RFI

Summary statistics for cross-validation (*k*-fold) of PLSR models for RFI and DMI of finishing steers and heifers are presented in Table 3.7. The R^2_{cv} and RMSE of the PLSR regression of RFI on BV, meal, and intensity traits (Daily-FB) were 0.33 and 0.43, respectively. This R^2_{cv} is lower than that reported in the previous chapter based on PLSR regression (0.33 vs. 0.39). Likely, increased trial variation in the current study impacted the R^2_{cv} value compared to the previous chapter. When day-to-day variation of BV, meal, and intensity traits (Var-FB) were added into the model, R^2_{cv} increased from 0.33 to 0.35, accounting for an additional 2% of the variation in individual animal RFI. The additional variance accounted for by day-to-day variation traits in the currently study is lower than that reported in the previous chapter (2% vs. 5%).

When ultrasound traits were added to the PLSR model for RFI, R^2_{cv} increased from 0.35 to 0.37 representing a 2% improvement in accounted variation. These results were lower than expected, as a 5% spearman's observed in the previous chapter. The spearman's rank correlation between observed and predicted RFI was 0.58 for the regression of RFI on Daily-FB alone, 0.60 when Daily-FB and Var-FB traits were included in the model, and 0.61 when ultrasound traits were added in combination with feeding behavior traits. Overall, these results indicate that a significant amount of variation in RFI can be explained by feeding behavior, the day-to-day variation of feeding behavior, and ultrasound traits.

For this study, PLSR models were also developed to derive expected DMI as was accomplished using MLR for the computation of RFI. Partial least squares regression and MLR models gave similar results with ADG and mid-test $BW^{0.75}$ accounting for

59% of the variation in DMI. When Daily-FB traits were added to the base model for RFI, R^2_{cv} increased from 0.59 to 0.76 and RMSE decreased from 0.74 to 0.64. Therefore, Daily-FB traits accounted for an additional 17% of the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. When Var-FB traits were added to the model, R^2_{cv} increased an additional 2% (0.76 vs. 0.78), which is similar to the previous chapter where a 3% increase was observed. In the previous chapter, Daily-FB and Var-FB traits also accounted for a larger proportion of additional variance as the R^2_{cv} increased from 0.43 to 0.71, representing a 28% increase in accounted variance. Although this agrees with the findings of the PLSR models for RFI using only feeding behavior traits in each study, it is important to note that feeding behavior traits may have been more influential in the previous chapter due to the poor associations found between performance and RFI (base model $R^2_{cv} = 0.43$). Overall, results from this study are comparable to those reported for MLR as Kayser and Hill (2013) found an 18% and 35% increase in model R^2 for Angus and Hereford bulls when HD duration was added to the base model (mid-test $BW^{0.75}$ and ADG) for RFI, respectively. Additionally, studies found daily bunk visit events to account for 20% (Kelly et al., 2010a) and daily bunk visit frequency and duration to account for 44% (de Haer et al., 1993) and 35% (Lancaster et al., 2009b) of the variation in DMI of growing heifers, pigs and growing bulls, respectively.

When ultrasound traits were added to the PLSR model for DMI, no change was observed in the R^2_{cv} despite RMSE being minimally reduced (0.63 vs. 0.62). These findings were unexpected as ultrasound traits accounted for an additional 2% of the variation in DMI in the previous chapter and 3 to 4% in other studies where standard linear regression models were used (Arthur et al., 2003; Basarab et al., 2003; Lancaster et al., 2009b). However, based on VIP scores (Table 3.8), gain and final back fat, and final LM area were influential in deriving expected DMI. While it is not surprising for carcass fat traits to be identified as influential by the PLSR model, no significant differences were observed in final LM area across RFI classes in this study or in the previous chapter, so it is unexpected that LM area traits had VIP scores greater than 0.80 in both studies.

Of the feeding behavior traits, BV duration and HD duration had the most influence on individual-animal variation in RFI (Table 3.8). These findings agree with the previous chapter as BV and HD durations had the highest VIP scores across feeding behavior traits for all models developed for composite Angus steers. Furthermore, numerous studies have found significant correlations between HD and BV durations and efficiency (Nkrumah et al., 2007; Lancaster et al., 2009a; Durunna et al., 2011; Kayser and Hill, 2013), further demonstrating the significant influence each of these traits has on feed efficiency. Based on criterion proposed by Wold (1966), a total of 11 feeding behavior traits were considered to be influential in accounting for the variation in RFI as they had VIP scores greater than 0.80. Despite differences in breed and gender between the current study and that reported in the previous chapter, 10 of the same feeding behavior traits had VIP scores greater than 0.80 for both studies. Furthermore, 9 of the 17 feeding behavior traits were considered to be influential in accounting for the variation in DMI (VIP > 0.08), however, only 4 of these feeding behavior traits had VIP scores > 0.80 in the previous chapter. More specifically, in comparing VIP scores for DMI models across studies, the previous chapter reported a higher VIP score for HD duration and lower VIP score for meal traits compared to the current study. Given the proposed associations between meal traits and individual-animal satiety mechanisms (Bailey, 2011), it is logical that meal traits would be more influential than most BV traits in predicting DMI of individual-animals as observed in the current study. Alternatively, BV traits would be expected to have stronger associations with RFI, as observed in the current study, since the energetic cost of eating, chewing, and ruminating, as well as physical activity are associated with the frequency and duration of BV events (Susenbeth et al., 1998). However, it is important to note that meal duration was found to be influential on both RFI and DMI models in the current study and in the previous chapter. Accordingly, meal duration may be associated with energetic expenditures, and individual-animal satiety mechanisms.

Similar results were observed for the day-to-day variation of feeding behavior traits as the day-to-day variation of BV frequency and duration were only influential for the RFI model, while the day-to-day variation of meal frequency and length were only influential for the DMI model. Although the associations between day-to-day variation traits and RFI and DMI are not well understood, these results further indicate a tie linking the day-to-day variation of BV events to the feed efficiency of animals. Potentially, increased day-to-day variation of BV events may be associated with increased incidences of metabolic disturbances, while the increased day-to-day variation of meal events may be more related to the alterations of gene expressions associated with hunger and satiety signals. However, no conclusions can be drawn as rumen parameters and gene expressions were not evaluated in the current study. Lastly, the day-to-day variation of HD duration was influential for both the RFI and DMI models in the current study, and in the previous chapter. However, for each of these studies, VIP scores of this trait were higher for the RFI model than for the DMI model. Head-down duration is described as an intensity trait in the current study as it is related to the intensity in which an animal consumes feed. Accordingly, it may be an indicator for social hierarchy rank, which would be expected to be more correlated with efficiency than intake given its association with activity. However, this theory cannot be validated as social behaviors were not evaluated in the current study.

Overall, the lack of association between BV frequency and DMI, and the strong associations between meal traits and DMI, may suggest that more animals were displaced from feed bunks "involuntarily" due to social hierarchy ranks or increased bunk competition in the current study compared to the previous chapter. Accordingly, BV events may have been more indicative of individual-animal hunger and satiety signals in the previous chapter than the current study. However, involuntary bunk displacements were not evaluated in either study, so no conclusions can be drawn.

In summary, feeding behavior patterns accounted for 35% of the variation in RFI and accounted for an additional 17% of the variation in DMI unaccounted for by ADG and mid-test $BW^{0.75}$. These results were lower than those reported in the previous chapter as they found feeding behavior traits to account for 47% of the variation in RFI and an additional 31% of the variation in DMI unaccounted for by the RFI base model.

Further, day-to-day variation of feeding behavior traits accounted for less of the total variance in RFI and DMI in the current study compared to the previous chapter. However, feeding behavior traits and the day-to-day variation of feeding behavior traits were found to be useful in accounting for individual-animal variance in both RFI and DMI. Accordingly, feeding behavior traits may serve as useful biomarkers for identifying feed efficient animals or for predicting individual-animal DMI.

Repeatability of feeding behavior traits

Repeatability estimates for performance, feed efficiency, and feeding behavior traits measured during the first 28 d or last 42 d of each trial are presented in Table 3.9. Repeatability estimates of ADG and DMI ranged from 0.27 to 0.38 and 0.77 to 0.87, respectively. These values are similar to those reported by Paddock (2010) between a 28 d receiving and 70 d growing period for ADG (r = 0.23), but higher than the value they reported for DMI (r = 0.58). In another study, lower repeatability estimates were reported for DMI (r = 0.61) and ADG (r = 0.11) for heifers across the growing and finishing period, and for DMI (r = 0.34) evaluated within the finishing period (Kelly et al., 2010b). For feed efficiency traits, strong repeatability estimates were observed for gain to feed ratio in the current study (r > 0.67), while moderate to strong estimates were observed for RFI (0.41 to 0.77). Previous studies reported similar estimates for RFI, however, low (0.03; Paddock, 2010) to moderate (0.37; Kelly et al., 2010b) repeatability estimates were reported for gain to feed ratio between a 28 d receiving and 70 d growing period and a 70 d growing and 70 d finishing period, respectively.

For feeding behavior traits, strong (> 0.50) repeatability estimates were consistently observed between periods for BV, meal, and intensity traits. Of these traits, the highest repeatability estimates were observed for BV and HD durations, and the ratios of HD duration with BV duration and meal duration. These results are similar to those reported by Paddock (2010) as they reported strong correlations (> 0.75) between BV and meal traits, with the highest correlation being reported for BV duration (r = 0.82). Strong repeatability estimates were also observed by Kelly et al. (2010b) for BV frequency (0.60) and BV eating rate (0.56) within the finisher period of heifers, but only a moderate correlation was observed for BV duration (0.37) in their study. For day-to-day variation traits, moderate to strong repeatability estimates were observed for all feeding behavior traits with the exception of max non-feeding interval SD. In general, the magnitude of the repeatability estimates were lower for day-to-day variation traits compared to the daily feeding behavior traits, however, these findings indicate a novel relationship between the day-to-day variance of feeding patterns for individual-animals across periods.

Overall, the findings reported in the current study indicate that daily feeding behavior patterns and the day-to-day variation of such feeding patterns are generally consistent across periods within the finisher phase of production. Additionally, they were found to be more repeatable than other production traits during the finisher period. Accordingly, these results provide implications for further research investigating the use of feeding behavior traits as biomarkers for feed intake or efficiency as they are associated with these traits and repeatable. Further, given the moderate to strong repeatability of RFI and DMI, and the strong repeatability of most feeding behavior traits, individual-animal feeding behavior measured during the early stages of the feeding period may be useful in predicting long-term feed efficiency or intake in finishing cattle.

Associations between 70-d RFI and 28-d feeding behavior traits

Based on the strong repeatability estimates reported for feeding behavior traits in this study, PLSR models were developed to evaluate the associations between feeding behavior traits measured during the first 28 d of the finisher period and feed efficiency of animals throughout the entire 70 d period. Summary statistics for cross-validation (*k*-fold) of these PLSR models for RFI and DMI of growing animals using feeding behavior traits measured during the first 28 d of each trial are presented in Table 3.10. Overall, BV, meal, and intensity traits measured during the first 28 d (28-d Daily-FB) accounted for 25% of the variation in RFI, which was 8% less than that observed using feeding behavior traits measured during the entire finishing period. Inclusion of day-to-day variation of BV, meal, and intensity traits measured during the first 28 d (28d Var-FB) increased the R^2_{cv} from 0.25 to 0.27, accounting for an additional 2% of the variance in RFI. These results agree with those reported using feeding behavior traits measured over the entire trials as day-to-day variation traits accounted for an additional 2% in those models as well. When initial ultrasound measurements of back fat depth, IMF, and LM area were added to the model, R^2_{cv} increased an additional 3%, which again agrees with the 2% increase observed for the previous models including gain and final ultrasound measurements. Overall, feeding behavior traits measured during the first 28 d of each study accounted for less of the variation in individual-animal RFI, however, a significant amount of variation was still accounted for by 28 d feeding behavior traits and initial ultrasound measurements (30%).

As before, PLSR models were also developed to derive expected DMI using performance, feeding behavior, and ultrasound traits measured within the first 28 d of each trial. For the base model, mid-test $BW^{0.75}$ and ADG measured during the first 28 d of each trial accounted for 48% of the variation in individual-animal DMI measured over the entire feeding period. As expected, 28 d performance data accounted for less of the variation than performance data determined over the entire trial, but only by 11% (48 vs. 59%). Inclusion of 28 d Daily-FB traits into the model increased R^2_{cv} from 0.48 to 0.63, accounting for an additional 15% of the variation in individual-animal DMI, which is comparable to the 17% increase observed when using performance and feeding behavior traits measured over the entire trial. When 28d Var-FB traits were added to the model, an additional 2% of the variance was accounted for, which agrees with the 2% increase observed for the previous model using Var-FB traits. Initial ultrasound traits did not improve model R^2_{cv}, which was also observed for gain and final ultrasound measurements when they were added to the model with Daily-FB and Var-FB traits.

Variable of importance in projection scores for PLSR models used to quantify the variation in RFI and DMI measured over the entire feeding period using performance, feeding behavior, and ultrasound traits measured during the first 28 d of each trial are presented in Table 3.11. Overall, VIP scores of feeding behavior traits were similar to those obtained for models using independent variables measured over the entire feeding period (Table 3.8). The only exceptions were for BV events per meal event for the RFI models and HD duration per BV duration for the DMI models. Accordingly, individual feeding behavior traits measured during the first 28 d or the entire trial appear to have similar influences on PLSR models for RFI and DMI. These results further indicate the use of feeding behavior traits as biomarkers for feed efficiency or intake as their associations with RFI and DMI are repeatable across periods within the finisher phase of production.

Overall, performance, feeding behavior, and ultrasound traits measured during the first 28 d of each study accounted for up to 30% of the variation in individual-animal RFI and 65% of the variation in individual-animal DMI determined over the entire feeding period. Although these traits accounted for less of the variation than traits measured over the entire period, these results indicate a strong association between feeding behavior traits measured during the beginning of the finishing period and feed efficiency and intake measured over the entire period. These findings provide implications for use of feeding behavior traits as biomarkers for feed efficiency or intake as short-term measurements of feeding behavior traits may provide useful information regarding the feed efficiency or intake of cattle during the entire finishing period.

Conclusion

The results from this study confirm that distinct differences exist between the feeding behavior patterns of animals with divergent feed efficiency. Specifically, efficient animals visited the bunk fewer times each day, spent less time consuming feed, and had reduced day-to-day variation in feeding behavior patterns. Overall, feeding behavior traits alone accounted for 35% of the variation in RFI and accounted for an additional 17% of the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. Ultrasound traits accounted for 2% of the variation in RFI, but only minimally improved the R^2_{cv} for the PLSR model deriving expected DMI.

Overall, feeding behavior traits in this study accounted for a significant portion of the individual-animal variation in RFI and DMI, with influential traits being repeatable across breed and gender types. Strong repeatability estimates were observed for most feeding behavior traits across the finishing period, with significant and consistent associations being observed between feeding behavior traits measured during the first 28 d of each trial and RFI and DMI measured during the entire feeding period. Based on these findings, feeding behavior traits may be useful bio-markers for RFI as they explain a significant proportion of the between-animal variation in feed efficiency, appear to be robust across variations in breed and gender, and are repeatable within the finishing phase of production. However, further research is warranted to evaluate the robustness of feeding behavior patterns across various diet types and to better understand the underlying mechanisms involved with the associations between feeding behavior and RFI.

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Table 3. 1. Effect of residual feed intake (RFI) on performance, efficiency, and ultrasound traits in heifers consuming a high-grain diet.

			RFI Class				*P*-value		
Item	Mean	SD	Low	Medium	High	SE	RFI	Breed	RFI × Breed
No. animals	408		120	169	119				
Performance and growth traits:									
Initial age, d	340	35	335	339	334	21	0.137	0.471	0.425
Initial BW, kg	281	36	277	275	283	14	0.095	0.001	0.005
Final BW, kg	388	49	387^{ab}	380^{b}	392^{a}	19	0.049	<.0001	0.010
ADG, kg/d	1.52	0.32	1.59^{a}	1.49^{b}	1.53^{ab}	0.08	0.042	<.0001	0.033
Initial hip height, cm	118	6	117	117	117	3	0.676	<.0001	0.010
DMI, kg/d	9.29	1.67	8.27^{a}	9.13^{b}	10.33^{c}	0.70	<.0001	<.0001	0.025
DMI SD, kg/d	2.79	0.68	2.52^{a}	2.68^{b}	3.00^{c}	0.26	<.0001	0.015	0.027
Feed efficiency traits:									
RFI, kg/d	0.000	0.923	-1.063^{a}	0.044^{b}	1.026^{c}	0.049	<.0001	0.537	0.690
RG, kg/d	0.000	0.223	0.165^{a}	-0.005^{b}	-0.097^{c}	0.020	<.0001	<.0001	0.152
G:F, kg/kg	0.165	0.028	0.192^{a}	0.163^{b}	0.149^{c}	0.007	<.0001	<.0001	0.241
Ultrasound traits:									
Final backfat depth, cm	0.650	0.238	0.607^{a}	0.640^{a}	0.705^{b}	0.071	0.002	<.0001	0.203
Final intramuscular fat, %	3.75	0.98	3.73	3.89	3.82	0.26	0.266	<.0001	0.003
Final LM area, cm^2	25.42	3.27	25.32	25.26	25.55	1.12	0.700	<.0001	0.460
Gain in backfat depth, cm	0.331	0.186	0.307^{a}	0.331^{a}	0.377^{b}	0.048	0.010	<.0001	0.453
Gain in intramuscular fat, %	0.517	0.684	0.466	0.528	0.567	0.220	0.506	<.0001	0.009
Gain in LM area, cm^2	8.04	2.40	8.10	8.07	8.38	0.34	0.497	<.0001	0.749

^{a,b,c} Means within row with different superscripts differ ($P < 0.05$).

Table 3. 2. Effect of residual feed intake (RFI) on performance, efficiency, and ultrasound traits in steers consuming a high-grain diet.

			RFI Class				*P*-value		
Item	Mean	SD	Low	Medium	High	SE	RFI	Breed	RFI × Breed
No. animals	320		98	121	101				
Performance and growth traits:									
Initial age, d	334	19	331	335	332	6	0.395	0.781	0.479
Initial BW, kg	290	46	290	294	285	33	0.164	<.0001	0.853
Final BW, kg	394	48	391	398	386	25	0.102	<.0001	0.393
ADG, kg/d	1.49	0.31	1.44	1.49	1.45	0.12	0.283	<.0001	0.043
Initial hip height, cm	119	5	120	119	118	1	0.089	0.001	0.147
DMI, kg/d	9.41	1.26	8.31^{a}	9.47^{b}	10.17^{c}	0.12	<.0001	<.0001	0.074
DMI SD, kg/d	2.10	0.39	1.89^{a}	2.13^{b}	2.24^{c}	0.05	<.0001	0.841	0.750
Feed efficiency traits:									
RFI, kg/d	0.030	0.875	-0.931^{a}	0.033^{b}	0.986^{c}	0.050	<.0001	0.776	0.781
RG, g/d	-0.002	0.216	0.097^{a}	-0.002^{b}	-0.125^{c}	0.021	<.0001	<.0001	0.247
G:F, kg/kg	0.158	0.028	0.173^{a}	0.157^{b}	0.141^{c}	0.014	<.0001	<.0001	0.305
Ultrasound traits:									
Final backfat depth, cm	0.518	0.207	0.501	0.518	0.528	0.073	0.692	<.0001	0.889
Final intramuscular fat, %	3.09	0.81	3.14	3.11	3.21	0.22	0.556	<.0001	0.506
Final LM area, cm^2	25.6	4.0	24.9	25.8	25.3	2.3	0.194	<.0001	0.829
Gain in backfat depth, cm	0.249	0.177	0.241	0.244	0.261	0.063	0.226	0.290	0.637
Gain in intramuscular fat, %	0.217	0.736	0.201	0.254	0.280	0.453	0.912	0.004	0.278
Gain in LM area, cm^2	6.90	2.68	6.66	6.86	6.82	0.94	0.861	<.0001	0.996

^{a,b,c} Means within row with different superscripts differ ($P < 0.05$).

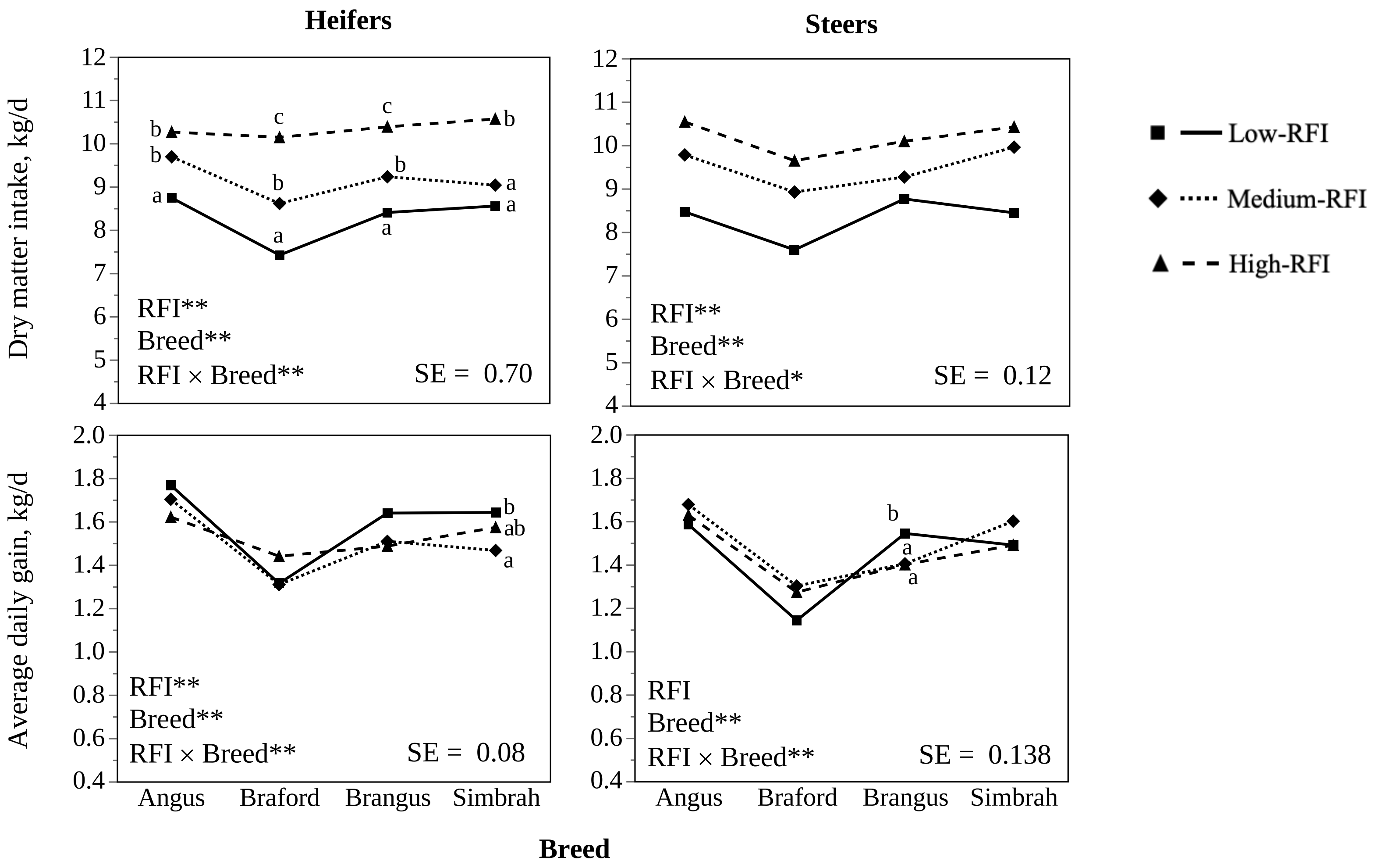

Figure 3. 1. Least squares means of DMI and ADG by breed for high, medium, and low residual feed intake (RFI; ± 0.50 SD from mean RFI; *P < 0.10; **P < 0.05) heifers (3 trials; N = 408) and steers (2 trials; N = 320) consuming high-grain finisher rations. Means within breeds with different letters differ (P < 0.05).

Table 3. 3. Effects of residual feed intake on feeding behavior traits in heifers consuming a high-grain diet.

			RFI Class				*P*-value		
Item	Mean	SD	Low	Medium	High	SE	RFI	Breed	RFI*Breed
No. animals	408		120	169	119				
Bunk visit traits:									
BV frequency, events/d	68.6	20.5	64.3^{a}	68.3^{b}	73.9^{c}	11.8	<.0001	0.128	0.581
BV duration, min/d	64.3	19.1	52.1^{a}	64.8^{b}	74.7^{c}	3.8	<.0001	<.0001	0.462
Max non-feeding interval, min	547	125	530	543	525	66	0.166	0.001	0.775
BV eating rate, g/min	0.155	0.044	0.173^{a}	0.149^{b}	0.146^{b}	0.005	<.0001	<.0001	0.095
Meal traits:									
Meal criterion, min	10.9	8.4	9.20	10.51	10.11	4.03	0.289	0.161	0.536
Meal frequency, events/d	9.91	5.12	10.6	10.3	10.4	2.9	0.848	0.003	0.424
Meal duration, min/d	139	37	122^{a}	135^{b}	152^{c}	12	<.0001	0.001	0.693
Meal length, min/event	19.8	12.7	15.3^{a}	19.1^{b}	20.6^{b}	6.7	<.0001	0.044	0.603
Meal size, kg	1.25	0.72	0.98^{a}	1.22^{b}	1.31^{b}	0.40	<.0001	<.0001	0.091
Meal eating rate, g/min	0.070	0.018	0.071	0.071	0.071	0.007	0.985	0.037	0.338
Intensity traits:									
HD duration, min/d	42.7	20.3	31.2^{a}	42.1^{b}	49.8^{c}	8.8	<.0001	<.0001	0.382
HD duration per BV duration	0.647	0.197	0.589^{a}	0.641^{b}	0.650^{b}	0.122	<.0001	0.007	0.826
HD duration per meal duration	0.301	0.116	0.246^{a}	0.310^{b}	0.323^{b}	0.044	<.0001	0.010	0.265
BV events per meal event	8.53	4.49	7.08^{a}	8.17^{b}	8.78^{b}	2.46	<.0001	<.0001	0.798
Day-to-day variation traits†:									
BV frequency SD, events/d	17.6	4.4	16.8^{a}	17.9^{b}	18.8^{c}	2.0	<.0001	0.232	0.979
BV duration SD, min/d	18.7	4.9	16.8^{a}	19.1^{b}	20.4^{c}	0.9	<.0001	<.0001	0.460
Max non-feeding interval SD, min	169	27	170	171	164	5	0.085	0.895	0.102
Meal frequency SD, events/d	2.93	1.66	3.12	3.14	3.05	0.96	0.740	<.0001	0.622
Meal duration SD, min/d	34.54	8.69	31.98^{a}	34.19^{a}	36.22^{b}	1.29	0.002	0.004	0.594
Meal length SD, min/event	6.13	4.01	4.69^{a}	5.93^{b}	6.36^{c}	1.89	<.0001	0.286	0.671
HD duration SD, min/d	12.47	5.00	10.06^{a}	12.60^{b}	13.77^{c}	1.79	<.0001	<.0001	0.548

† Day-to-day variation traits = day-to-day standard deviation for each trait.

[a,b,c] Means within row with different superscripts differ ($P < 0.05$).

Table 3. 4. Effects of residual feed intake on feeding behavior traits in steers consuming a high-grain diet.

			RFI Class				*P*-value		
Item	Mean	SD	Low	Medium	High	SE	RFI	Breed	RFI*Breed
No. animals	320		98	121	101				
Bunk visit traits:									
BV frequency, events/d	58.3	16.3	50.9^{a}	58.1^{b}	64.3^{c}	11.6	<.0001	0.610	0.069
BV duration, min/d	61.4	17.4	52.6^{a}	61.6^{b}	68.7^{c}	7.08	<.0001	<.0001	0.547
Max non-feeding interval, min	691	114	700	701	676	77	0.080	0.001	0.949
BV eating rate, g/min	0.16	0.05	0.17	0.17	0.16	0.02	0.078	<.0001	0.656
Meal traits:									
Meal criterion, min	16.8	7.03	17.5	15.9	15.8	0.98	0.228	0.013	0.599
Meal frequency, events/d	5.28	1.59	4.98^{a}	5.39^{ab}	5.51^{b}	0.61	0.061	0.186	0.161
Meal duration, min/d	137	33.3	123^{a}	133^{b}	146^{c}	17.8	<.0001	0.007	0.530
Meal length, min/event	29.2	9.62	27.4	28.2	30	1.12	0.200	0.043	0.565
Meal size, kg	1.91	0.56	1.77^{1}	1.92^{ab}	1.98^{b}	0.24	0.023	0.001	0.211
Meal eating rate, g/min	0.07	0.02	0.07	0.07	0.07	0.01	0.365	0.058	0.966
Intensity traits:									
HD duration, min/d	42.7	16.7	33.2^{a}	43.7^{b}	49.9^{c}	7.16	<.0001	<.0001	0.928
HD duration per BV duration	0.681	0.115	0.62^{a}	0.70^{b}	0.72^{b}	0.037	<.0001	0.384	0.981
HD duration per meal duration	0.312	0.097	0.28^{a}	0.33^{b}	0.34^{b}	0.016	<.0001	0.000	0.680
BV events per meal event	11.3	3.21	10.5^{a}	11.2^{ab}	12.0^{b}	0.99	0.005	0.024	0.206
Day-to-day variation traits†:									
BV frequency SD, events/d	14.7	3.3	13.4^{a}	14.8^{b}	15.7^{c}	1.5	<.0001	0.317	0.530
BV duration SD, min/d	16.7	3.9	15.2^{a}	17.0^{b}	17.8^{b}	1.0	<.0001	0.039	0.485
Max non-feeding interval SD, min	176	28	176	175	175	9	0.962	<.0001	0.290
Meal frequency SD, events/d	1.41	0.47	1.34	1.43	1.47	0.08	0.204	0.103	0.437
Meal duration SD, min/d	32.1	7.7	29.9^{a}	31.3^{ab}	33.3^{b}	2.2	0.016	0.019	0.746
Meal length SD, min/event	8.96	3.55	8.68	8.70	9.00	0.88	0.789	0.072	0.867
HD duration SD, min/d	11.8	4.0	9.9^{a}	12.2^{b}	13.3^{c}	1.3	<.0001	0.010	0.890

† Day-to-day variation traits = day-to-day standard deviation for each trait.

^{a,b,c} Means within row with different superscripts differ ($P < 0.05$).

Table 3. 5. Variable of importance scores for partial least squares regression (PLSR) models to predict residual feed intake (RFI) using as feeding behavior traits as independent variables.

	Heifer†				Steer†			
	Angus	Braford	Brangus	Simbrah	Angus	Braford	Brangus	Simbrah
No. animals	63	115	120	110	71	47	109	93
Bunk visit traits:								
BV frequency, events/d	**0.91**	**0.84**	**0.97**	**1.01**	**1.03**	**1.34**	**0.94**	**1.01**
BV duration, min/d	**1.45**	**1.69**	**1.94**	**1.40**	**1.40**	**1.35**	**1.40**	**1.27**
Max non-feeding interval, min	0.67	**0.83**	**0.87**	0.72	**0.95**	0.04	**0.84**	0.63
Meal traits:								
Meal frequency, events/d	0.61	0.73	0.75	0.58	0.70	0.28	**1.04**	0.56
Meal duration, min/d	**1.27**	**1.27**	**0.81**	**0.99**	**1.27**	**0.92**	**0.85**	**0.87**
Meal length, min/event	0.72	**0.80**	0.58	0.75	**1.19**	0.46	0.60	0.53
Intensity traits:								
HD duration, min/d	**1.11**	**0.90**	**1.21**	**1.38**	**1.21**	**1.54**	**1.27**	**1.64**
HD duration per BV duration	**0.91**	**1.23**	**0.91**	**1.13**	**0.87**	**1.48**	**1.12**	**1.72**
HD duration per meal duration	**0.92**	0.76	**1.02**	**1.42**	**0.88**	**0.91**	**1.25**	**1.40**
BV events per meal event	**0.85**	**0.82**	0.69	**0.91**	**1.12**	**0.90**	0.69	0.58
Day-to-day variation traits‡:								
BV frequency SD, events/d	**0.96**	0.75	**0.88**	**0.82**	**0.89**	**1.42**	**0.98**	**0.82**
BV duration SD, min/d	**1.08**	**1.26**	**1.45**	**0.93**	**0.83**	**1.06**	**1.13**	**1.03**
Max non-feeding interval SD, min	**1.25**	0.74	0.42	**0.92**	0.21	0.42	**0.91**	0.27
HD duration SD, min/d	0.58	**0.88**	**0.82**	0.61	**0.85**	0.04	**0.91**	0.60
Meal frequency SD, events/d	**1.18**	**1.16**	0.76	**0.84**	**1.20**	**0.91**	**0.85**	0.79
Meal duration SD, min/d	**0.85**	0.80	0.52	0.70	**0.82**	0.44	0.60	0.43
Meal length SD, min/event	**1.17**	**0.98**	**1.28**	**1.28**	**0.99**	**1.30**	**1.19**	**1.30**

† Variable of importance scores; values greater than 0.80 are in bold.

‡Day-to-day variation traits = day-to-day standard deviation for each trait.

Table 3. 6. Variable of importance scores for partial least squares regression (PLSR) models to predict residual feed intake (RFI) using as feeding behavior traits as independent variables.

	Heifers†	Steers†	Combined†
No. animals	408	320	728
Bunk visit traits:			
BV frequency, events/d	**1.06**	**1.04**	**0.99**
BV duration, min/d	**1.75**	**1.49**	**1.76**
Max non-feeding interval, min	0.70	**0.97**	**0.80**
Meal traits:			
Meal frequency, events/d	0.68	0.64	0.57
Meal duration, min/d	**1.11**	**0.98**	**1.11**
Meal length, min/event	0.71	0.63	0.69
Intensity traits:			
HD duration, min/d	**1.19**	**1.46**	**1.36**
HD duration per BV duration	**0.99**	**1.20**	**0.91**
HD duration per meal duration	**0.92**	**1.22**	**1.06**
BV events per meal event	0.77	0.73	0.75
Day-to-day variation traits‡:			
BV frequency SD, events/d	**0.84**	**0.95**	**0.89**
BV duration SD, min/d	**1.34**	**1.06**	**1.17**
Max non-feeding interval SD, min	0.68	0.62	0.66
HD duration SD, min/d	0.68	0.66	0.60
Meal frequency SD, events/d	**0.95**	**0.84**	**0.91**
Meal duration SD, min/d	0.68	0.58	0.67
Meal length SD, min/event	**1.22**	**1.24**	**1.28**

† Variable of importance scores; values greater than 0.80 are in bold.

‡Day-to-day variation traits = day-to-day standard deviation for each trait.

Table 3. 7. Summary statistics for cross-validation of partial least squares regression (PLSR) models for residual feed intake (RFI) or dry matter intake (DMI) using performance, feeding behavior, and ultrasound traits of finishing heifers and steers consuming a high-grain diet.

		Cross-validation		
Item	N	R^2_{cv}	RMSE	Spearman's
Residual feed intake PLSR models				
RFI = 28 d daily feeding behavior (28d Daily-FB)	728	0.33	0.43	0.58*
RFI = 28d Daily-FB + day-to-day variation of 28 d feeding behavior (28d Var-FB)	728	0.35	0.43	0.60*
RFI = 28d Daily-FB + 28d Var-FB + Ultrasound traits	705	0.37	0.43	0.61*
Dry matter intake PLSR models				
DMI = Mid-test $BW^{0.75}$ + ADG (Base model)	728	0.59	0.74	0.77*
DMI = Base model + 28d Daily-FB	728	0.76	0.64	0.87*
DMI = Base model + 28d Daily-FB + 28d Var-FB	728	0.78	0.63	0.88*
DMI = Base model + 28d Daily-FB + 28d Var-FB + Ultrasound traits	705	0.78	0.62	0.88*

* Correlations are different from zero at $P < 0.05$.

R^2_{cv} = coefficient of determination for cross-validation; RMSE = Root mean square error; Spearman's = Spearman's rank correlation between observed and predicted values.

Table 3. 8. Variable of importance scores for PLSR models used to quantify the variation in residual feed intake (RFI) and dry matter intake (DMI) using performance, feeding behavior, and ultrasound traits of growing heifers and steers consuming a high-grain diet.

	VIP Scores‡	
Trait	RFI	DMI
Bunk visit traits:		
BV frequency, events/d	**1.11**	0.477
BV duration, min/d	**1.88**	**1.37**
Max non-feeding interval, min	0.778	0.603
Meal traits:		
Meal frequency, events/d	0.538	**0.964**
Meal duration, min/d	**1.25**	**1.15**
Meal length, min/event	0.701	**1.25**
Intensity traits:		
HD duration, min/d	**1.51**	**1.04**
HD duration per BV duration	**0.919**	0.689
HD duration per meal duration	**1.11**	0.573
BV events per meal event	**0.814**	**1.06**
Day-to-day variation traits†:		
BV frequency SD, events/d	**0.910**	0.536
BV duration SD, min/d	**1.24**	0.712
Max non-feeding interval SD, min	0.644	0.631
Meal frequency SD, events/d	0.551	**1.00**
Meal duration SD, min/d	**0.968**	0.779
Meal length SD, min/event	0.602	**1.12**
HD duration SD, min/d	**1.38**	**0.843**
Ultrasound traits:		
Final backfat depth, cm	**0.961**	**1.04**
Final intramuscular fat, %	**0.897**	0.473
Final LM area, cm2	0.711	**1.11**
Gain in backfat depth, cm	**0.929**	**0.960**
Gain in intramuscular fat, %	0.721	0.703
Gain in LM area, cm2	0.595	0.612
Performance traits:		
ADG, kg/d	**-**	**1.83**
Metabolic BW, kg$^{0.75}$	**-**	**1.81**

† Day-to-day variation traits = day-to-day standard deviation for each trait.

‡ Variable of importance in projection scores for each independent variable included in the models for RFI and DMI.

Table 3. 9. Repeatability estimates for feeding behavior traits of growing heifers and steers consuming a high-grain diet.

	Heifers†			Steers†	
	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5
N	169	115	124	165	155
Performance and growth traits:					
ADG, kg/d	**0.36**	**0.38**	**0.27**	**0.41**	**0.28**
DMI, kg/d	**0.78**	**0.78**	**0.79**	**0.77**	**0.81**
Feed efficiency traits:					
RFI, kg/d	**0.55**	**0.41**	**0.77**	**0.74**	**0.69**
G:F, kg/kg	**0.70**	**0.75**	**0.78**	**0.78**	**0.67**
Bunk visit traits:					
BV frequency, events/d	**0.83**	**0.72**	**0.69**	**0.82**	**0.73**
BV duration, min/d	**0.88**	**0.76**	**0.86**	**0.83**	**0.89**
Max non-feeding interval, min	**0.75**	**0.61**	**0.71**	**0.63**	**0.69**
BV eating rate, g/min	**0.88**	**0.70**	**0.87**	**0.85**	**0.86**
Meal traits:					
Meal criterion, min	**0.71**	**0.51**	**0.58**	**0.72**	**0.68**
Meal frequency, events/d	**0.61**	**0.69**	**0.58**	**0.71**	**0.54**
Meal duration, min/d	**0.79**	**0.71**	**0.72**	**0.83**	**0.82**
Meal length, min/event	**0.70**	**0.68**	**0.58**	**0.78**	**0.78**
Meal eating rate, g/min	**0.74**	**0.82**	**0.74**	**0.77**	**0.80**
Intensity traits:					
HD duration, min/d	**0.88**	**0.81**	**0.86**	**0.86**	**0.90**
HD duration per BV duration	**0.88**	**0.85**	**0.81**	**0.89**	**0.91**
HD duration per meal duration	**0.85**	**0.81**	**0.80**	**0.88**	**0.84**
BV events per meal event	**0.72**	**0.68**	**0.57**	**0.80**	**0.76**
Day-to-day variation traits‡:					
BV frequency SD, events/d	**0.47**	**0.41**	**0.54**	**0.56**	**0.40**
BV duration SD, min/d	**0.51**	**0.55**	**0.63**	**0.55**	**0.47**
Max non-feeding interval SD, min	0.03	-0.05	**0.32**	0.08	**0.28**
Meal frequency SD, events/d	**0.51**	**0.53**	**0.42**	**0.59**	**0.47**
Meal duration SD, min/d	**0.39**	**0.35**	**0.64**	**0.49**	**0.42**
Meal length SD, min/event	**0.51**	**0.54**	**0.44**	**0.57**	**0.59**
HD duration SD, min/d	**0.59**	**0.61**	**0.73**	**0.66**	**0.63**

†Pearson correlations between feeding behavior traits measured during the first 28 d and last 42 days of each trial; significant correlations are bolded.

‡Day-to-day variation traits = day-to-day standard deviation for each trait.

Table 3. 10. Summary statistics for cross-validation of partial least squares regression (PLSR) models for residual feed intake (RFI) or dry matter intake (DMI) measured over the entire feeding period using performance and feeding behavior traits measured during the first 28d of each trial for growing heifers and steers consuming high-grain diet.

		Cross-validation		
Item	N	R^2_{cv}	RMSE	Spearman's
Residual feed intake PLSR models†				
RFI = Daily feeding behavior (Daily-FB)	728	0.25	0.39	0.50*
RFI = Daily-FB + day-to-day variation of feeding behavior (Var-FB)	728	0.27	0.40	0.52*
RFI = Daily-FB + Var-FB + initial ultrasound	709	0.30	0.41	0.55*
Dry matter intake PLSR models†				
DMI = Mid-test $BW^{0.75}$ + ADG (Base model)	728	0.48	0.75	0.70*
DMI = Base model + Daily-FB	728	0.63	0.73	0.79*
DMI = Base model + Daily-FB + Var-FB	728	0.65	0.72	0.80*
DMI = Base model + Daily-FB + Var-FB + initial ultrasound	709	0.65	0.71	0.81*

†Dependent variables measured over the entire feeding period for each trial and independent variables measured during the first 28d of each trial.

R^2_{cv} = coefficient of determination for cross-validation; RMSE = Root mean square error; Spearman's = Spearman's rank correlation between observed and predicted values.

Table 3. 11. Variable of importance in projection scores for PLSR models used to quantify the variation in residual feed intake (RFI) and dry matter intake (DMI) measured over the entire feeding period using performance, feeding behavior, and ultrasound traits measured during the first 28 d of each trial for growing heifers and steers consuming a high-grain diet.

	VIP Scores‡	
Trait	RFI	DMI
28 d bunk visit traits:		
BV frequency, events/d	**1.12**	0.458
BV duration, min/d	**1.73**	**1.34**
Max non-feeding interval, min	0.736	0.563
28 d meal traits:		
Meal frequency, events/d	0.536	**0.945**
Meal duration, min/d	**1.22**	**0.974**
Meal length, min/event	0.612	**1.16**
28 d intensity traits:		
HD duration, min/d	**1.34**	**1.06**
HD duration per BV duration	**0.984**	**0.937**
HD duration per meal duration	**0.894**	0.748
BV events per meal event	0.764	**1.04**
28 d day-to-day variation traits‡:		
BV frequency SD, events/d	**0.835**	0.631
BV duration SD, min/d	**1.31**	0.763
Max non-feeding interval SD, min	0.654	0.529
HD duration SD, min/d	0.581	**1.03**
Meal frequency SD, events/d	**0.916**	0.443
Meal duration SD, min/d	0.517	**1.02**
Meal length SD, min/event	**1.34**	**0.884**
Initial ultrasound traits:		
Initial back fat depth, cm	0.680	**0.822**
Initial intramuscular fat, %	**1.12**	0.609
Initial LM area, cm^2	**1.04**	**0.911**
28 d performance traits:		
ADG, kg/d	**-**	**1.65**
Metabolic BW, $kg^{0.75}$	**-**	**1.97**

† Variable of importance in projection scores for partial least squares regression (PLSR) models for individual-animal RFI or DMI measured over the entire trial using independent variables measured during the first 28 d or the entire trial period (Trial).

‡ Day-to-day variation traits = day-to-day standard deviation for each trait.

CHAPTER IV

APPLICATION OF CHEMOMETRICS TO PREDICT INDIVIDUAL-ANIMAL FEED INTAKE AND EFFICIENCY USING PERFORMANCE AND FEEDING BEHAVIOR TRAITS IN FINISHING STEERS AND HEIFERS

Introduction

Increasing competition for land, water, and grain, as well as growing societal concerns about the environment, are forcing the livestock industry to increase production outputs, with fewer, more expensive inputs, while also reducing the environmental impact of the industry. Given that feed is the largest variable input cost for production, and is related to enteric methane emissions, the economic and environmental sustainability of the livestock industry will rely on the efficiency use of feed by cattle. Accordingly, a great deal of research has investigated methods to select cattle with favorable genotypes for feed efficiency. Research in this area has identified residual feed intake (**RFI**) as an ideal trait for use in selection programs as it accounts for the variation between individual animals' feed efficiency, independent of growth and production, and is moderately heritable (Schenkel et al., 2004; Williams et al., 2011). Efficient or low-RFI cattle have been shown to have reduced feed intake (Nkrumah et al., 2004; Lancaster et al., 2009b; Hafla et al., 2013; Baldassini et al., 2018; Lam et al., 2018) and decreased methane emissions (Hegarty et al., 2007; Basarab et al., 2013) compared to their inefficient or high-RFI counterparts with no impact on growth and performance.

Unfortunately, favorable selection for RFI has been limited by the absence of an affordable method for accurately quantifying individual-animal DMI.

Currently, the industry relies on prediction equations published by the National Research Council (**NRC**) to estimate DMI of animals. These equations have been developed with considerations for both diet composition and energy requirements of the animal, using factors such as gender, age, body weight, physiological state, level of production, nutrient content of the diet, climate, and frame size. The simplicity and ease of application of these models make them advantageous for estimating intake of animals, however current equations have limited ability to measure between-animal variation, hindering the precision of individual-animal determinations (Anele et al., 2014). Accordingly, researchers have worked to identify bio-markers, which are associated with feed efficiency or DMI, repeatable, and measurable in large scale operations, for inclusion into current models to improve individual-animal predictions.

Feeding behavior patterns have been identified as potential bio-markers for feed efficiency as distinctive differences have been reported between the feeding behavior patterns of animals with divergent RFI (Nkrumah et al., 2006; Lancaster et al., 2009b; Kelly et al., 2010a; Gomes et al., 2013; Alende et al., 2016). Furthermore, feeding behavior traits accounted for 13 to 44% of the variation in RFI in previous studies (Lancaster et al., 2009b; Kayser and Hill, 2013; Miller, 2016), and were found to be moderately heritable (Nkrumah et al., 2007) and repeatable (Gibb et al., 1998; Kelly et al., 2010b). Accordingly, inclusion of feeding behavior traits into current prediction models has considerable potential for improving estimations of feed efficiency or DMI.

In the previous chapters, inclusion of feeding behavior traits into the base model for RFI (Mid-test $BW^{0.75}$ and ADG) accounted for an additional 25 to 17% of the variation in individual-animal DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. Similar results were observed by Halachmi et al. (2016) as inclusion of feeding behavior traits to the NRC model which included FCM, DIM, and BW, improved the model accuracy by 38%. Based on these results, feeding behavior patterns may be indicative of variations in individual-animal feed efficiency or DMI, warranting their inclusion into current prediction models.

The objective of this study was to develop prediction models for DMI and RFI using performance, feeding behavior, and ultrasound traits of growing cattle consuming a high-grain diet.

Material and methods

All animal care and use procedures were in accordance with the guidelines for use of Animals in Agricultural Teaching and Research as approved by the Texas A&M University Institutional Animal Care and Use Committee.

Experimental animals and design

Data were collected from 1 study utilizing 498 Angus-based composite steers (Study 1; initial BW = 309.8 ± 57.7 kg; age = 289.1 ± 15.9 d), and 2 studies utilizing 408 heifers (Study 2; initial BW = 280.8 ± 35.9 kg; age = 340.1 ± 35.1 d) and 321 steers (Study 3; initial BW = 290.9 ± 45.9 kg; age = 333.5 ± 19.1 d) composed of Brangus, Braford, Simbrah, and Angus breeds. For each study, animals were randomly assigned to pens equipped with electronic feed bunks (GrowSafe Systems LTD., Airdrie, AB, Canada) and adapted to a high-grain feedlot diet consisting of approximately 73.7% dry rolled corn, 6% chopped hay, 6% cottonseed meal, 6% cottonseed hulls, 5% molasses, 2.5% premix, and 0.8% urea (ME = 3.0 Mcal/kg DM; CP = 12.6% DM) for 28 d. Following adaptation, ad libitum feed intake, performance, and feeding behavior traits were measured for a minimum of 70 d.

For each trial, BW was measured at 14-d intervals and hip height (HH) and ultrasound measurements of 12th rib-fat (**BF**) depth, LM area, and intramuscular fat percentage (**IMF**) were collected on d 0 and 70. Ultrasound measurements were collected by a certified technician using an Aloka 500-V instrument with a 17-cm, 3.5-MHz transducer (Corometrics Medical Systems Inc., Wallingford, CT). Collected images were sent to the Centralized Ultrasound Processing laboratory (Ames, IA) for analysis.

Diet samples were collected weekly, composited by weight at the end of each trial, and sent to Cumberland Valley Analytical Services Inc. (Hagerstown, MD) for chemical analysis.

Computation of traits

Individual animal feed intake was computed using a subroutine of the GrowSafe 4000E software (Process feed intakes) as described by Parsons et al. (2019). For each trial, data was deleted for a pen when the assigned feed disappearance (**AFD**) of an individual bunk in a pen was below 90% or the average AFD of the pen was less than

95%. When data was deleted due to system failure, daily intake values were determined by linear regression of DMI on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC).

Linear regression of serial BW data on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC) was used to determine mid-test $BW^{0.75}$ and ADG. Residual feed intake was computed as the difference between actual and expected DMI from the linear regression of mean DMI on mid-test $BW^{0.75}$ and ADG as described by Koch et al. (1963), with trial included in the model as a fixed effect. Steers and heifers were ranked by RFI and classified into one of three RFI phenotypic groups; low (< 0.5 SD), medium (± 0.5 SD) or high (> 0.5 SD).

Initial hip height (**IHH**) and age at the start of the trial were used to calculate frame score using the following equations for either heifers or steers (Beef Improvement Federation, 1991):

$$\text{Frame score for heifers: } -11.548 + (0.4723 \times \text{IHH}) - (0.0239 \times \text{Age}) + (0.0000146 \times \text{Age}^2) + (0.0000759 \times \text{IHH} \times \text{Age})$$

$$\text{Frame score for steers: } -11.7086 + (0.4878 \times \text{IHH}) - (0.0289 \times \text{Age}) + (0.00001947 \times \text{Age}^2) + (0.0000334 \times \text{IHH} \times \text{Age})$$

where IHH is initial hip height in cm and Age is the days of age at the start of the trial.

Estimates of dry matter required

Adjusted final shrunk BW (**AFSBW**) was determined for individual animals using three methods published by Guiroy et al. (2001), Baker et al. (2006), and Fox et al.

(1988) to account for various individual-animal measurements. The first and second method were modified from the equations published by Guiroy et al. (2001) and Baker et al. (2006), respectively, and accounted for initial ultrasound measurements of BF depth, IMF, and LM area using the following equations to adjust empty body fat (**EBF**):

$$\text{Method 1: } \mathrm{EBF} = 17.76107 \times (4.68142 \times \mathrm{BF}) + (0.01945 \times \mathrm{pHCW}) + (0.81855 \times \text{quality grade}) - (0.06754 \times \text{LM Area}) \text{ (Guiroy et al., 2001)}$$

$$\text{Method 2: } \mathrm{EBF} = (39.9535 \times \mathrm{BF}) - (0.1384 \times \text{LM area}) + (0.0867 \times \mathrm{pHCW}) - (0.0897 \times \mathrm{BF} \times \mathrm{pHCW}) - 1.3690 \text{ (Baker et al., 2006)}$$

where BF is initial ultrasound back fat depth, quality grade was estimated using initial ultrasound measurements of IMF (%), LM area is initial LM area measured by ultrasound, and pHCW was predicted HCW ((pHCW = EBW – 30.26)/1.362).

For methods 1 and 2, AFSBW was then calculated using the following equation by Guiroy et al. (2001):

$$\mathrm{AFSBW} = ((\mathrm{EBW} + (28 - \mathrm{EBF}) \times 14.26)/0.891$$

For the third method, AFSBW was adjusted for gender and frame score using the equation described by Fox et al. (1988) for steers and heifers:

$$\text{AFSBW for heifers} = 26.7 \times \text{Frame score} + 293.2$$

$$\text{AFSBW for steers} = 33.35 \times \text{Frame score} + 366.52$$

Weight equivalent to the (NRC, 1984) medium-framed steer (EQSBW) was then computed for each method using the following equation:

$$\mathrm{EQSBW}\ (\mathrm{kg}) = \mathrm{SBW} \times (\ 478\ \mathrm{kg} \div \mathrm{AFSBW}\ )$$

where SBW is average BW × 0.96 and AFSBW is final SBW adjusted for ultrasound traits (Methods 1 and 2) or frame score by gender (Method 3).

To calculate dry matter required, net energy requirements for maintenance (**NE$_m$**) and gain (**NE$_g$**) were calculated for each method as described by NASEM (2016) guidelines using the following equations:

$$\mathrm{NE_m}\ (\mathrm{Mcal/d}) = 0.077 \times \mathrm{SBW}^{0.75}$$

$$\mathrm{NE_g}\ (\mathrm{Mcal/d}) = 0.0625 \times \mathrm{EQSBW}^{0.75} \times \mathrm{EBG}^{1.097}$$

where EQSBW is equivalent empty BW and EBG is empty body gain (0.891 × SBW gain).

Estimates of individual dry matter requirements (**DMR**) were then calculated using the following equation for each of the 3 methods evaluated:

$$\mathrm{DMR}\ (\mathrm{kg/d}) = \frac{\text{Required } \mathrm{NE_m}\ (\mathrm{Mcal/d})}{\text{Dietary supply of } \mathrm{NE_m}\ (\mathrm{Mcal/kg})} + \frac{\text{Required } \mathrm{NE_g}\ (\mathrm{Mcal/d})}{\text{Dietary supply of } \mathrm{NE_g}\ (\mathrm{Mcal/kg})}$$

Computation of feeding behavior traits

Feeding behavior traits were computed based on the frequency and duration of individual animal bunk visits (**BV**) and meal events as described by Parsons et al. (2019). Bunk visit events commenced when an animals' electronic identification (**EID**) tag was detected by a feed bunk and ended when the duration of the time between the last 2 consecutive EID readings exceeded 100-s, the EID tag was detected in another feed bunk, or the EID of another animal was detected at the same feed bunk (Mendes et al., 2011). Bunk visit frequency and duration were then defined as the number and the sum of duration of BV events recorded during a 24-hour period, regardless of whether feed was consumed, respectively. The interval between BV events was defined as the non-feeding interval (**NFI**), with maximum NFI being defined as the longest NFI during a 24-hour period. Head down (**HD**) duration was computed as the sum of EID tag readings detected each day, multiplied by the scan rate of the GrowSafe system, which was 1.0 reading per second (Jackson et al., 2016).

Meals were defined as the clusters of BV events that are differentiated from the next meal by a nonfeeding interval that is longer compared with the nonfeeding intervals within a meal (Bailey et al., 2012). The longest nonfeeding interval considered to be a part of a meal is defined as the meal criterion. Meal criterion was estimated by fitting a 2-pool, Gaussion-Weibull bimodal probability density function to the $\log_{10}$-transformed interval lengths between BV events for each animal using the Meal Criterion Calculation Software (MCC; ver. 1.7.6836.33854; http://nutritionmodels.tamu.edu). Meal criterion was defined as the intersection of the Gaussion-Weibull probability density functions (Bailey et al., 2012). Meal criterion was used to cluster bunk visit events into meals, with meal frequency, length, and duration being defined as the number of meal events, average meal event length, and sum of length of meal events recorded each day, respectively (Miller, 2016).

Day-to-day variation of feeding behavior traits were calculated as the SD of the residuals of actual vs. predicted values based on linear regression of feeding behavior traits on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC). Day-to-day variation was calculated for BV frequency and duration, HD duration, maximum NFI, meal frequency, meal duration, and meal length. Additionally, 3 ratio traits were computed; BV frequency per meal event, HD duration per meal event, and HD duration per BV event.

Overall, seventeen feeding behavior traits were evaluated, including frequency and duration of BV and meal events, HD duration, meal length, maximum non-feeding interval, corresponding day-to-day variation (SD) of these traits, and ratios of HD duration per BV duration, HD duration per meal duration, and BV events per meal event.

Statistical Analysis

To generate phenotypic correlation coefficients, performance, feed efficiency, and feeding behavior traits were adjusted for the random effect of trial, then used in the multivariate platform of JMP (SAS Inst. Inc., Cary, NC) to obtain phenotypic correlations.

To evaluate the repeatability of performance, feed efficiency, and feeding behavior traits, individual-animal means were computed within the first 28 d and the last 42 d of each trial. All variables were then adjusted within Study for the random effect of trial, and repeatability estimates generated using Pearson correlation coefficient estimates between adjusted means measured during the first 28 d and the last 42 d of each Study.

Preliminary partial least squares regression (**PLSR**) models for DMI were developed using DMR computed from 3 independent sets of equations to compare the various methods in which DMR can be estimated for finishing steers and heifers. For each of these PLSR models, the optimal number of components were determined by minimizing the root mean squared error (**RMSE**) of prediction using the *k*-fold cross-validation procedure in JMP (SAS Inst. Inc., Cary, NC), and all independent variables were retained in the model. The *k*-fold cross-validation technique involves the partitioning of observations into *k* subsets, which are used iteratively as validation sets for models developed using the remaining observations. To compare each of these models, differences between the model residuals were evaluated by *t* test using the fit model procedures in JMP, and cross-validation RMSE and R^2 were evaluated.

Partial least squares regression models were also developed to predict RFI and DMI in this study, using cross-validation and independent-validation techniques. For cross-validation models, *k*-fold cross validation was used as described above, such that all observations were used in both the calibration and validation. For independent-validation techniques, PLSR models for DMI and RFI were calibrated using data from Studies 1 and 2, and independent-validation conducted on Study 3. For prediction of RFI, 3 PLSR models were developed: 1) included feeding behavior traits; 2) included feeding behavior and ultrasound traits; 3) included feeding behavior, ultrasound, and frame size as independent variables.

For prediction of DMI, empirical and mechanistic models were developed to evaluate which approach provides the most robust prediction model for DMI. For empirical DMI models, ADG and mid-test $BW^{0.75}$ were included as independent variables to develop the base model. Two additional empirical models were then developed off the base model to predict DMI: 1) Base model plus feeding behavior traits; and 2) Base model plus feeding behavior and ultrasound traits as independent variables. For mechanistic DMI models, 3 PLSR models were developed: 1) included DMR based on Fox et al. (2001); 2) included DMR plus feeding behavior traits; and 3) included DMI plus feeding behavior and ultrasound traits as independent variables.

To evaluate the model performance using data collected during the first 28 d of each trial, PLSR cross-validation models were developed for RFI and DMI using performance and feeding behavior traits measured during the first 28 d of each trial. For these models, mid-test $BW^{0.75}$, ADG, and frame size, or DMR estimates based on 28 d measurements were included with feeding behavior traits measured during the first 28 d, and initial ultrasound measurements of BF depth, IMF, and LM area as independent variables.

For each of the PLSR prediction models, independent variables were excluded if the variable of importance in projection (VIP) score was less than 0.80. This variable selection technique was proposed by Wold (1966), to ensure the robustness of the PLSR prediction models. Predictive accuracy of the models was evaluated by the coefficient of determination for cross-validation ($\mathbf{R^2_{cv}}$) and independent-validation ($\mathbf{R^2_{v}}$), and the precision of each model evaluated using the RMSE of cross-validation and independent-validation. Additionally, the bias between observed and PLSR predicted values were determined, with differences between mean observed and PLSR predicted values being evaluated by *t* test using the fit model procedures in JMP (SAS Inst. Inc., Cary, NC).

For this study, mean comparisons with *P*-values ≤ 0.05 were declared to be significant, and *P*-values ≤ 0.10 were considered tendencies.

Results and discussion

Relationship between performance, feed efficiency, and feeding behavior traits

Pearson correlations between performance, feed efficiency, and feeding behavior traits of steers and heifers consuming a high-grain diet are presented in Table 4.1. Average daily gain was strongly correlated with G:F (0.65; $P < 0.01$). These results are similar to those reported previously (Lancaster et al., 2009a; Hafla et al., 2013; Kayser and Hill, 2013), and indicate that selection for improved G:F may result in increased mature body weight (Herd and Bishop, 2000). As expected, RFI was highly correlated with DMI (0.71; $P < 0.01$), but not ADG (0.00; $P > 0.05$).

Dry matter intake was positively correlated with BV frequency and duration (0.12 and 0.19, respectively), however, the magnitude of the correlations were small. The magnitude of the correlations observed between RFI and BV frequency and duration were higher (0.39 vs. 0.54, respectively), indicating that these traits are more indicative of individual-animal variations in feed efficiency than DMI. Alternatively, meal duration was slightly more correlated with DMI (0.40) than RFI (0.34). Given that the energetic cost of eating, chewing, and ruminating, as well as physical activity are associated with the frequency and duration of BV events (Susenbeth et al., 1998), it is logical that BV traits would be more correlated with feed efficiency than DMI. Further, meal traits would be expected to be more representative of individual-animal satiety mechanisms, and subsequent DMI, than BV traits (Bailey, 2011), supporting the findings of the current study.

Of the feeding behavior traits, BV and HD durations had the strongest correlations with RFI (0.54 and 0.54, respectively). Previous studies have also found significant correlations between RFI and BV and HD durations of cattle (Nkrumah et al., 2007; Lancaster et al., 2009a; Durunna et al., 2011; Kayser and Hill, 2013), supporting the current findings. Additionally, BV frequency, meal duration, HD duration per BV duration, HD duration per meal duration, and the day-to-day variation of BV frequency, BV duration, and HD duration moderately correlated with RFI (0.31 to 0.41; $P < 0.01$).

In general, the magnitude of the phenotypic correlations between RFI and feeding behavior traits were higher compared to those between DMI and feeding behavior traits, suggesting that feeding behavior traits may be more predictive of RFI than DMI.

Prediction of dry matter intake

The 3 DMR-based PLSR models used to predict DMI of finishing steers and heifers are presented in Table 4.2. Of the 3 equations used to estimate DMR, the equation based on Guiroy et al. (2001) provided the highest R^2_{cv} and lowest RMSE (0.50 and 0.98, respectively). However, no significant differences ($P > 0.05$) in RMSE were observed across the 3 models, and R^2_{cv} ranged minimally from 0.47 to 0.49. These results indicate that model performance was minimally affected by the equation used to compute DMR. Because the equation based on Fox et al. (1988) did not require ultrasound data, this DMR equation was used to further evaluate the accuracy of DMI prediction models.

Cross- and independent-validation results of empirical and mechanistic PLSR models to predict DMI are presented in Table 4.3. Cross-validation R^2 and RMSE of the empirical base model (ADG and mid-test $BW^{0.75}$) were 0.58 and 0.91, respectively. When feeding behavior traits were added to the base model, R^2_{cv} increased from 0.58 to 0.74, and RMSE decreased from 0.91 to 0.71. These findings indicate that inclusion of feeding behavior traits improved the accuracy and precision of the PLSR model to predict DMI, accounting for an additional 16% of the variation in individual-animal DMI unaccounted for by ADG or mid-test $BW^{0.75}$. When ultrasound traits were included with feeding behavior traits to the base model, R^2_{cv} and RMSE were minimally improved. Independent-validation R^2 and RMSE of the empirical models for DMI ranged from 0.48 to 0.68 and 0.09 to 0.18, respectively. Overall, R^2_v and RMSE values were improved upon inclusion of feeding behavior traits into the base model (R^2_v 0.68 vs. 0.48; RMSE 0.73 vs. 0.92), however no improvements were observed upon inclusion of ultrasound traits. Overall, R^2_v was lower than R^2_{cv}, however the model error was not different across validation procedures, indicating that each of these models were robust in predicting DMI across independent data sets. Each empirical model was also useful in predicting mean DMI as bias between observed and predicted DMI were low for both cross- and independent-validation models (Bias < 0.18 kg/d).

Cross-validation R^2 and RMSE were 0.49 and 1.00, respectfully, for the mechanistic model including DMR alone as an independent variable to predict DMI.

These results are lower than those obtained for cross-validation of the empirical base model, likely as the DMR estimates rely on coefficients determined using previous independent data sets. It is therefore logical, that the empirical model developed in the current study would have improved R^2_{cv} as coefficients were determined using the data from the current study. However, when evaluating independent-validation results, the mechanistic model appears to be somewhat advantageous over the empirical model as R^2_v and RMSE were slightly improved. These results indicate that when predicting an independent data set, the mechanistic approach, in which coefficients are determined using previous independent data sets from a variety of populations, enables a more robust prediction of DMI. When feeding behavior traits were included with DMR in the PLSR model to predict DMI, R^2_{cv} and R^2_v were 0.65 and 0.62, respectively. Although these values are lower than those obtained upon inclusion of feeding behavior traits to the empirical models, the independent-validation RMSE and Bias were reduced (RMSE 0.61 vs. 0.73; Bias -0.01 vs 0.18), further indicating that the mechanistic approach is advantageous in predicting DMI of independent data sets. It is important to note that these differences may be even greater, favoring the mechanistic approach, in future research in which models are used to predict DMI of independent trails that may be more variable than the trials evaluated in the current study. Inclusion of ultrasound traits to the model including DMR and feeding behavior traits as independent variables slightly improved the cross-validation results, but resulted in increased error and bias of the independent-validation. These results and those obtained for the empirical models, indicate that for the current study, ultrasound traits were not useful in improving the prediction of DMI, especially across independent data sets.

Overall, the most robust PLSR model to predict DMI was determined to include DMR (based on Fox et al., 2001) and feeding behavior traits as independent variables. This model accounted for 65% of the variation in individual-animal DMI based on cross-validation, and 62% of the variation in individual-animal DMI of the validation data set. Similar cross-validation results were reported by Johnson et al. (2017) for the prediction of individual-animal DMI based on fecal NIRS (R^2_{cv} ranged from 60 to 69%), however, their model was not useful in predicting DMI of independent data sets ($R^2_v = 0.05$).

Individual-animal intake is driven by a complex series of mechanisms that are highly variable within and among animals (Grovum et al., 1998). The complexity of these mechanisms has hindered estimation techniques as it is difficult to predict how these mechanisms will interact with different diet and animal conditions. However, there is evidence to suggest that feed intake is controlled by physical factors such as ruminal fill and digesta passage when ruminants are consuming a less digestible, low-energy diet, and by the energy demands of the animal or metabolic factors when consuming a highly digestible, high-energy diet (NASEM, 2016). Based on these concepts, predictive equations have been developed to predict DMI with considerations for both the composition of the diet and the energy requirements of the animal. Anele et al. (2014) evaluated 4 equations to predict DMI in individual-animals using BW and NE concentrations of the diet and reported a range in r^2 of 0.13 to 0.25. These results indicate the need for additional factors to be considered in predictive equations to better estimate the energy demands of the animal. In the current study, a mechanistic approach to developing prediction models for DMI was determined to provide the most robust prediction of individual-animal DMI for independent data sets. While this approach provided the lowest validation RMSE, it also provides opportunity for accounting for additional group and individual-animal variables that affect energy requirements such as breed and environmental factors. Inclusion of such factors into the equation used to estimate DMR may improve future PLSR prediction models for DMI.

Prediction of residual feed intake

Cross- and independent-validation results of PLSR models to predict RFI are presented in Table 4.4. Cross-validation R^2 and RMSE for the prediction of RFI using feeding behavior traits alone as independent variables were 0.34 and 0.71, respectively. When ultrasound traits were added to the PLSR model for RFI, R^2_{cv} increased from 0.34 to 0.36, accounting for an additional 2% of the variation in individual-animal RFI. These findings support previous literature as positive correlations between RFI and backfat have been consistently observed in cattle (Arthur et al., 2001; Nkrumah et al., 2004; Schenkel et al., 2004; Lancaster et al., 2009a). Inclusion of frame score to the PLSR model for RFI increased R^2_{cv} an additional 2%. Based on these results, feeding behavior traits, ultrasound traits, and frame score are warranted for inclusion into prediction models for RFI as they each account for variation in individual-animal RFI.

Independent-validation R^2 and RMSE for the prediction of RFI using feeding behavior traits alone were 0.31 and 0.76, respectively. As expected, the R^2_v was lower than the reported R^2_{cv}, however, the model still accounted for a significant portion of the between animal variation in RFI, and resulted in little bias (0.12 kg/d). Inclusion of ultrasound traits to the PLSR model for RFI improved R^2_v (0.36 vs. 0.31) and RMSE (0.73 vs. 0.76), but increased the model bias from 0.12 to 0.16. Further addition of frame score into the model reduced bias from 0.16 to 0.00, and accounted for an additional 2% of the variation in individual-animal RFI (0.38 vs. 0.36). Overall, independent-validation results indicated that feeding behavior traits, ultrasound traits, and frame score were robust in predicting individual-animal RFI of independent data sets. However, the overall model R^2_v values were poor ($R^2_v < 0.60$).

To evaluate the usefulness of the PLSR predicted RFI values to identify animals with divergent RFI, the PLSR predicted RFI values of the independent validation set were used to classify steers and heifers into low-, med-, and high-RFI classes based on ± 0.50 SD from the mean PLSR predicted RFI. Based on this procedure, 49% of animals were classified correctly when feeding behavior traits alone were used to develop the PLSR model. When ultrasound traits and frame score were included 47 and 51%, respectively, were classified correctly into low-, med-, and high-RFI classes. Additionally, only 9, 7, and 5% animals were classified across 2 RFI groups of that observed (low-RFI to high-RFI or high-RFI to low-RFI) when feeding behavior traits, feeding behavior plus ultrasound traits, and feeding behavior, ultrasound, and frame scores were included as independent variables in the PLSR model, respectively. Based on these results, PLSR equations may provide opportunity for producers to identify animals with divergent feed efficiency for selection or culling purposes with minimal risk of negative impacts to their operations.

Application of feeding behavior traits measured early during the finisher period to predict DMI or RFI

Repeatability estimates for performance, feed efficiency, and feeding behavior traits measured during the first 28 d or last 42d of each trial are presented in Table 4.5. Across the 3 studies, repeatability estimates for ADG and DMI ranged from 0.11 to 0.35 and 0.67 to 0.79, respectively. Paddock (2010) reported a similar repeatability estimate between a 28 d receiving and 70 d growing period for ADG (r = 0.23), but found a lower correlation for DMI (r = 0.58) than the current study. An additional study reported repeatability estimates for DMI and ADG of heifers across the growing and finishing period of 0.61 and 0.11, respectively, which agree with the findings of the current study (Kelly et al., 2010b). However, when the repeatability of DMI was evaluated within the finishing period of the same study, a lower correlation was reported (r = 0.34). Across studies, repeatability of RFI ranged from 0.55 to 0.72, which agrees with values reported in previous studies (Kelly et al., 2010b; Paddock, 2010).

Strong (> 0.50) repeatability estimates were observed for all BV, meal, and intensity traits evaluated. These results are similar to those reported previously as Paddock (2010) reported strong correlations (> 0.75) between BV and meal traits across the grower and finishing period, and Kelly et al. (2010b) found strong repeatability estimates for BV frequency (0.60) and BV eating rate (0.56) within the finisher period. In the current study, significant correlations were also observed for all but one of the day-to-day variation traits, however, the repeatability estimates were generally lower than those obtained for daily feeding behavior traits.

Overall, these results indicate a consistency of feeding behavior patterns and the day-to-day variation of such patterns within the finisher phase of production. Additionally, feeding behavior traits were found to be more repeatable than other production traits during the finisher period.

Given the repeatability estimates observed for feeding behavior traits during the finisher period, PLSR models were developed to evaluate the usefulness of feeding behavior traits measured early during the finishing period to predict RFI and DMI of the entire finishing period. Cross-validation results of PLSR models for DMI and RFI using performance, feeding behavior, and ultrasound traits measured during the entire trial (70-d) and during the first 28 d of each trial (28-d) are presented in Figure 4.1. The R^2_{cv} and RMSE of the empirical DMI model developed using 28-d traits were 0.60 and 0.88, respectively. As observed in the cross-validation models using 70-d measurements, the mechanistic DMI model developed using 28-d traits accounted for less of the variance in individual-animal DMI than the empirical model. Likely this is a factor of the cross-validation procedure as the coefficients for ADG and mid-test $BW^{0.75}$ were determined within the data set, while the coefficients for the mechanistic model were determined using independent data sets. While the PLSR models developed using 28-d traits were less predictive of DMI than those developed using traits measured over the entire 70-d feeding period, 28-d measurements were useful in accounting for 47 to 60% of the variation in individual-animal DMI. Further, no bias was found between observed and PLSR predicted DMI for either the empirical or mechanistic models. Further research is warranted to evaluate the robustness of these models across independent data sets.

However, these preliminary models do account for more of the individual-animal variation in DMI than those published previously by Anele et al. (2014) using BW and NE concentrations of the diet (r^2 of 0.13 to 0.25). Based on these findings, 28-d measurements of performance, feeding behavior, and ultrasound measurements may be useful in predicting DMI to improve management decisions of a livestock operation.

Similar to the DMI models, 28-d feeding behavior, ultrasound, and frame score measurements accounted for less of the variation in individual-animal DMI than 70-d measurements (0.30 vs 0.37). However, PLSR predicted RFI values based on 28-d traits were useful in correctly classifying 50% of animals into low-, med-, and high-RFI groups, with only 6% of animals being classified across 2 RFI groups (low-RFI vs. high-RFI or high-RFI vs. low-RFI). Accordingly, 28-d measurements of feeding behavior, ultrasound, and frame score may be useful in identifying animals with divergent RFI phenotypes for improving production efficiency.

Conclusion

Favorable selection for RFI has been limited by the absence of an affordable method for accurately quantifying individual-animal DMI. In production settings where direct measurements of DMI are not feasible, the industry relies on the use of prediction equations published by the National Research Council (**NRC**) to estimate DMI of animals. Although the simplicity and ease of application of prediction models make them advantageous for estimating DMI, current equations have limited ability to measure between-animal variation, hindering the precision of individual-animal determinations (Anele et al., 2014). In the current study, feeding behavior traits accounted for an additional 20% of the between-animal variation in DMI unaccounted for by ADG and mid-test $BW^{0.75}$, and 11% unaccounted for by DMR based on equations from Fox et al. (2001). These results indicate the usefulness of feeding behavior traits to account for additional between-animal variation in DMI, warranting their inclusion into future prediction models for DMI. Further, PLSR predicted RFI values, from the PLSR model developed to predict RFI using feeding behavior traits, were useful in classifying 91% of animals within 1 RFI class of that originally observed (low-RFI vs. high-RFI or high-RFI vs. low-RFI). Based on these findings, development of PLSR equations to predict RFI provides opportunity for producers to identify animals with divergent feed efficiency for selection or culling purposes with minimal risk of negative impacts to their operation.

Ongoing development of biosensor-based technologies to quantify feeding behavior patterns will provide opportunities to predict DMI and RFI in support of precision nutrition, and reduce the costs of identifying feed-efficient cattle. Given the strong repeatability estimates observed between feeding behavior patterns during the first 28-d and the last 42-d of the finishing period, opportunities may also exist to measure feeding behavior for a short duration to predict long term DMI and RFI. However, further research is warranted to determine the optimal measurement period for feeding behavior patterns, and to evaluate the robustness of PLSR-based models to predict DMI and RFI across independent data sets.

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Table 4. 1. Pearson correlations between performance and feed efficiency and feeding behavior traits in steers and heifers (3 Studies; n = 1,225).

Item[1]	ADG	DMI	G:F	RFI
ADG	**-**	**0.59**	**0.65**	0.00
DMI	**0.59**	**-**	**-0.20**	**0.71**
Bunk visit traits:				
BV frequency, events/d	**0.12**	**0.27**	**-0.11**	**0.39**
BV duration, min/d	**0.19**	**0.50**	**-0.25**	**0.54**
Max non-feeding interval, min	**-0.12**	**-0.10**	-0.05	**-0.09**
Meal traits:				
Meal frequency, events/d	**-0.09**	-0.06	-0.05	**0.07**
Meal duration, min/d	**0.28**	**0.40**	-0.04	**0.34**
Meal length, min/event	**0.22**	**0.26**	0.02	**0.14**
Intensity traits:				
HD duration, min/d	**0.13**	**0.45**	**-0.28**	**0.54**
HD duration per BV duration	-0.01	**0.26**	**-0.25**	**0.38**
HD duration per meal duration	-0.04	**0.25**	**-0.29**	**0.38**
BV events per meal event	**0.16**	**0.23**	-0.02	**0.19**
Day-to-day variation traits[2]:				
BV frequency SD, events/d	-0.05	**0.12**	**-0.17**	**0.31**
BV duration SD, min/d	0.02	**0.24**	**-0.22**	**0.34**
Max non-feeding interval SD, min	**-0.21**	**-0.22**	**-0.07**	**-0.09**
Meal frequency SD, events/d	**-0.15**	**-0.09**	**-0.10**	**0.06**
Meal duration SD, min/d	**0.06**	**0.14**	**-0.06**	**0.16**
Meal length SD, min/event	**0.15**	**0.18**	0.02	**0.08**
HD duration SD, min/d	0.00	**0.28**	**-0.27**	**0.41**

[1] Performance, feed efficiency, and feeding behavior traits were adjusted for the random effect of trial to generate phenotypic correlation coefficients; correlations in bold are different from zero at $P < 0.0$; RFI = residual feed intake.

[2] Day-to-day variation traits = day-to-day standard deviation for each trait.

Table 4. 2. Comparison of dry matter required (DMR) equations to predict dry matter intake (DMI) of growing steers and heifers using partial least squares regression (PLSR) models.

Model[1]	DMR equation components[2]	N	Cross-validation[3]	
			RMSE	R^2_{cv}
Based on Guiroy et al. (2001)	BF, LMA, pHCW, QG, and BW	1205	0.98	0.50
Based on Baker et al. (2006)	BF, LMA, pHCW, and BW	1217	1.02	0.47
Based on Fox et al. (1988)	HH, Age, BW, gender	1220	1.00	0.49

[1] Dry matter required (DMR) estimated using three independent sets of equations were included as independent-variables to predict individual-animal DMI.

[2] BW is mid-test $BW^{0.75}$ and ADG measured during the entire trial. The remaining components are based on initial measurements: BF is back fat (cm); LMA is LM area (cm); pHCW is predicted HCW ((pHCW = EBW - 30.26)/1.362); QG is quality grade estimated from initial intramuscular fat (4 = Select, 5 = Choice-, 6 = Choice, 7 = Choice+, and 8 = Prime); HH is hip height (cm), Age is age in d.

[3] R^2_{cv} = coefficient of determination for cross-validation; RMSE = Root mean square error.

Table 4. 3. Validation of empirical and mechanistic models to predict dry matter intake in growing steers and heifers.

	Cross-validation[1]					Independent-validation[2]				
Item	N	RMSE	R^2_{cv}	Bias	*r*	N	RMSE	R^2_{v}	Bias	*r*
Empirical models for DMI[3]										
Base model (ADG + MBW + frame score[4])	1220	0.91	0.58	0.00	0.76*	320	0.92	0.48	0.09	0.70*
Base model + feeding behavior traits	1220	0.71	0.74	0.00	0.86*	320	0.73	0.68	0.18	0.82*
Base model + feeding behavior + ultrasound traits	1211	0.70	0.75	0.00	0.87*	316	0.73	0.68	-0.11	0.82*
Mechanistic models for DMI[3]										
DMR (based on Fox et al., 2001)	1220	1.00	0.49	0.00	0.70*	320	0.90	0.51	0.17	0.71*
DMR + feeding behavior traits	1220	0.83	0.65	0.00	0.80*	320	0.61	0.62	-0.01	0.79*
DMR + feeding behavior + ultrasound traits	1220	0.79	0.68	0.00	0.82*	317	0.79	0.63	0.10	0.79*

[1] Cross-validation was accomplished using *k*-fold cross-validation in which samples were randomly subdivided into 7 groups, with all groups being used for calibration and validation, iteratively.

[2] Independent-validation was accomplished using data from Studies 1 and 2 (6 trials; n = 904) for calibration and data from Study 3 for validation (2 trials; n = 321).

[3] Independent variables were excluded from each model if variable of importance in projection (VIP) scores were < 0.80.

[4] Frame score was calculated by gender according to the Beef Improvement Federation guidelines 1991).

RMSE = Root mean square error; R^2_{cv} = coefficient of determination for cross-validation; R^2_{v} = coefficient of determination for validation, Bias = (∑ observed data/N) – (∑ predicted NRS data/N), *r* = Spearman's rank correlation between observed and predicted values.

Table 4. 4. Validation of partial least squares regression (PLSR) models to predict residual feed intake (RFI) in growing steers and heifers.

	Cross-validation[1]					Independent-validation[2]				
PLSR models for RFI[3]	N	RMSE	R^2_{cv}	Bias	*r*	N	RMSE	R^2_{v}	Bias	*r*
Feeding behavior traits	1225	0.71	0.34	0.00	0.58*	321	0.76	0.31	0.12	0.55*
Feeding behavior + ultrasound traits	1215	0.69	0.36	0.00	0.60*	311	0.73	0.36	0.16	0.60*
Feeding behavior + ultrasound traits + frame score[4]	1212	0.68	0.38	0.00	0.61*	311	0.71	0.38	0.00	0.62*

[1] Cross-validation was accomplished using *k*-fold cross-validation in which all samples were used for calibration and validation iteratively.

[2] Independent-validation was accomplished using data from Study 1 and 2 (6 trials; n = 904) for calibration and data from Study 3 for validation (2 trials; n = 321).

[3] Independent variables were excluded from each model if variable of importance in projection (VIP) scores were less than 0.80.

[4] Frame score was calculated by gender according to the Beef Improvement Federation guidelines (1991).

RMSE = Root mean square error; R^2_{cv} = coefficient of determination for cross-validation; R^2_{v} = coefficient of determination for validation, Bias = (∑ observed data/N) – (∑ predicted NRS data/N), *r* = Spearman's rank correlation between observed and predicted values.

Table 4. 5. Repeatability estimates for feeding behavior traits of growing steers and heifers consuming high-grain finisher diets.

Item[1]	Study 1	Study 2	Study 3
N	497	407	321
Gender	Steers	Heifers	Steers
Performance and growth traits:			
ADG, kg/d	**0.11**	**0.34**	**0.35**
DMI, kg/d	**0.67**	**0.78**	**0.79**
Feed efficiency traits:			
RFI, kg/d	**0.55**	**0.60**	**0.72**
Bunk visit traits:			
BV frequency, events/d	**0.63**	**0.76**	**0.80**
BV duration, min/d	**0.75**	**0.82**	**0.85**
Max non-feeding interval, min	**0.66**	**0.72**	**0.66**
Meal traits:			
Meal frequency, events/d	**0.55**	**0.63**	**0.63**
Meal duration, min/d	**0.65**	**0.75**	**0.83**
Meal length, min/event	**0.59**	**0.67**	**0.76**
Intensity traits:			
HD duration, min/d	**0.83**	**0.84**	**0.87**
HD duration per BV duration	**0.89**	**0.84**	**0.90**
HD duration per meal duration	**0.81**	**0.83**	**0.86**
BV events per meal event	**0.52**	**0.60**	**0.79**
Day-to-day variation traits[2]:			
BV frequency SD, events/d	**0.44**	**0.43**	**0.50**
BV duration SD, min/d	**0.40**	**0.24**	**0.22**
Max non-feeding interval SD, min	**0.17**	0.05	**0.19**
Meal frequency SD, events/d	**0.54**	**0.46**	**0.51**
Meal duration SD, min/d	**0.42**	**0.46**	**0.46**
Meal length SD, min/event	**0.44**	**0.48**	**0.57**
HD duration SD, min/d	**0.59**	**0.63**	**0.64**

[1] Pearson correlations between feeding behavior traits measured during the first 28 d and last 42 days of each trial; Within Study, variables were adjusted for the random effects of trial (3 trials in Study 1; 3 trials in Study 2; 2 trials in Study 3); Correlations different from zero are bold (*P* < 0.05).

[2] Day-to-day variation traits = day-to-day standard deviation for each trait.

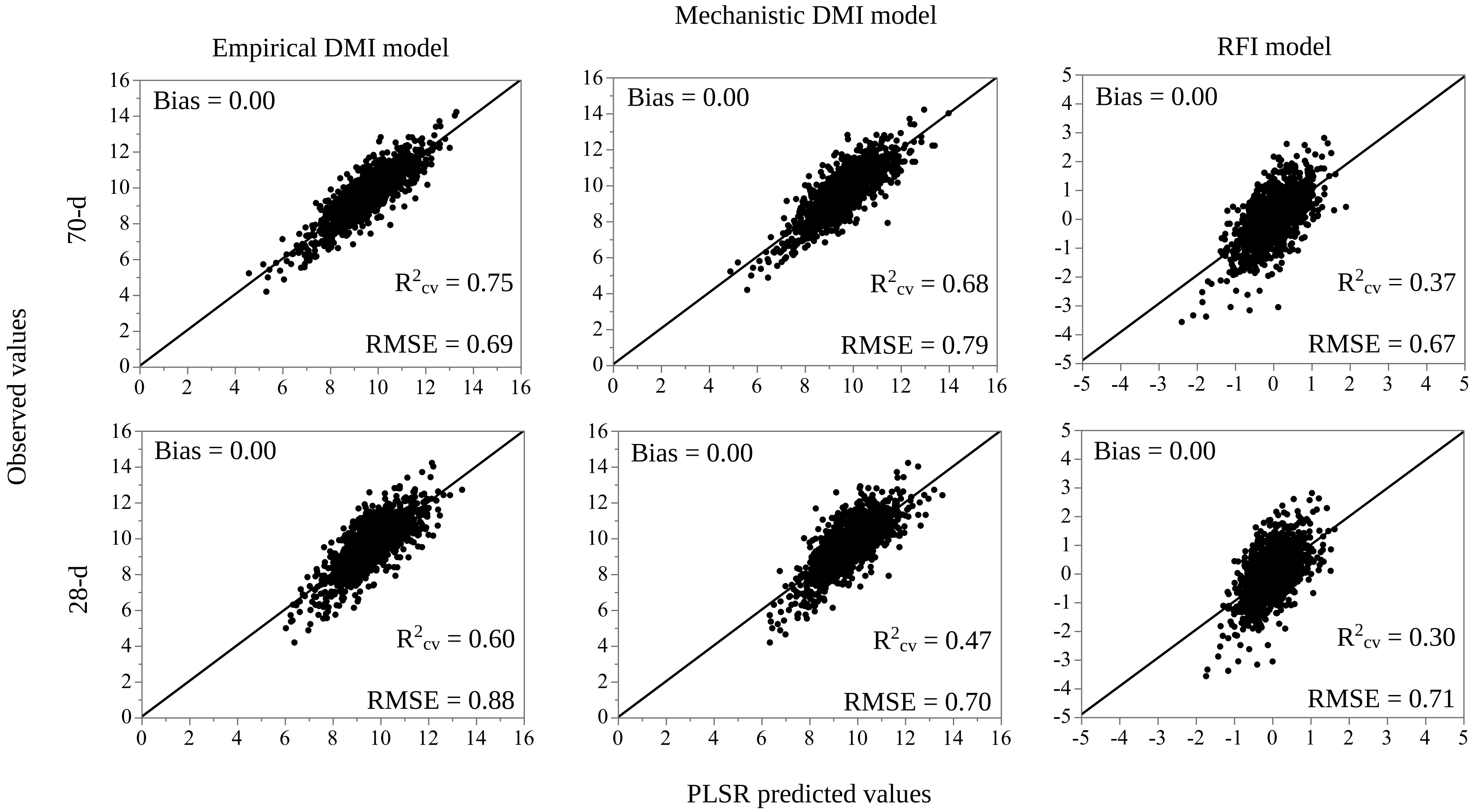

Figure 4. 1. Cross-validation results of partial least squares regression (PLSR) models for dry matter intake (DMI) and residual feed intake (RFI) using performance, feeding behavior, and ultrasound traits measured during the entire trial (70-d) or during the first 28 d of each trial (28-d). Independent variables were excluded from each model if variable of importance in projection (VIP) scores were less than 0.80. Empirical DMI model included mid-test BW0.75, ADG, feeding behavior, and ultrasound traits; Mechanistic DMI model included dry matter required (DMR) based on the Fox et al. (2001), feeding behavior, and ultrasound traits; RFI model included feeding behavior, ultrasound, and frame size.

CHAPTER V

CHARACTERIZATION OF FEEDING BEHAVIOR PATTERNS IN GROWING HOLSTEIN HEIFERS WITH DIVERGENT RFI

Introduction

The efficient use of feed by dairy cattle is critical for the economic success of dairy operations as feed is the largest variable input cost of production, accounting for a majority of the total farm expenses. Residual feed intake has been recognized as an ideal trait for use in selection programs for improved feed efficiency as it is moderately heritable (Schenkel et al., 2004) and accounts for the variation in individual animals' feed efficiency, independent of growth and production. Efficient or low-RFI dairy heifers consumed 13 to 20% less feed (Williams et al., 2011; Waghorn et al., 2012; Connor et al., 2019) compared to their inefficient or high-RFI counterparts with no impact on growth and performance. However, application of favorable selection programs for feed efficiency have been limited by the absence of an applicable method for determining individual animal intake, especially for large populations. Accordingly, research has aimed to identify biological determinants of feed efficiency that are practical for application in commercial operations.

Current literature has identified numerous mechanisms associated with variations in feed efficiency such as protein turnover, tissue metabolism, stress, digestibility, heat increment, fermentation, physical activity, body composition, and feeding patterns

(Richardson and Herd, 2004; Nkrumah et al., 2007; Lancaster et al., 2009b; Kayser and Hill, 2013). However, the mechanisms regulating individual-animal feed efficiency have yet to be fully understood. Recent advancements in electronic RFID technology have enabled the development of large-scale systems capable of measuring individual-animal feeding behavior patterns for large numbers of animals. Research regarding the associations between individual-animal feeding behavior patterns and feed efficiency are warranted. Such associations are likely, as energetic costs associated with feeding activities such as time spent feeding, physical activity, and rate of eating, impact daily energetic cost (Susenbeth et al., 1998; Lancaster et al., 2009b).

In beef cattle, distinct differences in feeding behavior patterns have been observed in cattle with divergent RFI phenotypes, such that low-RFI animals visit the bunk fewer times per day (Nkrumah et al., 2006; Alende et al., 2016), have lower daily feeding durations (Nkrumah et al., 2006; Gomes et al., 2013) and consume DM at slower rates (Lancaster et al., 2009b; Kelly et al., 2010a) compared to high-RFI animals. In growing dairy heifers, similar results were reported by Green et al. (2013) for groups with divergent RFI, as the most efficient heifers (10%) had fewer meals and reduced daily feeding durations compared to the most inefficient heifers (10%). However, only weak correlations were reported for feeding behavior traits and RFI when all animals were considered for analysis. Further, Williams et al. (2011) did not observe a difference in the feeding duration of growing dairy heifers, however efficient heifers did consume feed at a slower rate than inefficient heifers in their study.

In lactating dairy cows, activity, feeding behavior, and unidentified activity accounted for 26.5, 21.3, and 10.6% of the variation in residual energy intake (REI), respectively (Fischer et al., 2018). However, apparent confounding results were observed by the authors between behavior, activity, digestibility, and rumen-temperature so it was not possible to draw a conclusion on biological traits and their association with feed efficiency in their study. Nevertheless, daily bunk visit (**BV**) events accounted for 20% of the variation in DMI of growing beef heifers (Kelly et al., 2010a), and daily BV frequency and duration accounted for 44% (de Haer et al., 1993) and 35% (Lancaster et al., 2009b) of the variation in DMI in pigs and growing bulls, respectively. Although few studies have investigated the associations between feeding behavior patterns and RFI in growing dairy heifers, results indicate the presence of a similar relationship between feeding behavior patterns and RFI. Therefore, further investigation is warranted in examining the relationship between feeding behavior patterns and feed efficiency in growing dairy heifers, especially given that feeding behavior traits were found to be highly repeatable (Gibb et al., 1998; Kelly et al., 2010b), and moderately heritable (Nkrumah et al., 2007).

The objectives of this paper were to characterize feeding behavior patterns of growing Holstein heifers with divergent RFI phenotypes, quantify the between-animal variation in feed efficiency accounted for by performance and feeding behavior traits of these animals, and to evaluate the use of PLSR to predict individual-animal RFI and DMI.

Material and methods

Experimental animals and design

Data were collected from 38 trials utilizing 1,787 growing Holstein heifers (initial BW = 277 ± 66 kg; age = 287 ± 65 d). For each trial, heifers were housed in pens with 8 electronic feed bunks (GrowSafe Systems LTD., Airdrie, AB, Canada) and offered *ad libitum* feed and clean drinking water. Heifers were adapted to a diet consisting of approximately 50% corn silage, 26% triticale, 13% soybean hulls, 3% premix, 3% corn grain, 2.5% soybean meal, 1.5% clover hay, and 1% wheat straw (ME = 2.4 Mcal/kg DM; CP = 12.3% DM) for a minimum of 21 d. Following adaptation, feed intake, performance, and feeding behavior traits were measured for a minimum of 70 d. For each trial, a minimum of 3 serial BW were measured for each animal during the 70 d feeding period.

Computation of traits

Individual animal feed intake was computed using a subroutine of the GrowSafe 4000E software (Process feed intakes) as described by Parsons et al. (2019). For each trial, data was deleted for a pen when the assigned feed disappearance (**AFD**) of an individual bunk in a pen was below 85% or the average AFD of the pen was less than 90%. When data was deleted due to system failure, daily intake values were determined by linear regression of DMI on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC).

Linear regression of serial BW data on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC) was used to determine mid-test $BW^{0.75}$ and ADG. Residual feed intake was computed as the difference between actual and expected DMI from the linear regression of mean DMI on MBW and ADG as described by Koch et al. (1963). Trial was included as a fixed effect in this model, with mid-test $BW^{0.75}$ and ADG accounting for 59% of the variation in DMI. Heifers were ranked by RFI and classified into one of three RFI phenotypic groups; low (< 0.5 SD), medium (± 0.5 SD) or high (> 0.5 SD).

Feeding behavior traits were computed based on the frequency and duration of BV and meal events as described by Parsons et al. (2019). Bunk visit events commenced when an animals' electronic identification (**EID**) tag was detected by a feed bunk and ended when the duration of the time between the last 2 consecutive EID readings exceeded 100-s, the EID tag was detected in another feed bunk, or the EID of another animal was detected at the same feed bunk (Mendes et al., 2011). Bunk visit frequency and duration were defined as the number and the sum of duration of BV events recorded during a 24-h period, regardless of whether feed was consumed, respectively. The interval between BV events was defined as the non-feeding interval (**NFI**), with maximum NFI being defined as the longest NFI during a 24-h period. Head down (**HD**) duration was computed as the sum of EID tag readings detected each day, multiplied by the scan rate of the GrowSafe system, which was 1.0 reading per second (Jackson et al., 2016). Time to bunk (**TTB**) was computed as the interval between feed delivery and each animal's first BV event each day.

Meals were defined as the clusters of BV events that are differentiated from the next meal by a nonfeeding interval that is longer compared with the nonfeeding intervals within a meal (Bailey et al., 2012). The longest nonfeeding interval considered to be a part of a meal is defined as the meal criterion. Meal criterion was estimated by fitting a 2-pool, Gaussion-Weibull bimodal probability density function to the $\log_{10}$-transformed interval lengths between BV events for each animal using the Meal Criterion Calculation Software (MCC; ver. 1.7.6836.33854; http://nutritionmodels.tamu.edu). Meal criterion was defined as the intersection of the Gaussion-Weibull probability density functions (Bailey et al., 2012). Meal criterion was used to cluster bunk visit events into meals, with meal frequency, length, and duration being defined as the number of meal events, average meal event length, and sum of length of meal events recorded each day, respectively (Miller, 2016).

Day-to-day variation of feeding behavior traits were calculated as the SD of the residuals of actual vs. predicted values based on linear regression of feeding behavior traits on day of trial using the Standard Least Squares procedure of JMP (SAS Inst. Inc., Cary, NC). Day-to-day variation was calculated for BV frequency and duration, HD duration, maximum NFI, TTB, meal frequency, meal duration, and meal length. Additionally, 3 ratio traits were computed; BV frequency per meal event, HD duration per meal event, and HD duration per BV event.

Overall, 19 feeding behavior traits were evaluated, including frequency and duration of BV and meal events, HD duration, meal length, maximum non-feeding interval, TTB, corresponding day-to-day variation (SD) of these traits, and ratios of HD duration per BV duration, HD duration per meal duration, and BV events per meal event.

Statistical Analysis

To evaluate the effect of RFI classification on performance, feed efficiency, and feeding behavior traits, a mixed model (JMP; SAS Inst. Inc., Cary, NC) was used that included the random effect of trial and fixed effect of RFI classification. Tukey-Kramer test was used to evaluate the difference among treatment means. To generate phenotypic correlation coefficients, performance, feed efficiency, and feeding behavior traits were adjusted for the random effect of trial, then used in the multivariate platform of JMP (SAS Inst. Inc., Cary, NC) to obtain phenotypic correlations.

Preliminary partial least squares regression (**PLSR**) models were developed to quantify the variation in RFI and DMI explained by performance and feeding behavior traits in JMP (SAS Inst. Inc., Cary, NC). For each of the preliminary models, optimal number of components were determined by minimizing the root mean squared error of prediction (**RMSEP**) using the k-fold cross-validation procedure. This cross-validation technique involves the partitioning of observations into *k* subsets, which will be used iteratively as validation sets for models developed using the remaining observations. Further, for each of the preliminary PLSR models, all original independent variables were retained, with variables of importance in projection (**VIP**) scores being used to identify traits to be used in subsequent prediction models for RFI and DMI.

For model development, feeding behavior traits were divided into 3 categories: BV and meal traits, intensity traits, and day-to-day variation of feeding behavior traits. Five preliminary models were developed for RFI: 1) included BV and meal traits; 2) included intensity traits; 3) included day-to-day variation of feeding behavior traits (**Var-FB**); 4) included BV, meal, and intensity traits (**Daily-FB**); and 5) included BV, meal, intensity, and the day-to-day variation of feeding behavior traits as independent variables.

Since performance and growth traits are known to influence DMI, preliminary PLSR models for DMI were derived from an initial model that included mid-test BW$^{0.75}$ and ADG as independent variables (base model). The base model was used to compare the R^2 and RMSE of the remaining preliminary models for DMI which included the base model: 1) plus BV and meal traits; 2) plus BV, meal and intensity traits; and 3) plus BV, meal, intensity and day-to-day variation of feeding behavior traits as independent variables.

Partial least squares regression models were also developed to predict RFI and DMI in this study, using cross-validation procedures as described above. For prediction of RFI, BV, meal, intensity, and day-to-day variation traits were included as independent variables. For prediction of DMI, mid-test BW$^{0.75}$ and ADG were included with BV, meal, intensity, and day-to-day variation traits as independent variables. For each of the prediction models, independent variables were excluded if the VIP score was less than 0.80. This variable selection technique was proposed by Wold (1966), to ensure the robustness of the PLSR prediction models. Predictive accuracy of the models was evaluated by the coefficient of determination for cross-validation ($\mathbf{R^2_{cv}}$), and model precision evaluated using the RMSE. Additionally, the bias between observed and PLSR predicted values were determined, and differences between mean observed and PLSR predicted values, as well as model residuals across years, months, and age of cattle were evaluated by *t* test using the fit model procedures in JMP (SAS Inst. Inc., Cary, NC).

Finally, to evaluate the application of PLS to identify animals with divergent RFI the Contingency Platform in JMP (SAS Inst. Inc., Cary, NC) was used to compare observed RFI class with RFI class based on PLS predicted RFI.

Results and discussion

Intake, performance, and feed efficiency

Effects of RFI classification on performance and efficiency traits in growing dairy heifers are presented in Table 5.1. As expected, low-RFI animals consumed 24% less feed and had 33% higher G:F than their high-RFI counterparts, with no differences in initial or final BW or ADG. These results agree with other studies which reported a 13 to 20% reduction in feed consumption of low-RFI dairy heifers compared to their high-RFI counterparts (Williams et al., 2011; Waghorn et al., 2012; Connor et al., 2019).

Feeding behavior traits

The effect of RFI classification on feeding behavior traits in growing dairy heifers is presented in Table 5.2. Low-RFI heifers had 22% fewer ($P < 0.001$) BV events and spent 21% less ($P < 0.001$) time at the bunk each day compared to high-RFI heifers.

In beef cattle, previous studies have reported similar results as low-RFI animals visited the bunk fewer times per day (Golden et al., 2008; Durunna et al., 2011) and had lower daily feeding durations (Durunna et al., 2011). In dairy heifers, Green et al. (2013) observed a 5% increase in the total daily feeding duration of the 10% least efficient heifers compared to the 10% most efficient heifers, however in another study, no differences were observed amongst dairy heifers with divergent RFI (Williams et al., 2011). In regard to eating rate, no differences were observed between the BV eating rate of low- and high-RFI dairy heifers in the current study. Bunk visit frequency and eating rates were not evaluated in either of the previous studies involving dairy heifers.

In the current study, low-RFI heifers had longer meal criterion ($P < 0.001$), which corresponded to reduced ($P < 0.001$) daily meal frequency of low-RFI heifers compared to high-RFI heifers. Further, low-RFI heifers spent 4% less ($P < 0.001$) time consuming meals each day and had 16% greater ($P < 0.001$) meal length than high-RFI heifers. These results agree with those reported for growing Holstein-Friesian heifers as low-RFI heifers had 23% fewer meal events each day that were also 16% longer in length compared to their high-RFI counterparts (Green et al., 2013). However, in the current study, compared to high-RFI heifers, low-RFI heifers had lower ($P < 0.001$) meal eating rates, which is in contrast to results reported by Green et al. (2013) and Williams et al. (2011) as they observed a 14 and 15% increase in the meal eating rates of inefficient heifers compared to their efficient counterparts, respectively. For beef cattle, results have been inconsistent with some studies reporting slower meal eating rates for low-RFI cattle compared to their nonefficient counterparts (Lancaster et al., 2009b;

Fitzsimons et al., 2014), and others reporting higher meal eating rates for low-RFI cattle (Kayser and Hill, 2013). Overall, the associations between meal traits and RFI are less consistent than for BV traits, which is likely a reflection of the variation in methods used determine meal criterion as individual-animal meal criterion values were determined in the current study, while previous studies have used a standard meal criterion value across animals.

Compared to high-RFI heifers, low-RFI heifers appeared to be less assertive in their feeding patterns as they had a 45% reduction in their HD duration, took 10 min longer ($P < 0.001$) to approach the bunk following feed delivery, and had 43 and 33% reductions in their HD duration per BV duration and HD duration per meal duration, respectively. Although HD durations have not been reported in growing dairy cattle, Kayser and Hill (2013) found a 31% reduction in HD duration for low-RFI Hereford and Angus bulls compared to their high-RFI counterparts, which is in agreement with the current study. Similar reductions were also observed by Lancaster et al. (2009b) for efficient Brangus heifers compared to their nonefficient counterparts, and for steers and heifers in the previous chapters.

Compared to low-RFI heifers, high-RFI heifers exhibited greater ($P < 0.001$) day-to-day variation in DMI, BV frequency and duration, HD duration, and meal frequency, and less day-to-day variation in max non-feeding interval and TTB. Although these results agree with those reported in the previous chapters, low-RFI heifers in the current study also exhibited more day-to-day variation in meal duration and length, which contrasts with the results reported for beef cattle previously. These results are the first to report on the associations between RFI and day-to-day variation of feeding patterns in dairy cattle. In beef cattle, day-to-day variations in individual-animal intake and pen intake have been found to negatively correlate with G:F of cattle (Galyean et al., 1992; Stock et al., 1995; Soto-Navarro et al., 2000). The literature suggests that increased day-to-day variation in DMI can be attributed to metabolic disorders in cattle (Gibb and McAllister, 1999) or can directly predispose cattle to metabolic disorders (Galyean et al., 1992). Accordingly, nutritionist and feedlot managers generally attribute metabolic disturbances such as subclinical acidosis to increased daily intake variation (Gibb and McAllister, 1999; Soto-Navarro et al., 2000; Pritchard and Bruns, 2003; Schwartzkopf-Genswein et al., 2003). However, in the current study, incidences of acidosis would be unexpected as the heifers were consuming a high-roughage corn silage diet. Further, high-RFI animals maintained higher levels of DMI compared to low-RFI animals throughout the study. Alternatively, the differences in the day-to-day variation of heifers with divergent RFI phenotypes in the current study may be associated with differences in digestibility (Cooper et al., 1997) or appetite signaling mechanisms (Perkins et al., 2014) as discussed in the previous chapters. However, these mechanisms were not evaluated in the current study, so no determinations can be made. Regardless, the results from this study further indicate the associations between day-to-day variation of feeding patterns and RFI, warranting further research to investigate the mechanisms responsible for such associations.

Pearson correlations between performance, feed efficiency, and feeding behavior traits in growing Holstein heifers are presented in Table 5.3. As expected, the strongest correlation was observed between DMI and RFI, which agrees with previous studies (Nkrumah et al., 2007; Lancaster et al., 2009a; Montanholi et al., 2009; Kelly et al., 2010a; Williams et al., 2011; Green et al., 2013). Additionally, as expected, no correlation was observed between ADG and RFI. Of the feeding behavior traits, strong correlations ($r > 0.50$) were observed between RFI and HD duration, HD duration per BV duration, HD duration per meal duration, BV frequency, and the day-to-day variation of HD duration. Overall, the correlation observed between HD duration and RFI in the current study agrees with values previously reported for Angus or Hereford bulls (0.37 to 0.52; Lancaster et al., 2009b; Kayser and Hill, 2013) and composite Angus steers (0.57; Parsons, 2018). Head down duration, HD duration per meal duration, and BV duration also had strong correlations ($r > 0.50$) with DMI in this study. In comparing BV, meal, and intensity traits, meal traits had the lowest correlations between RFI and DMI. Given that meal traits are generally considered to be the most biologically relevant feeding behavior trait, as they are less impacted by social hierarchy, bunk competition, and environmental changes as compared to BV traits (Bailey, 2011), these results were unexpected. However, associations between meal traits and RFI have been inconsistent, and therefore, these results are not unfounded. The correlation between meal frequency and RFI ($r = 0.27$) in the current study was higher than the correlation reported in numerous studies (ranged from 0.05 to 0.18; Robinson and Oddy, 2004; Nkrumah et al., 2007; Montanholi et al., 2009; Green et al., 2013; Lin et al., 2013), comparable to the correlation reported for Angus bulls (0.26; Lancaster et al., 2009b), and lower than the correlation reported by Kelly et al. (2010a) for growing beef heifers (0.45). Overall, all feeding behavior patterns of growing Holstein heifers in the current study significantly correlated with RFI, and all except meal duration significantly correlated with DMI. Further, only weak (< 0.17) correlations were observed between feeding behavior traits and ADG. These results further reveal the existence of strong associations between feeding behavior patterns and RFI, and suggest that feeding behavior patterns may be useful indicators for DMI or RFI.

Overall, results from this study indicate that distinctive differences exist in the feeding behavior patterns of growing Holstein heifers with divergent RFI. More specifically, low-RFI heifers visited the bunk fewer times each day, had lower daily feeding durations, and less day-to-day variation in BV and intensity traits.

PLSR to quantify associations between feeding behavior and RFI

Summary statistics for PLSR models developed to quantify the variation in RFI accounted for by feeding behavior patterns are presented in Table 5.4. Bunk visit and meal traits accounted for 32% of the variation in RFI, while intensity traits accounted for 29%, and day-to-day variation of BV, meal, and intensity traits accounted for 33%. When BV, meal, and intensity traits were included together as independent variables, they did not additively explain the variation in RFI. However, intensity traits did explain an additional 9% of the variation in RFI unexplained by BV and meal traits, with an additional 2% of the variation being explained upon inclusion of day-to-day variation traits into the model. Although the number of independent variables were not identical across models, which may have impacted the results, these findings indicate that BV, meal, intensity, and day-to-day variation traits each account for proportions of the variation in RFI (Figure 5.1). Overall, feeding behavior traits accounted for 43% of the variation in RFI, with 57% of the variation in individual-animal RFI being unaccounted for in this study.

In addition to feeding behavior traits, performance and growth traits are known to influence DMI. Thus, PLSR models were also developed to quantify the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. The first of these models was used as the base model from which to compare the R^2_{cv} and RMSE of the remaining models and included mid-test $BW^{0.75}$ and ADG as independent variables (base model). Alone, the base model accounted for 51% of the variation in individual-animal DMI. Inclusion of BV and meal traits to the base model accounted for an additional 17% of the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. Further, sequential inclusion of intensity traits accounted for an additional 5%, and inclusion of day-to-day variation traits accounted for an additional 1% of the variation in DMI. These findings are illustrated in Figure 5.1. Overall, feeding behavior traits accounted for 23% of the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG, with only 26% of the variation in DMI being unexplained in this study.

Overall, feeding behavior patterns accounted for more of the variation in feed efficiency than feed consumption (43% vs 23%), which is similar to the results observed for steers and heifers presented in previous chapters. Further, feeding behavior traits did significantly account for variation in individual-animal DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. Differences in energetic cost of eating, chewing, and ruminating, as well as physical activity associated with BV frequency and duration may have been associated with the observed variation in RFI. Specifically, high-RFI animals may have had increased energetic costs due to increased BV frequency and duration. This idea is supported as energy expenditures associated with eating have been shown to be strongly related to time spent eating (Susenbeth et al., 1998), which was longer in high-RFI animals compared to low-RFI animals in this study. Additionally, Susenbeth et al. (1998) found a positive correlation between time spent standing and total energy expenditure. Although activity data was not measured in this study, increased BV frequency and duration of high-RFI animals may be related to increased activity as positive correlations between physical activity and RFI have been reported in ruminants (Herd et al., 2004) and non-ruminants (Luiting et al., 1991; Bunger et al., 1998). Lastly, although the literature is sparse in regards to the impacts of day-to-day variation of feeding patterns on RFI and DMI, results from this study further indicate a relationship.

Based on the distinctive differences observed in feeding behavior patterns of dairy heifers with divergent RFI phenotypes, feeding behavior traits may serve as useful biomarkers for identifying animals with divergent feed efficiency. Previously, researchers have used multiple linear regression (MLR) models to quantify the associations between feeding behavior traits and RFI, with feeding behavior traits accounting for 13 to 44% of the variation observed in individual-animal RFI (Lancaster et al., 2009b; Kayser and Hill, 2013; Miller, 2016). In the current study, BV, meal, intensity, and day-to-day variation of feeding behavior traits accounted for 43% of the variation in individual-animal RFI and 23% of the variation in individual-animal DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. These results indicate that feeding behavior traits may be useful biomarkers for RFI or DMI, warranting inclusion of such traits into future prediction models for RFI or DMI.

PLSR to predict RFI and DMI using feeding behavior traits

Prediction models for RFI and DMI were developed using performance, growth, and feeding behavior data as presented in the previous section. Based on the results presented in Table 5.4, BV, meal, intensity, and day-to-day variation traits were considered as independent variables in the prediction model for RFI, as they each accounted for additional variation. For the prediction of DMI, mid-test $BW^{0.75}$ and ADG were also considered as independent variables in addition to BV, meal, intensity, and day-to-day variation traits, as they also accounted for additional variation. Variable of importance scores and equation coefficients for the PLSR prediction models for RFI and DMI are presented in Table 5.5. Based on criterion proposed by Wold (1966), independent variables were excluded from the prediction model if VIP score exceeded 0.80. Thus, the coefficients are presented for only those independent variables included in the final prediction model that had VIP scores greater than 0.80.

Of the feeding behavior traits, HD duration, HD duration per BV duration, HD duration per meal duration, and the day-to-day variation of HD duration had the highest VIP scores for the RFI model, indicating that they were the most influential traits in predicting individual-animal RFI. Given the strong correlations observed between these traits and RFI, these results were expected. For the DMI model, HD duration per meal duration, meal frequency and length, and the day-to-day variation of meal length, were the feeding behavior traits with the highest VIP scores. Unlike for the RFI model, these results were not as expected as moderate correlations were observed between meal traits and DMI. However, given the proposed associations between meal traits and individual-animal satiety mechanisms (Bailey, 2011), it is logical that meal traits would be more influential than most BV traits in predicting DMI of individual-animals as observed in the current study.

Cross-validation results for PLSR models developed to predict RFI and DMI are presented in Figure 5.2. The model developed to predict RFI included 10 feeding behavior traits as independent variables and resulted in cross-validation R^2 (R^2_{cv}) and root mean square error (RMSE) of 0.41 and 0.54, respectively. No differences ($P = 0.99$) were observed between the mean observed and PLSR predicted RFI values for this model. Although feeding behavior traits only accounted for 41% of the variation in individual-animal RFI, they were useful in correctly classifying 56% of heifers into low-, medium-, or high-RFI classes, with only 3% of heifers incorrectly classified across 2 RFI groups (low-RFI to high-RFI or high-RFI to low-RFI). Further, 76% of the most- and least-efficient heifers (± 10%) were correctly classified. These results indicate that PLSR models to predict RFI using feeding behavior traits may be useful in identifying animals with favorable feed efficient phenotypes for selection as there is only a 3% chance of.mis-classifying an animal across divergent RFI groups.

The prediction model for DMI included mid-test $BW^{0.75}$, ADG, and 10 feeding behavior traits as independent variables. Cross-validation R^2 and RMSE of this prediction equation were 0.70 and 0.79, respectively. Further, no differences ($P = 0.98$) were observed between observed and PLSR predicted DMI. Thus, this equation accounted for 70% of the variation in individual-animal DMI, which is comparable to results previously reported for the prediction of DMI by the n-alkane technique (18 to 86%; Berry et al., 2000; Ferreira et al., 2007; Olivan et al., 2007; Hafla et al., 2012), fecal NIRS methods (60 to 69%; Johnson et al., 2017), or by empirical equations (54 to 81%; Hoffman et al., 2008; Oliveira and Ferreira, 2016). However, the current model appears to be more robust in predicting independent data sets, as the R^2 of validation for PLSR prediction models developed using data from the 2017 trials (n = 607) to predict the 2018 trials (n = 1180) or from the first 19 trials (n = 905) to predict the last 19 trials (n = 881) were 0.68 and 0.71, respectively. When an independent validation was completed by Johnson et al. (2017), validation R^2 of the fecal NIRS prediction model was reduced from 0.69 to 0.05, indicating that the current model lacked the diversity and size necessary to predict DMI of independent data sets. When these empirical models were applied to the current data set, the models accounted for 36 to 41% of the variation in individual-animal DMI, which was lower than that observed for the PLSR model for DMI. Thus, the current PLSR model accounted for more of the variation in individual-animal DMI than the evaluated empirical models. However, further testing of the current model will be required to evaluate its' robustness when applied outside the boundaries of the studied system (Pulina et al., 2013).

Residuals from the PLSR model to predict RFI and DMI are plotted by year, month, and initial age of animals at the start of each trial in Figure 5.3. Although significant differences ($P < 0.05$) were observed in the means across years, months, and age, there were no obvious patterns observed in regards to model performance.

In summary, feeding behavior traits accounted for 41% of the variation in individual-animal RFI, with PLSR-predicted RFI being able to correctly classify 56% of heifers into low-, medium-, and high-RFI groups, with only 3% of animals being incorrectly classified across 2 RFI groups (low-RFI to high-RFI or high-RFI to low-RFI). Further, feeding behavior traits in combination with ADG and mid-test $BW^{0.75}$ accounted for 70% of the variation in individual-animal DMI, which was greater than that obtained using previously developed empirical equations. The PLSR model to predict DMI was found to be robust across years, months, and age of animals, further indicating the robustness of feeding behavior patterns in predicting individual-animal DMI.

Conclusion

This study provides evidence that strong associations exist between daily feeding behavior patterns and the day-to-day variation of such patterns and RFI in growing Holstein heifers. Specifically, efficient heifers visited the bunk fewer times each day, spent less time consuming feed, and had reduced day-to-day variation in DMI and feeding behavior patterns. These distinct differences in feeding behavior patterns accounted for 43% of the variation in RFI and explained 29% of the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. When feeding behavior traits were used to develop prediction models for RFI, 41% of the variation in RFI was accounted for in the cross-validation set, with predicted RFI values being useful in classifying heifers into low-, medium-, and high-RFI groups. For prediction of DMI, feeding behavior traits in combination with ADG and mid-test $BW^{0.75}$ accounted for 70% of the variation in DMI of the cross-validation, and 68 to 71% of the variation when independent validation was accomplished.

Based on the results from this study, feeding behavior patterns may serve as useful biomarkers for RFI and DMI, providing livestock managers the opportunity to make informed management decisions to improve the precision in which they meet the nutrient requirements of their animals, or to select for animals with superior feed efficiency. However, further research is warranted to evaluate additional variables for inclusion into prediction models, as well as to evaluate the performance of these prediction models across various production systems.

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Table 5. 1. Effects of residual feed intake (RFI) on performance, growth, and feed efficiency of Holstein heifers consuming a corn-silage TMR.

Item	Mean	SD	Low	Medium	High	SE	P-value
No. animals	1,787		497	762	528		
Performance and growth traits:							
Initial age, d	287	65	285	282	282	9	0.255
Initial BW, kg	277	66	270	271	270	9	0.753
Final BW, kg	384	73	376	379	377	10	0.558
ADG, kg/d	1.07	0.24	1.08	1.08	1.08	0.03	0.876
DMI, kg/d	9.13	1.71	7.79^{a}	9.10^{b}	10.30^{c}	0.17	<.0001
DMI SD, kg/d	1.67	0.37	1.54^{a}	1.63^{b}	1.80^{c}	0.04	<.0001
Feed efficiency traits:							
G:F, kg/kg	0.119	0.026	0.140^{a}	0.119^{b}	0.105^{c}	0.002	<.0001
RFI, kg/d	0.00	1.09	-1.28^{a}	-0.01^{b}	1.21^{c}	0.02	<.0001

^{a,b,c} Means within row with different superscripts differ ($P < 0.05$).

Table 5. 2. Effects of residual feed intake (RFI) on feeding behavior traits in Holstein heifers consuming a corn-silage TMR.

Item	Mean	SD	Low	Medium	High	SE	P-value
No. animals	1787		497	762	528		
Bunk visit traits:							
BV frequency, events/d	107	31	96^a	105^b	122^c	4	<.0001
BV duration, min/d	114	33	100^a	120^b	126^c	3	<.0001
Max non-feeding interval, min	434	56	438	433	431	4	0.092
BV eating rate, g/min	87.1	29.4	86.7^a	81.6^b	87.5^a	3.3	<.0001
Meal traits:							
Meal criterion, min	7.99	5.10	10.74^a	7.63^b	6.10^c	0.33	<.0001
Meal frequency, events/d	11.0	3.6	9.7^a	11.0^b	11.9^c	0.2	<.0001
Meal duration, min/d	232	44	230^a	233^a	240^b	4	<.0001
Meal length, min/event	25.2	11.1	27.7^a	25.3^b	23.9^c	0.8	<.0001
Meal size, g	0.904	0.291	0.870^a	0.900^a	0.941^b	0.021	0.000
Meal eating rate, g/min	41.0	11.7	35.4^a	40.6^b	44.6^c	1.2	<.0001
Intensity traits:							
HD duration, min/d	61.8	30.0	43.9^a	65.5^b	79.9^c	2.8	<.0001
Time to bunk, min	99.9	35.8	105.1^a	96.7^b	95.0^b	3.0	<.0001
HD duration per BV duration	0.525	0.155	0.421^a	0.533^b	0.629^c	0.014	<.0001
HD duration per meal duration	0.266	0.119	0.189^a	0.283^b	0.332^c	0.009	<.0001
BV events per meal event	10.7	4.6	10.7^a	10.5^a	11.4^b	0.5	<.0001
Day-to-day variation traits†:							
BV frequency SD, events/d	24.6	7.3	23.0^a	24.3^b	27.3^c	0.9	<.0001
BV duration SD, min/d	27.6	5.3	26.6^a	28.1^b	28.5^b	0.4	<.0001
Max non-feeding interval SD, min	120	24	123^a	119^b	117^b	2	<.0001
Meal frequency SD, events/d	2.60	0.92	2.26^a	2.62^b	2.82^c	0.06	<.0001
Meal duration SD, min/d	44.9	9.6	47.0^a	44.5^b	44.2^b	0.7	<.0001
Meal length SD, min/event	7.48	3.59	8.36^a	7.46^b	6.85^c	0.23	<.0001
HD duration SD, min/d	15.8	5.8	12.5^a	16.5^b	19.0^c	0.5	<.0001
Time to bunk SD, min	100	23	104^a	99^b	98^b	2	<.0001

† Day-to-day variation traits = day-to-day standard deviation for each trait

^{a,b,c} Means within row with different superscripts differ ($P < 0.05$).

Table 5. 3. Pearson correlations between performance and feed efficiency and feeding behavior traits in growing Holstein heifers (38 trials; n = 1,787).

Item	ADG	DMI	G:F	RFI
ADG	**-**	**0.42**	**0.56**	0.00
DMI	**0.42**	-	**-0.47**	**0.78**
Bunk visit traits:				
BV frequency, events/d	0.03	**0.24**	**-0.19**	**0.50**
BV duration, min/d	0.23	**0.51**	**-0.25**	**0.41**
Max non-feeding interval, min	**-0.07**	**-0.05**	-0.04	**-0.06**
Meal traits:				
Meal frequency, events/d	**0.10**	**0.29**	**-0.15**	**0.27**
Meal duration, min/d	0.03	0.00	0.02	**0.14**
Meal length, min/event	**-0.08**	**-0.23**	**0.12**	**-0.13**
Intensity traits:				
HD duration, min/d	**0.14**	**0.54**	**-0.34**	**0.56**
Time to bunk, min	**-0.17**	**-0.26**	**0.05**	**-0.13**
HD duration per BV duration	0.00	**0.45**	**-0.41**	**0.60**
HD duration per meal duration	**0.14**	**0.57**	**-0.37**	**0.52**
BV events per meal event	**-0.08**	**-0.10**	0.00	**0.10**
Day-to-day variation traits†:				
BV frequency SD, events/d	**-0.05**	**0.13**	**-0.17**	**0.35**
BV duration SD, min/d	0.02	**0.17**	**-0.15**	**0.21**
Max non-feeding interval SD, min	**-0.11**	**-0.13**	0.01	**-0.13**
Meal frequency SD, events/d	**0.07**	**0.27**	**-0.17**	**0.26**
Meal duration SD, min/d	**-0.15**	**-0.25**	**0.07**	**-0.11**
Meal length SD, min/event	**-0.13**	**-0.27**	**0.11**	**-0.16**
HD duration SD, min/d	0.02	**0.41**	**-0.36**	**0.51**
Time to bunk SD, min	**-0.16**	**-0.26**	**0.07**	**-0.14**

RFI = residual feed intake;

† Day-to-day variation traits = day-to-day standard deviation for each trait

Correlations in bold are different from zero at $P < 0.05$.

Table 5. 4. Summary statistics for cross-validation of partial least squares regression (PLSR) models to quantify the variation in residual feed intake (RFI) and dry matter intake (DMI) accounted for by performance, growth, and feeding behavior traits of growing Holstein heifers consuming a corn-silage TMR.

	Cross-validation		
Item	RMSE	R^2_{cv}	Spearman's
Residual feed intake PLSR models			
RFI = BV and meal traits	0.90	0.32	0.56*
RFI = Intensity traits	0.92	0.29	0.53*
RFI = day-to-day variation of feeding behavior (Var-FB)	0.90	0.33	0.57*
RFI = BV, meal, and intensity traits (Daily-FB)	0.84	0.41	0.64*
RFI = Daily-FB + Var-FB	0.83	0.43	0.65*
Dry matter intake PLSR models			
DMI = Mid-test $BW^{0.75}$ + ADG (Base model)	1.20	0.51	0.72*
DMI = Base model + BV and meal traits	0.96	0.68	0.83*
DMI = Base model + Daily-FB	0.89	0.73	0.86*
DMI = Base model + Daily-FB + Var-FB	0.87	0.74	0.86*

*Correlations differ from zero ($P < 0.05$).

R^2_{cv} = coefficient of determination for cross-validation; RMSE = Root mean square error; Spearman's = Spearman's rank correlation between observed and predicted values.

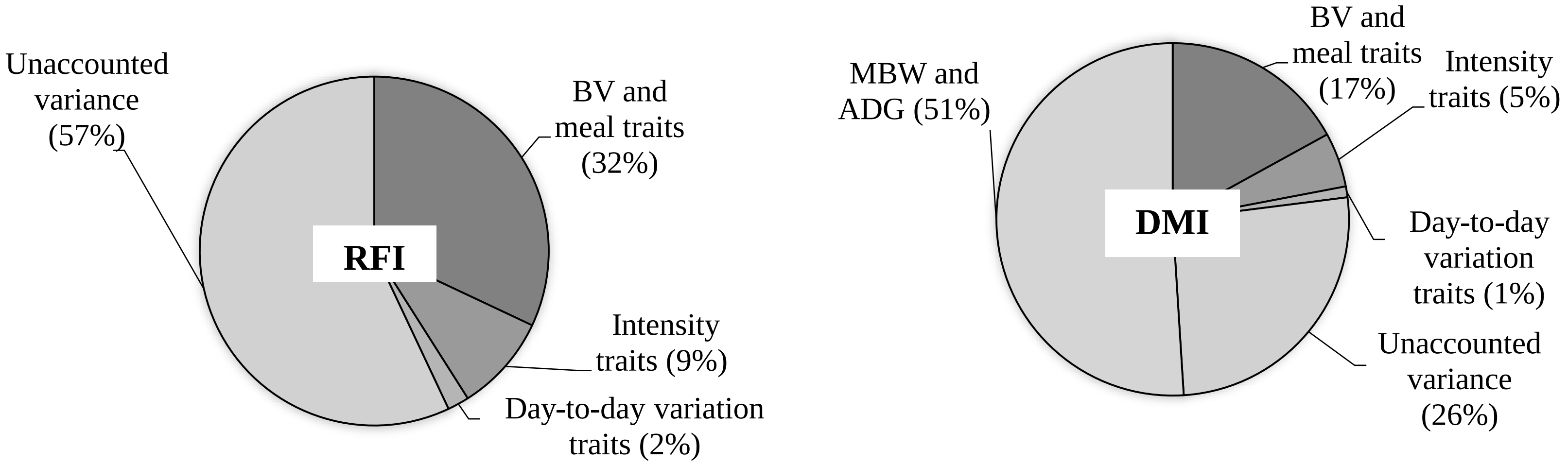

Figure 5. 1. Contribution of BV and meal traits to residual feed intake (RFI) and performance, BV and meal traits to dry matter intake (DMI), and the additional contribution of intensity traits and day-to-day variation traits upon sequential inclusion into the PLSR model using data from growing Holstein heifers (38 Trials; n = 1,787) consuming a corn-silage TMR.

Table 5. 5. Variable of importance scores and equation coefficients for partial least squares models to predict residual feed intake (RFI) and dry matter intake (DMI) in growing Holstein heifers (38 trials; n = 1,787).

	RFI model†		DMI model†	
Trait	VIP	Coefficient	VIP	Coefficient
Bunk visit traits:				
BV frequency, events/d	**1.26**	0.013	0.580	-
BV duration, min/d	**1.23**	0.021	**0.900**	0.005
Max non-feeding interval, min	0.582	-	0.541	-
Meal traits:				
Meal frequency, events/d	**0.890**	0.032	**1.03**	0.134
Meal duration, min/d	0.562	-	0.612	-
Meal length, min/event	0.508	-	**1.06**	-0.034
Intensity traits:				
HD duration, min/d	**1.54**	-0.041	**0.939**	0.004
Time to bunk, min	0.669	-	0.708	-
HD duration per BV duration	**1.69**	5.33	0.781	-
HD duration per meal duration	**1.50**	3.040	**1.15**	2.41
BV events per meal event	0.484	-	**0.968**	0.135
Day-to-day variation traits‡:				
BV frequency SD, events/d	**0.966**	-0.020	0.485	-
BV duration SD, min/d	**0.817**	0.006	0.454	-
Max non-feeding interval SD, min	0.628	-	0.415	-
Meal frequency SD, events/d	**0.885**	0.037	**0.908**	-0.119
Meal duration SD, min/d	0.594	-	**0.816**	-0.006
Meal length SD, min/event	0.585	-	**1.09**	0.024
HD duration SD, min/d	**1.45**	0.012	0.756	-
Time to bunk SD, min	0.675	-	**0.817**	0.001
Performance traits:				-
ADG, kg/d	**-**	-	**1.77**	2.22
Metabolic BW, $kg^{0.75}$	**-**	-	**2.26**	0.091

† Variable of importance in projection (VIP) scores and equation coefficients for partial least squares regression (PLSR) models for RFI and DMI; VIP scores greater than 0.80 are in bold.

‡ Day-to-day variation traits = day-to-day standard deviation for each trait.

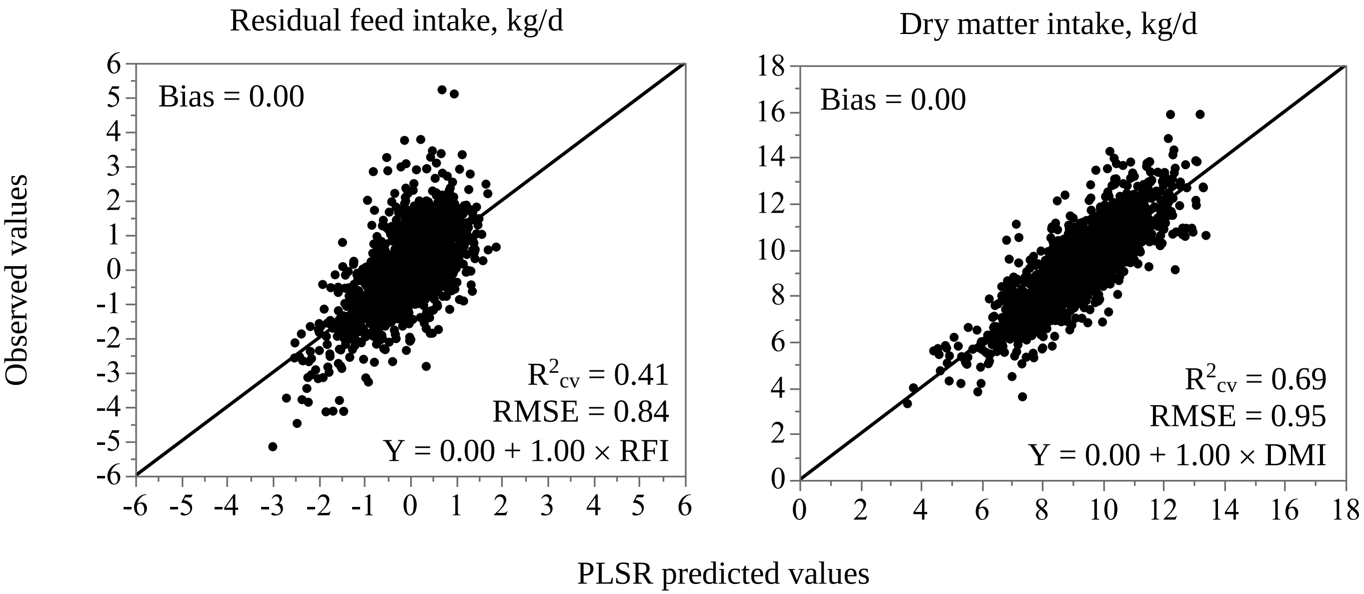

Figure 5. 3. Cross-validation R2 (R2cv), root mean square error (RMSE), bias ((Σ observed data/N)- (Σ predicted data/N)), and spearmans rank correlation (Spearmans) of partial least squares regression models to predict residual feed intake (RFI) and dry matter intake (DMI) using performance, growth, and feeding behavior traits as independent variables. Variables were excluded from the model if variable of importance in projections scores were less than 0.80. Data from 1,787 growing Holstein heifers from 38 trials were used to develop the prediction models.

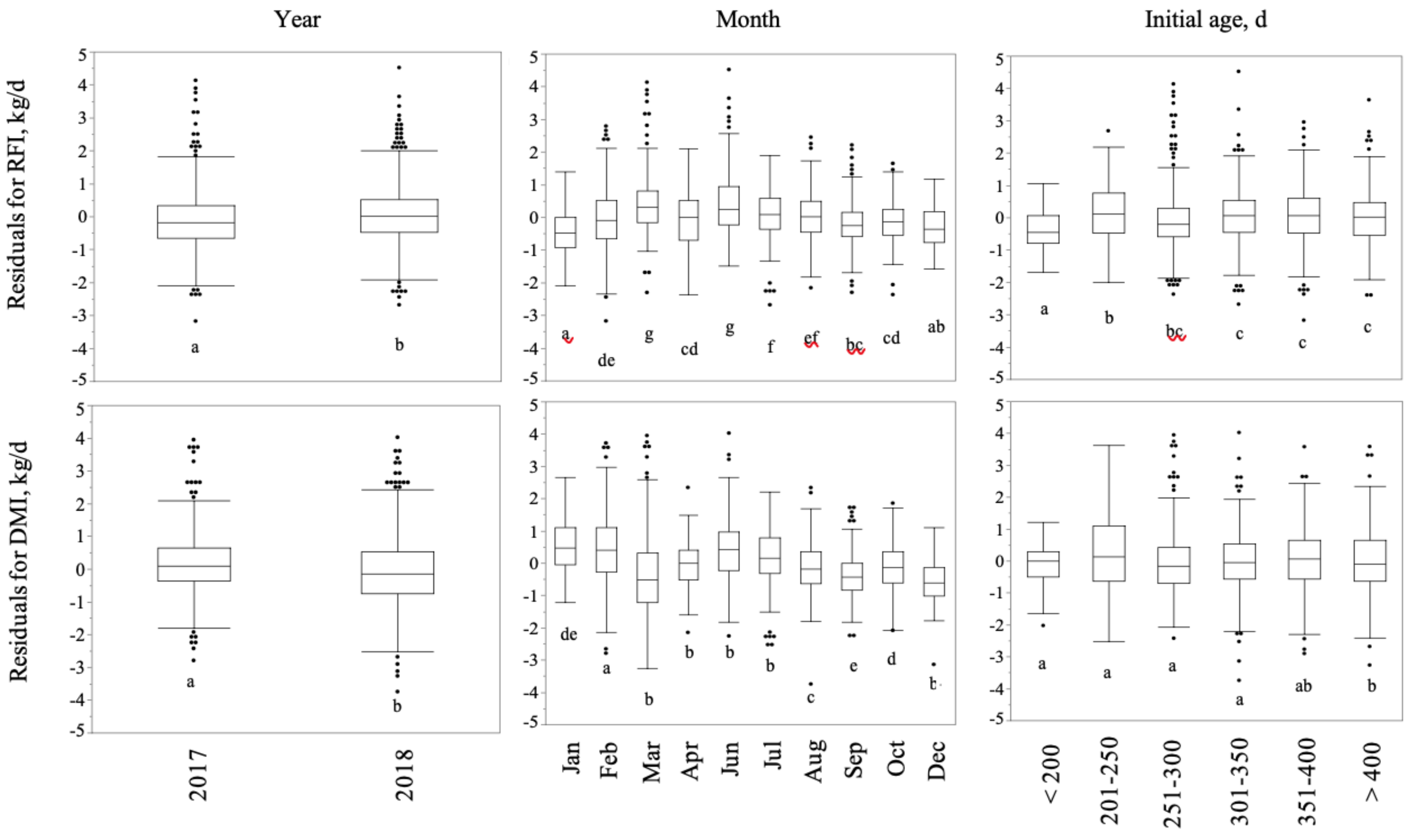

Figure 5. 4. Residuals from partial least squares regression models to predict residual feed intake (RFI) and dry matter intake (DMI) by the year (n = 607 in 2017; n = 1180 in 2018), month (n = 76 in Jan; n = 248 in Feb; n =149 in Mar; n = 156 in Apr; n = 171 in Jun; n = 158 in Jul; n = 227 in Aug; n = 218 in Sep, n = 308 in Oct, and n = 76 in Dec), and age of animals (< 200 n = 88; 201-250 n = 485; 251-300 n = 591; 301-350 n = 312; 351-400 n = 198; > 400 n = 112) at the start of each trial. The PLSR model for RFI included feeding behavior traits as independent variables, and the PLSR model for DMI included mid-test BW0.75, ADG, and feeding behavior traits as independent variables. Models excluded traits based on having variable of importance in projection scores less than 0.80. Means with different letters differ ($P < 0.05$).

CHAPTER VI

CONCLUSIONS

Efficient use of feed by cattle is critical to the economic success of livestock operations as feed accounts for the largest input cost of production. Residual feed intake (RFI) has been identified as an ideal trait for use in selection programs to improve efficiency as efficient animals consume less feed compared to their non-efficient counterparts, independent of growth and production. Unfortunately, RFI is an expensive trait to measure so researchers are working to identify biomarkers that can be used to predict DMI or RFI.

Results from this study indicate that distinctive differences exist in the feeding behavior patterns of cattle with divergent RFI phenotypes. Specifically, across breeds and genders, low-RFI cattle had fewer BV events, lower daily BV and meal durations, and lower HD durations each day compared to their high-RFI counterparts. Low-RFI animals also exhibited less day-to-day variations in their feed consumption and feeding behavior patterns compared to high-RFI animals. These distinct differences were useful in accounting for 35 to 47% of the variation in RFI, and 17 to 29% of the variation in DMI unaccounted for by mid-test $BW^{0.75}$ and ADG. Further, PLSR predicted RFI values, based on feeding behavior traits alone, were useful in identifying animals with divergent RFI, as less than 10% of cattle were classified across 2 RFI groups of that observed (low-RFI to high-RFI or high-RFI to low-RFI).

Based on the results of this study, ongoing development of biosensor-based technologies to quantify feeding behavior patterns will provide opportunities to predict DMI in support of precision nutrition and reduce cost of identifying feed-efficient cattle. However, further research is necessary to improve current understanding of mechanisms that contribute to variation in individual-animal feed efficiency and to evaluate the robustness of PLSR models across varying production systems.