EFFECTS OF RESIDUAL FEED INTAKE CLASSIFICATION ON TEMPERAMENT, CARCASS COMPOSITION, AND FEEDING BEHAVIOR TRAITS IN GROWING SANTA GERTRUDIS HEIFERS

A Thesis

by

JUSTIN ANTHONY RAMIREZ

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Chair of Committee,	Gordon E. Carstens
Co-Chair of Committee,	Luis O. Tedeschi
Committee Member,	Andy D. Herring
Head of Department,	H. Russell Cross

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ABSTRACT

Objectives of this study were to evaluate the associations of feed intake, feeding behavior, temperament, and carcass composition with performance and feed efficiency traits in growing heifers. Santa Gertrudis heifers (n = 369) with initial BW of (275.3 ± 37.4 kg) were used in this study. Intake and feeding behavior traits were collected for 70 d using a GrowSafe system while consuming a forage-based diet (ME = 2.19 Mcal/kg DM). Heifers were weighed at 14-d intervals and ultrasound traits measured on d 0 and 70. Residual feed intake was computed by regression of DMI on mid-test $BW^{0.75}$ and ADG, and heifers classified into low, medium, and high RFI (± 0.50 SD) groups. A 2-population distribution model was fit to $\log_{10}$-transformed non-feeding interval lengths to estimate meal criterion (MC), which was used to compute meal traits (frequency and duration). As expected, RFI was positively correlated with DMI (r = 0.72; $P < 0.001$), but not with initial BW or ADG. Residual feed intake was negatively correlated with G:F (r = -0.72; $P < 0.001$) and RG (r = -0.49; $P < 0.001$). In contrast to previous studies, RFI was not correlated with ultrasound LM area or back-fat thickness measured on day 70 of the trials. Residual feed intake was positively correlated ($P < 0.05$) with bunk visit (BV) frequency (r = 0.45) and duration (r = 0.35), and meal duration (r = 0.31), but negatively correlated with MC (r = -0.25). The R^2 of the base RFI model (ADG, mid-test $BW^{0.75}$) was 0.48, which increased to 0.69 with the inclusion of backfat thickness and feeding behavior traits (BV frequency and duration, MC, meal frequency and duration, and time to bunk). Heifers with low-RFI phenotypes had 21.5 and 23.2% lower ($P <$

0.001) DMI and G:F compared to high-RFI heifers. Heifers with low RFI had lesser (*P* < 0.001) BV frequency (64.7 vs 80.6 ± 1.6 events/d) and duration (95.7 vs 113.4 ± 3.6 min/d), higher (*P* < 0.01) MC (9.45 vs 8.12 ± 0.55 min) and greater (*P* = 0.39) time to bunk (TTB; 67.9 vs 58.3 ± 3.5 min) compared to high-RFI heifers. Between-animal variation in RFI was not associated with differences in ultrasound measurements of carcass composition in this study. However, variation in feeding behavior traits account for 41% additional variance in DMI beyond that associated with carcass ultrasound, ADG, and mid-test $BW^{0.75}$. The longer MC observed in low-RFI heifers suggests that these heifers take longer to initiate subsequent meals compared to high-RFI heifers, and demonstrate that heifers with divergent RFI have distinctive feeding behavior patterns.

DEDICATION

I would first like to thank my Lord and Savior, Jesus Christ, for giving me the strength and ability to be in the position I am in, as with God, all things are possible, Matthew 19:26. I would like to dedicate this thesis to my parents, Mauro and Elma Ramirez, for instilling morals such as strong faith, hard work, and dedication, which has made me the man I am today. I would like to also dedicate this thesis to those closest to me for their undying support when times were tough throughout my graduate student career.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Overview

Increased volatility and costs of feed ingredients has prompted renewed interest in selection programs focused on improving genetic merit for feed efficiency while meeting environmental standards. Traditionally, beef cattle selection has been focused on growth traits such as yearling weight and postweaning average daily gain (Parnell et al., 1994). However, selection for growth may lead to increases in feed intake and thus feed costs (Archer et al., 1999; Nkrumah et al., 2004). It is well known in the industry that the largest variable expense associated with beef production is feed cost (Archer et al., 1999; Arthur et al., 2001a; Moore et al., 2009). Feed cost for maintenance is estimated to characterize 60 to 65% of the total feed requirements for the cowherd, with considerable variation among individual animals independent of BW (Arthur et al., 2001a; Montano-Bermudez et al., 1990). However, the variation in maintenance requirements is believed to be greater than variation used to support growth, gestation and lactation requirements (Ferrell and Jenkins, 1985).

Barlow (1984) previously suggested that any noticeable improvements in gross efficiency appear to be more than offset by higher maintenance requirements when selection was based on growth. Improving ADG by 10% increases profits by 20%, whereas, profitability increases 43% by improving feed efficiency 10% (Fox et al., 2001). Therefore, selecting cattle with lower maintenance requirements and improved feed utilization would greatly reduce production cost. Maintenance energy requirements are believed to be moderately heritable (Carstens et al., 1989) suggesting that selection for efficient beef cattle may be achievable. Thus, it is necessary to understand the biological mechanisms responsible for contributing variation to energy maintenance requirements, as they are inherently reflected in the variation in feed efficiency (Archer et al., 1999).

Feed Efficiency

Multiple traits are currently being considered by the industry to select for improved feed efficiency including residual feed intake (RFI), residual gain (RG), and residual intake and BW gain (RIG); all of which have unique attributes compared to ratio-based traits (e.g., gain/feed ratio). Gain to feed ratio (G:F) and feed to gain ratio (F:G) have been traditional traits used by the industry to measure feed efficiency, and to evaluate the effects of diet quality, environment, and management practices in growing and finishing cattle (Carstens and Tedeschi, 2006). Feed to gain ratio is moderately heritable (Crews, 2005), but it grossly measures feed efficiency and therefore does not attempt to partition feed intake into growth or maintenance components (Nkrumah et al., 2004). Negative correlations reported by Lancaster et al. (2009a) between F:G and ADG (r_p = -0.72) demonstrate there is an inverse relationship between ADG and F:G, such that selection for lower F:G in growing bulls will result in increases in genetic merit for growth. Furthermore, low correlations between F:G of weaned heifers and mature cows suggests that favorable selection for F:G may not improve the efficiency of feed use in the breeding cow herd (Archer et al., 2002). Moreover, postweaning genetic correlations between postweaning F:G and mature BW ranging between -0.24 and -0.95 (Koots et al., 1994) and -0.54 (Archer et al., 2002) demonstrates that selection for improved (i.e., decreased) F:G in postweaning bulls will increase the genetic responses in mature size and maintenance requirements of the cow herd (Arthur et al., 2001b; Crews, 2005; Herd and Bishop, 2000; Nkrumah et al., 2004). Because ratio-based traits are comprised of two traits, the ability to predict changes of the trait in future generations becomes increasingly difficult, such that results may favor one trait over the other and vice versa (Gunsett, 1984). Therefore, is it is essential for breeding programs to use a feed efficiency trait that is independent of growth traits and associated with biologically relevant processes (Carstens and Tedeschi, 2006).

Koch et al. (1963) proposed the concept of residual feed intake (RFI) as an alternative measure of feed efficiency defined as the difference between an animal's actual feed intake and expected feed requirements based on body size and gain over time. The linear regression model used to calculate RFI is as follows:

$$y = \beta_0 + \beta_1(\text{ADG}) + \beta_2(\text{MBW}) + \text{RFI}$$

where y is dry matter feed intake (DMI), β_0 is the regression intercept, β_1 is the partial regression of DMI on ADG, and β_2 is the partial regression of DMI on mid-test $BW^{0.75}$ (MBW; Koch et al., 1963). Animals that consumed less than expected feed will to be considered more efficient and have negative RFI values.

Previous research has demonstrated that RFI is moderately heritable (Arthur et al., 2001a; Herd and Bishop, 2000) and responds to selection (Herd et al., 2003). Selection for low-RFI improves feed efficiency by decreasing feed intake without effecting growth performance (Archer et al., 1999) and overall mature size (Herd et al., 2003). Residual feed intake better reflects inherent inter-animal variation in metabolic processes associated with efficient utilization of feed (Carstens and Tedeschi, 2006; Herd and Arthur, 2009). The metabolic contributions that have an impact on the differences in RFI between animals described by Herd and Arthur (2009) are represented in Figure 1.1.

Differences in body composition are believed to account for about 5% of the variation observed in RFI (Richardson and Herd, 2004). It has been suggested that low-RFI cattle may be leaner based on evidence of genetic and phenotypic relationships with RFI and backfat (BF) thickness (Herd and Pitchford, 2011). Research findings by Arthur et al. (2001a) concluded that BF thickness was weakly correlated phenotypically (r_p = 0.14) and genetically (r_g = 0.17) with RFI in heifers and bulls. Similarly, Arthur et al. (1997) found RFI was phenotypically correlated (r_p = 0.19) with BF thickness. Nkrumah et al. (2007a) found that steers with low-RFI had greater lean meat yields as a result of 16.1% lesser BF thickness, 23.7% lesser BF gain, and 18.7% lesser carcass grade fat than high-RFI steers. Based on estimated genetic correlations of RFI with BF thickness, intramuscular fat (IMF), and rump fat adjusted to constant carcass weight (0.58 ± 0.14, 0.25 ± 0.17, and 0.79 ± 0.16 respectively), Robinson and Oddy (2004) concluded that selection for reduced RFI is likely to decrease BF thickness and IMF. However, Nkrumah et al. (2004) determined that RFI was independent of ultrasound marbling score and Basarab et al. (2003) did not observe significant phenotypic or genetic correlations with RFI and initial and final ultrasound marbling scores. However,

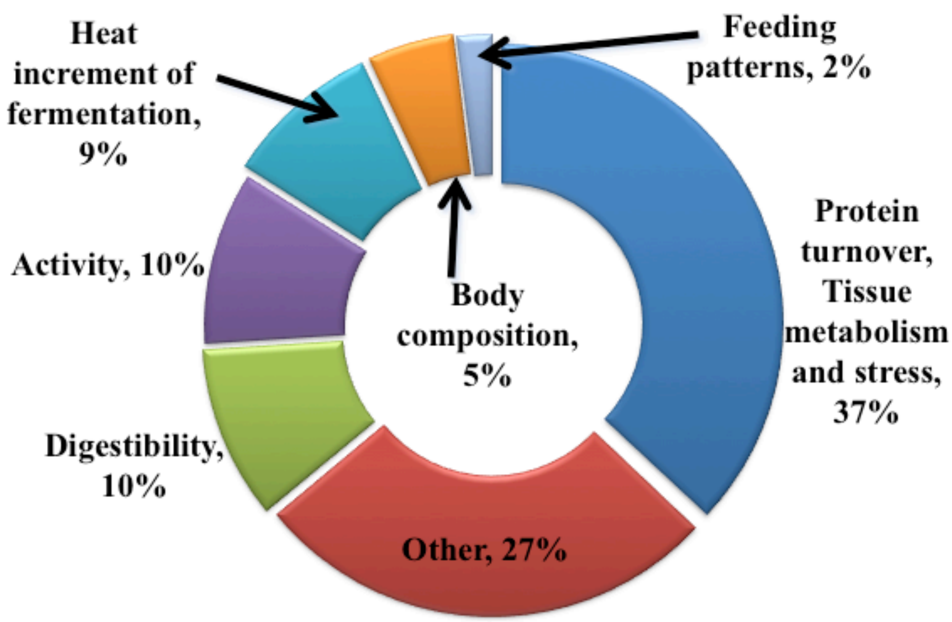

Figure 1.1. Contributions of biological mechanisms to variation in residual feed intake (Richardson and Herd, 2004).

Basarab et al. (2003) did find that RFI was significantly correlated phenotypically with gain in ultrasound marbling score (r_p = 0.22), such that low-RFI cattle have less gain in marbling scores than high-RFI cattle.

Golden et al. (2008) determined that LM area and BF thickness did not differ (P > 0.10) among efficient and inefficient Angus steers. Results reported by Nkrumah et al. (2004) also determined that RFI was independent of LM area in crossbred steers and bulls, which is in agreement with Arthur et al. (2001b) who also found the relationship between RFI and LM area to be non-significant. Similar findings were reported by Lancaster et al. (2009b) in Brangus heifers.

Conclusions reached by Herd and Bishop (2000) determined that RFI was negatively correlated both genetically and phenotypically with expected lean content (r = -0.43 and -0.22 respectively) and lean growth rate (r = -0.47 and -0.33 respectively) in Hereford cattle, which adds validity that low-RFI animals may be leaner than high-RFI contemporaries. It has been suggested that 1 kg of fat requires more energy than 1 kg of lean tissue (Robinson and Oddy, 2004; SCA, 1990), such that high-RFI animals with greater fat deposition require more dietary energy than low-RFI contemporaries, and therefore are likely to be less efficient. There is, however, more variation in efficiency of deposition of lean gain than fat gain as a result of greater variation in protein turnover than in fat (Herd and Arthur, 2009). Collectively, protein turnover, tissue metabolism and stress are suggested to account for 37% of the variation in RFI (Richardson and Herd, 2004).

It has been suggested that as feed intake increases, the ability to digest feed will decrease, which accounts for 10% of the variation in RFI (Herd and Arthur, 2009). In addition, since RFI is a trait selecting for animals with considerably lower intake, animals that eat less feed for the same performance could be expected to have less energy expended as heat increment (Herd and Arthur, 2009). Basarab et al. (2003) found that low-RFI steers retained 12% less energy and produced 9.3% less heat than high-RFI steers. The heat increment of fermentation has been suggested to account for 9% of the variation in RFI (Richardson and Herd, 2004). Further description of additional mechanisms contributing to the variation in RFI (stress, feeding patterns, and activity) will later be discussed.

Residual BW gain (RG) is a feed efficiency trait similar to RFI, however; calculation of RG involves regression of ADG on DMI and mid-test $BW^{0.75}$ (Crowley et al., 2010). Residual BW gain is the difference between actual and expected daily gain relative to body size and feed intake (Koch et al., 1963), however in contrast to RFI, a greater or positive value is desired. Research presented by Berry and Crowley (2012a) found RG to be phenotypically negatively correlated with RFI and F:G ($r = -0.40$ and -0.71 respectively), positively correlated with ADG ($r = 0.70$), but independent of DMI ($r = 0.00$) as expected. In addition, heritability estimates determined for growing cattle for RG were 0.28 (Koch et al., 1963) and 0.62 (Crowley et al., 2010), suggest that selection for greater RG (more efficient) will result in more efficient animals with higher ADG and lower RFI and F:G.

Residual intake and BW gain (RIG) is a newly proposed trait that retains favorable characteristics of RFI and RG such that it reduces feed intake and increases daily gain while minimally affecting BW (Berry and Crowley, 2012a). Calculation of RIG is determined as the sum of RG and -1 x RFI, both of which are standardized to a variance of 1. Standardization of RFI and RG allows for their equal expression in determining RIG. Residual feed intake is multiplied by -1 in order to have a favorable comparison with a positive RG value. Favorable selection for RIG may be possible, such that Berry and Crowley (2012b) reported moderate heritability results of 0.36 ± 0.06, which is consistent with RFI heritability estimates (0.39 ± 0.06) determined by Arthur et al. (2001b). Research conducted by Berry and Crowley (2012b) determined that RIG was phenotypically correlated with RFI and DMI (r_p = -0.85 and -0.34 respectively) in a negative manner, yet positively correlated with RG and ADG (r_p = 0.36 and 0.41 respectively). In addition, least squares means results confirmed that high-bulls had lower RFI and DMI (-0.71 and 10.4 kg/d respectively) and higher RG and ADG (0.19 and 1.81 kg/d respectively), such that favorable selection for RIG resulted in animals with greater efficiency gaining 21.5% more while consuming 5.45% less feed. Interest in RIG selection is not only confined to cattle; Willems et al. (2013) reported genetic correlations of RIG in turkeys with feed intake (-0.41) and body weight gain (0.43) signifying that high RIG groups (more efficient) had both lowest ($P < 0.001$) feed intake and highest ($P < 0.001$) body weight gain relative to medium and low groups (less efficient).

Animal Feeding Behavior Characteristics

Innovative technologies such as those considered in the GrowSafe system (i.e., radio frequency (RF) identification, wireless communication, RF detection, and software design) have provided the industry with feeding systems equipped with analytical programs designed exclusively for examining feeding behavior in large groups of animals (GrowSafe, 2009). Measuring individual animal feed intake and behavior in large groups remained difficult until RFID-based technology was developed in the mid-1970s (Eradus and Jansen, 1999). While the costs associated with measuring individual feed intake in cattle are expensive and time consuming (Archer et al., 1999) with estimates ranging from $150 to more than $200 per head (Crews, 2005), technologies (i.e., GrowSafe) have simplified the collection of individual feed intake and have allowed for more extensive research in determining and understanding the variability associated with the phenotypic expression of efficiency (Golden et al., 2008).

Research presented by Lancaster et al., (2009a) determined that feeding behavior traits (meal duration, head down duration, and eating rate) were moderately correlated positively with DMI in Angus bulls, such that animals with greater DMI had longer feeding durations, larger meals, and greater meal eating rates. Phenotypic correlations presented by Kelly et al. (2010b) found DMI moderately correlated with eating rate (0.43) and feeding events (0.31), suggesting animals with greater DMI had greater feeding events and faster eating rates. It has been found that individual animal feeding behavior is repeatable Gibb et al. (1998); and therefore may be used to predict differences in animal performance and efficiency (Nkrumah et al., 2007b). Findings from Gibb et al. (1998), Kelly et al. (2010b), and Nkrumah et al. (2007a) suggest that individual animal feeding behavior is generally consistent within and between the phases of productions (i.e., growing and finishing) in crossbreed heifers and steers. However, results from Golden et al. (2008) varied, such that feeding behavior intake patterns repeated in efficient and inefficient crossbred steers up until animals reached a BW (391 and 381 kg, respectively) close to d 47 and 31 respectively. Therefore, conceivable differences in methodology used in obtaining and processing data (Tolkamp et al., 2000) may be related to divergent results reported among trials examining feeding behavior. In addition, researchers have shown that variation in feeding behavior may also be influenced by animal type, diet composition, management system, environment, health, and social activities such as competition for feeder space (Dobos and Herd, 2008; Gibb et al., 1998; Tolkamp et al., 2000).

There are diverse methods used in collecting individual feed intake and behavior data, such as the Calan gate and GrowSafe systems. The Calan gate system is a common method used for measuring feed intake; however the technology incorporated in the system limits its use in measuring intake in large groups of animals. Whereas, the GrowSafe System® is capable of measuring individual animal intake and feeding behavior traits in large groups of animals using radio frequency identification (RFID) tags. The antenna located within the rim of the feed bunk reads the RFID tag as the animal enters the bunk via the neck bars. A wireless signal is then sent to a data-acquisition computer and assigns feed disappearance and bunk visit data to individual animals.

Feeding behavior traits typically measured during feeding behavior studies are bunk visit (BV) frequency and duration, feeding bout (FB) frequency and duration, meal frequency and duration, eating rate, and meal size. Bunk visit frequency (event/d) is measured as the number of visits the animal makes to the feeding bunk on a daily basis regardless of whether or not feed was consumed. Bunk visit duration (min/d) is the summation of time the animal is at the feed bunk in a 24 h period. A feeding bout is defined in this study as visits to the bunk with recorded (> 0 g) feed consumption. A meal event, depicted on Figure 1.2, consists of a cluster of BV events that can be distinguished from the next meal event by a non-feeding interval. Meal frequency (MF) is calculated based on the total number of meal events per day and meal duration (min/d) is the sum of time within each meal throughout each day. Additional meal traits such as, meal length (min/event), meal size (kg/event), and eating rate (g/min) can be determined once meal traits have been computed. The consistency between feeding patterns and physiological factors affecting satiety have been suggested to be a more appropriate rationale for grouping bunk visits into meals in contrast to the notion that cattle have random feedings (Morgan et al., 2000; Tolkamp and Kyriazakis, 1999a). Kelly et al. (2010b) found moderate to strong repeatability of feeding behavior traits ranging from 0.40 to 0.76 ($P < 0.001$) between the growing and finishing phases of crossbred heifers. Random feeding events are longer intervals that incorporate the total number of bunk visits per animal, which potentially can contain involuntary feed bunk removals caused by social hierarchy, feeding pressures, and/or trough composition (Tolkamp et al., 2000). Tolkamp et al. (1998) concluded that clustering feeding bouts into meals using the

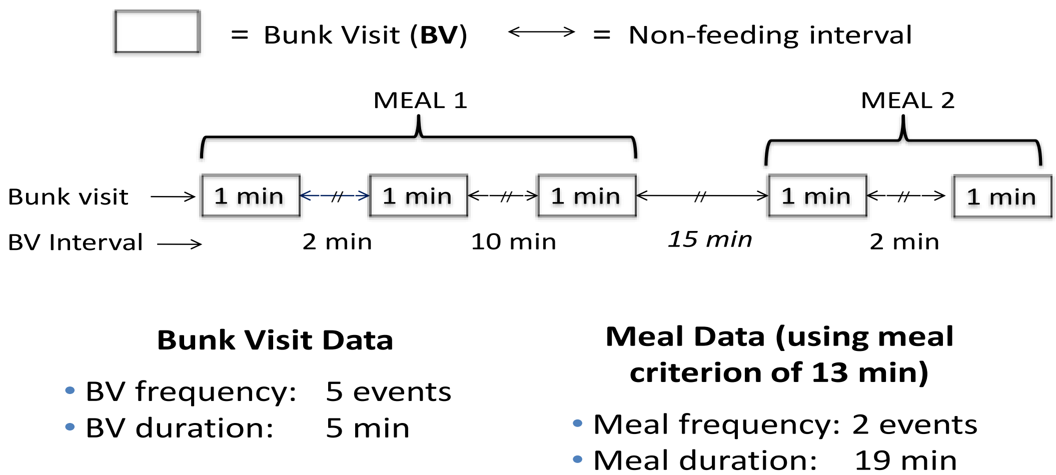

Figure 1.2. Feeding behavior and meal traits definition representation (Mendes et al., 2011).

satiety concept is the most biologically appropriate method of analyzing feeding behavior.

Meal criterion (MC) is determined after analyzing feeding behavior traits. It is the estimate of the longest non-feeding interval that is still considered to be part of a meal (Yeates et al., 2001; Yeates et al., 2002). Meals consist of clusters of feeding events separated by short intervals (Mayes and Duncan, 1986). Analysis of feeding behavior may be affected by the methodology used in collecting the data, thereby altering the accuracy of the measurements and increasing the difficulty of comparing results across experiments (Tolkamp et al., 2000; Yeates et al., 2001). Quantitative estimation of MC allows for feeding events to be clustered into meals in a repeatable fashion (Berdoy, 1993), thus providing an additional understanding of relationships associated with feeding behavior (Tolkamp and Kyriazakis, 1999a). Estimation of meal criterion has previously been measured using multiple techniques, such as two and three-population models to determine which combination provides the best biological and statistical description of pooled observations (Yeates et al., 2001). Earlier research from Tolkamp and Kyriazakis (1999a) suggests a 2-pool Gaussian distribution possesses a better biological foundation than previous quantitative methods that do not depict a clear biological explanation. An example of one such method is a negative exponential distribution, which results from a behavioral feeding event beginning independently of the previous event of the same type (Berdoy, 1993). A straight line with a negative slope is expected from log transformation of a negative exponential (Tolkamp and Kyriazakis, 1999a). Distributing negative exponentials of both intervals within and between meals will result in the formation of two straight lines in the shape of a “broken stick” (Slater and Lester, 1982). Research from Tolkamp and Kyriazakis (1999a) evidently reveals that a “broken stick” model poorly fits the data sets when compared to log-survivorship curves generated from models (G-W and G-G) based on the satiety concept.

Calculating meal criterion using the satiety concept can be attained by fitting a log-transformed equation to non-feeding interval data with a 2-pool Gaussian distribution (Tolkamp and Kyriazakis, 1999b, 1999a). The initial pool represents the non-feeding intervals within the meal, while the secondary pool represents the intervals between meals as demonstrated in Figure 1.3. The intersection of the two distributions will determine the meal criterion. Supportive research ($t = 4.20$, $df = 7$, $P < 0.005$) from Yeates et al. (2001) is consistent with other findings (Bailey et al., 2012; Tolkamp and Kyriazakis, 1999a) demonstrating that a 2-pool Gaussian distribution model is not only statistically a better model, but also serves as a better biological fitment of individual cows that is significantly superior to other models. A Gaussian-Weibull (G-W) distribution model will be used in this study to analyze meal data based on suggestive findings from Bailey et al. (2012) indicating the G-W distribution was the best fitment for non-feeding intervals in beef cows.

Factors Affecting Animal Behavior

Environmental conditions including as temperature, wind, precipitation, and humidity (Hohenboken, 1985; Tolkamp et al., 2000) coupled with diet composition, affect behavioral patterns in cattle by altering their internal body temperature

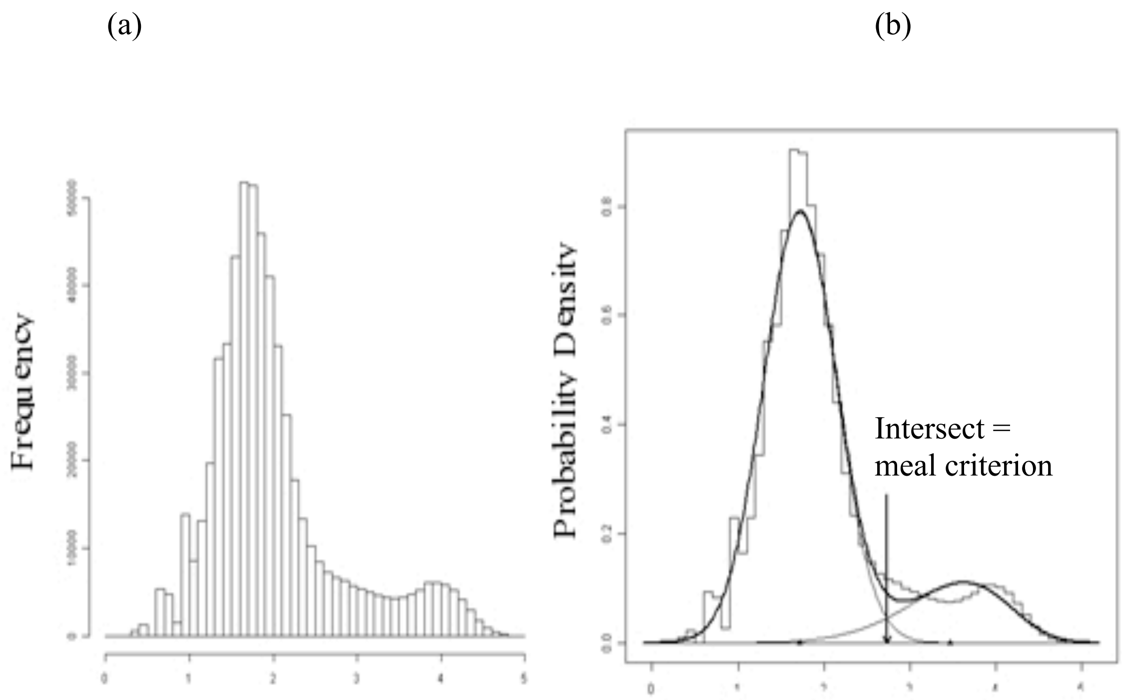

Figure 1.3. Histogram of $\log_{10}$-transformed non-feeding intervals (panel a; Intervals less than 2 s have been removed), and graphical representation of the G-W combination with a bin width of 0.1 $\log_{10}$ units (panel b; Intervals less than 2 s have been removed, Bailey et al., 2012).

(Allen, 2000; Beede and Collier, 1986; West, 2003). Research indicates exposure to hot weather and humidity for extended intervals will subject cattle to greater risks of developing heat stress (Forbes, 2007; Hahn, 1997; Prescott et al., 1994). Animals enduring heat stress develop higher energy maintenance requirements and poorer growth rates over time (Beede and Collier, 1986). Cattle actively seek shade as a physiological response to humidity and hot temperatures in order to dissipate heat and regulate body temperature (Bennett et al., 1985; Blackshaw and Blackshaw, 1994; Forbes, 2007). A shade structure reduces heat load exposure to animals by 30% or more by absorbing solar radiation (Bond et al., 1967). Although it is important for cattle to regulate body temperature (Turner, 1984), unproductive behavior may arise when the necessity for seeking shade reduces feed intake (Bennett et al., 1985). Research suggests that one mechanism by which cattle reduce the heat load is through DMI reduction (Mader et al., 2002). Cattle instinctively reduce intake in order to avert elevated body temperatures caused from digestion and other biological mechanisms. Normal body temperatures in beef cattle range between 36.7 and 39.1°C. Data from Mader et al. (2002) determined that temperature can be reduced by 0.5°C or more ($P < 0.05$) when feed intake is restricted during parts of the day.

Research has shown that not all breeds of cattle respond accordingly due to their genotypic (Beatty et al., 2006) and phenotypic (Mader et al., 2002) influential differences (Colditz and Kellaway, 1972). Dark coated *Bos taurus* and *Bos indicus* cattle have been found to generate higher body temperatures than light coated contemporaries when free access to water was unavailable, however when water was freely accessible, elevated body temperatures were only observed in *B. taurus* cattle (Finch, 1986). This is because *B. taurus* have higher loading heat at the skin than *B. indicus* and must evaporate substantially more sweat to maintain body temperatures (Blackshaw and Blackshaw, 1994). Findings from Beatty et al. (2006), are in agreement with previous studies (Brown-Brandl et al., 2005; Colditz and Kellaway, 1972; Hahn, 1997), suggesting that heat stress reduces feed intake in *B. taurus* cattle (P < 0.0 01) at a significantly higher degree than *B. indicus* cattle (P = 0.14).

Dry matter intake has shown to be affected by the physical and chemical natures of the dietary ingredients used in the ration (Allen, 2000). Intake is a function derived of meal size and meal frequency that is determined by animal and dietary factors that affect hunger and satiety (Allen, 2000). Findings from Golden et al. (2008) revealed that daily eating bouts of feed efficient steers were greater when eating high concentrate diets (14.5 events/d) as opposed to consuming a "receiving diet" (11.0 events/d) that contained 8% (DM) grass hay. In addition, Beauchemin et al. (1994) reported that DMI reduced (P < 0.01) by nearly 3 kg/d when forage content increased from 35 to 65% with diets containing long chopped alfalfa hay. Meal initiations and cessations are dictated by responses sent from satiety centers in the brain via mechanisms from visceral organs including distention and hypertonicity triggered in the reticulo-rumen (RR), metabolic receptors in the liver, and chemical and osmotic receptors within the digestive tract (Allen, 2000; Forbes, 1996; Forbes, 1986). Proper ruminal function requires adequate particle length (Lammers et al., 1996). Reduced particle size decreases the time spent chewing and may decrease ruminal pH (Woodford and Murphy, 1988). Decreased ruminal pH results from decreased saliva production available to buffer the rumen, which is also a precursor of acidosis (Lammers et al., 1996). Particle size has also been found to reduce intake in cattle. Beauchemin et al. (1994) determined that DMI was reduced by 0.5 kg/d ($P < 0.01$) with diets containing short chopped forage. Particle size has also been found to decrease ruminal acetate to propionate ratio along with pH, which subsequently reduces milk fat percentage (Grant et al., 1990; Shaver, 1990).

Research has shown that animal feeding behavior varies in animals relative to their utilization of feed. Findings by Robinson and Oddy (2004) determined that RFI was positively correlated phenotypically and genetically with BV duration ($r_p = 0.16$ and $r_g = 0.35$ respectively) and BV frequency ($r_p = 0.18$ and $r_g = 0.43$ respectively). Likewise, Montanholi et al. (2009) observed positive correlations between RFI and BV duration (0.24) and BV frequency (0.35), in addition to eating rate (0.44), and meal size (0.41) in growing steers. Nkrumah et al. (2007b) found RFI moderately correlated phenotypically with feeding duration and head down duration (0.49 and 0.50 respectively) but weakly correlated with feeding frequency (0.18). Durunna et al. (2011) determined that high-RFI steers had a 13.7% greater feeding frequency and 13.5% longer feeding duration than low-RFI steers, demonstrating that high-RFI steers expended more energy in feeding behaviors associated with ingestion of feed to and from the feed bunks. In contrast, Basarab et al. (2003) found no differences between RFI class for FB frequency and duration. Lancaster et al. (2009a) examined the relationship between feeding behavior and RFI and found that variation in feeding behavior traits (head-down duration, meal frequency, and meal duration) accounted for 35% of the variation in RFI not explained by ADG, MBW, and ultrasound traits. Therefore, these findings reinforce that the reasons for variation of RFI in cattle are still not fully understood but are likely to contain differences in feeding behavior (Richardson and Herd, 2004).

Temperament in Cattle

Animal temperament may be defined as an animal's behavioral response to handling (Burrow and Corbet, 1999) and other stressors, such as unfamiliar situations (Petherick et al., 2009). Based on subjective assessment of temperament, cattle with more excitable temperaments tend to have lower BW gains (Voisinet et al., 1997). Traditional methods existing for measuring temperament in cattle include chute score and pen score. Chute score measures the temperament of cattle while held in a squeeze chute with head restrained (Grandin, 1993). Cattle are then ranked 1 to 5 based on the amount of movement, where 1 indicates minimal movement and 5 indicating continuous struggle (Burdick et al., 2011). Analysis of temperament by pen score is based on the reactivity of animals while unrestrained in small groups (3 to 5) typically inside a pen. A human observer approaches each animal and assigns a score between 1 and 5; where 1 the animal is docile and 5 the animal is aggressively attempting to evade the observer (Burdick et al., 2011). These methods however, are subjective in nature, and therefore allow for human error and/or bias to affect an animal's temperament evaluation.

Exit velocity (EV) was developed by Burrow et al. (1988) to be a more objective method to evaluate temperament. Exit velocity is a measure of the speed in which an animal traverses a fixed distance while exiting a confined area, typically a squeeze chute after processing (Burdick et al., 2011). Exit velocity is calculated as the distance, in which 1.8 m has become the standard typically used, divided by the time the animal took to traverse 1.8 m (Burdick et al., 2011; Burrow et al., 1988; Prayaga and Henshall, 2005). Research by Curley et al. (2006) evaluated these methods (EV, chute and pen score) and determined that EV may have greater utility than methodologies of subjective nature (pen score and chute score). In addition, the author also noted that all measurements of temperament revealed that there was an adaption as the animals interacted more with humans over the 120 d of data collection, while noting EV and pen score fluctuated less than chute score.

Use of EV may indicate a direct representation of cattle management, as well as the design of the handling facilities (Cooke et al., 2011). Research in beef cattle has demonstrated that negative weak to moderate correlations exist between EV with BW, ADG, and DMI (Brown, 2005; Fox et al., 2004; Nkrumah et al., 2007b). Research presented by Fox et al. (2004) and Brown (2005) reported negative phenotypic correlations of EV with DMI (r_p = -0.34 and -0.31 respectively) and ADG (r_p = -0.25 and -0.26 respectively) for Bonsmara bulls and Santa Gertrudis steers. Research findings by Nkrumah et al. (2007b) also determined that EV was phenotypically correlated negatively with DMI and ADG (r_p = -0.35 and -0.26 respectively), such that animals with greater EV had suppressed intakes and gains. Although Elzo et al. (2009) was unable to detect significant correlations of EV with ADG in Angus, Brahman, and Angus x Brahman crossbred cattle, a negative relationship was found to exist between

EV and DMI (-0.29 ± 0.09; $P < 0.001$), providing additional reference that calves that consumed more feed exited the chutes at a slower rate (numerically lower EV).

According to research presented by Curley et al. (2006), EV is positively correlated with cortisol concentration ($r = 0.26$; $P < 0.05$), such that animals exiting the chutes at faster rates are likely to possess greater cortisol concentrations. The concentration of cortisol increases when it is subsequently released from the adrenal gland in response to stress via corticotropin-releasing hormone and vasopressin release from the hypothalamus and adrenocorticotropic hormone from the pituitary gland. Research has determined that high cortisol concentrations are negatively correlated with growth rates in growing calves (Nikolic et al., 1996), suggesting that animals with greater cortisol levels have suppressed growth rates and therefore grow slower than their contemporaries with lower cortisol levels.

It has been suggested that excitable temperament can impair reproductive performance of beef females (Cooke et al., 2011; Wettemann and Bossis, 2000). Temperament was found to be negatively associated with body condition score (BCS) in growing calves (Cooke et al., 2009; Petherick et al., 2009), but not in mature cows (Sandelin et al., 2005). Poor BCS has typically been associated with reduced conception rates and longer intervals from calving to first estrus (Wagner et al., 1988). A study measuring temperament on Nelore (*B. indicus*) beef cows (Cooke et al., 2011) using EV found a 25% reduction in pregnancy rates between cows with the highest EV (36%) compared to cows with the lowest exit velocities (48.2%). Earlier research from Hafez and Lindsay (1965) determined that dairy cattle with both very calm and very excitable temperaments had lower conception rates than cattle with moderate temperaments.

Heritability estimates for temperament in beef cattle, as assessed by EV, range from lower values of 0.11 and 0.20 (Hoppe et al., 2010) to moderate estimates of 0.34 (Rolfe et al., 2011), 0.35 (Burrow and Corbet, 1999) and 0.49 (Nkrumah et al., 2007b). Earlier findings from Burrow et al. (1988) determined that heritability for temperament was repeatable in bulls measured at weaning (0.48 ± 0.21) and at 18 mo of age (0.44 ± 0.21), whereas, in females there was a significant decline in the heritability estimate from weaning (0.58 ± 0.23) to 18 mo of age (0.21 ± 0.18), suggesting there is an effect of sex. In addition, moderate heritability estimates were also observed in Nelore (Carneiro et al., 2006) and other *Bos indicus* (Burrow and Corbet, 1999; Hearnshaw and Morris, 1984) breeds of cattle. Given that EV has shown to be moderately heritable, it has been suggested that EV be incorporated an indicator trait for temperament and used a selection criteria in beef cattle (Curley et al., 2006; Nkrumah et al., 2007b). Therefore, selection for animals with calm temperament cattle can be expected to improve animal welfare, and to also increases profits due to better performance (Voisinet et al., 1997).

Several studies have measured the relationships between EV and feed efficiency traits in growing cattle (Brown, 2005; Fox et al., 2004; Lancaster et al., 2005a; Nkrumah et al., 2007b). In summary, these studies found that EV was weakly correlated with DMI and ADG, but not with F:G and RFI, which is in agreement with findings from Elzo et al. (2009). Reports from Nkrumah et al. (2007b) determined that EV did not differ among low and high RFI steers. Likewise, Richardson et al. (2000) concluded that first generation cattle divergently selected for high and low RFI did not differ in EV when measured over a 2 wk period on 4 d. While weak to moderate negative correlations have been found between EV with ADG and DMI, the absence of relationship with RFI and G:F suggests that although cattle with aggressive temperaments as assessed by EV consume less feed and grow slower, they are not necessarily less feed efficient.

CHAPTER II

ASSOCIATIONS OF PERFORMANCE AND FEED EFFICIENCY TRAITS WITH FEED INTAKE AND FEEDING BEHAVIOR TRAITS IN GROWING SANTA GERTRUDIS HEIFERS

Introduction

The increase in cost of feed commodities has renewed interest in identifying animals that are more efficient at utilizing feed. The costs of feed is widely known as the largest variable expense in beef production (Parnell et al., 1994). Historically, feed to gain ratio (F:G) or its reciprocal, G:F (gain to feed ratio), were the most common and widely used traits used in the industry to describe the efficiency of feed utilization in beef cattle (Archer et al., 1999). Feed to gain ratio is a useful trait to evaluate the effects diet quality, environment, and management practices on production efficiency of beef cattle production systems (Carstens and Tedeschi, 2006; Nkrumah et al., 2007a). In addition, F:G is a moderately heritable trait (h^2 = 0.50; (Koots et al., 1994) that is strongly correlated (r_g > -0.50) with growth traits in cattle (Carstens and Kerley, 2009). Thus, favorable selection for F:G will increase genetic merit for growth and mature size in breeding females (Arthur et al., 2001b; Herd and Bishop, 2000; Nkrumah et al., 2004). Moreover, F:G is ratio based trait that is comprised of two traits, such that the ability to predict change of the trait in future generations becomes increasingly difficult, and therefore, limits the utility of F:G in breeding programs (Nkrumah et al., 2004). In order to improve the utilization of feed in cattle, selection should incorporate a trait that better reflects inter-animal differences in net feed efficiency while minimally affecting mature size and maintenance requirements (Arthur et al., 2001c; Carstens and Kerley, 2009).

Residual feed intake (RFI) was proposed as an alternative feed efficiency trait to identify animals that consume less feed relative to body size and level of production (Koch et al., 1963). Studies measuring heritability of RFI in beef cattle range from weak estimates of 0.14 and 0.28 (Koch et al., 1963) to moderate estimates of 0.44 and 0.43 by Arthur et al. (1997) and Arthur et al. (2001b), respectively. These results suggest that selection for animals divergent in RFI is possible. Moreover, RFI is strongly correlated phenotypically with DMI and F:G, but independent of ADG and BW (Carstens and Tedeschi, 2006; Herd and Arthur, 2009; Nkrumah et al., 2004), which is expected since RFI, by definition, is phenotypically independent of production traits. Residual feed intake is calculated as the difference between actual DMI and predicted DMI determined from linear regression of DMI on mid-test $BW^{0.75}$ and ADG (Koch et al., 1963). Selection to improve genetic merit for RFI will reduce animal feed intakes and while having minimal influences on productivity or mature size (Archer et al., 1999; Carstens and Tedeschi, 2006).

Additional feed efficiency traits including residual gain (RG) (Koch et al., 1963) and residual intake and gain (RIG) (Berry and Crowley, 2012a) have also been suggested as alternative measures of feed efficiency in beef cattle. Residual gain is a feed efficiency trait similar to RFI, however; calculation of RG involves regression of ADG on DMI and mid-test $BW^{0.75}$ (Crowley et al., 2010). Residual gain is the difference between actual and expected daily gain relative to body size and feed intake (Koch et al., 1963). Residual intake and gain combines the favorable characteristics of RFI and RG, such that it reduces feed intake and increases daily gain while minimally affecting BW (Berry and Crowley, 2012a). Calculation of RIG is determined as the sum of RG and -1 x RFI, both of which are standardized to a variance of 1. Standardization of RFI and RG allows for their equal expression in calculating RIG. Residual feed intake is multiplied by -1 in order to have a favorable comparison with a positive RG value.

Recent development of state-of-the-art technologies (i.e., GrowSafe System) have provided the industry with easier less expensive methods of collecting individual feed intakes on a commercial scale, and have also facilitated a better understanding of the biological processes associated with feed efficiency in animals (Golden et al., 2008). However, the cost of measuring feed intake with current technology remains expensive with an estimated range from $150 to more than $200 per head (Crews, 2005). Thus, indicator traits such as feeding behavior traits that are predictive of feed efficiency would be beneficial to identify animals with genetic merit for feed efficiency at a lower cost (Archer et al., 1999; Carstens and Kerley, 2009). Feeding behavior traits (e.g., BV frequency and duration) have been found to be weakly to moderately correlated with RFI (Kelly et al., 2010a; Lancaster et al., 2009b; Montanholi et al., 2009; Nkrumah et al., 2007b). Golden et al. (2008) determined that low-RFI steers had 17.6% fewer BV than high-RFI steers, which was similar to reports from Kelly et al. (2010a) where low-RFI heifers had 22% fewer BV events. Lancaster et al. (2009a) determined that meal frequency and duration accounted for 35% of the variation in intake not explained by the

RFI base model that included BW, ADG, and carcass composition. These findings suggest there may be merit in use of feeding behavior traits as indicators of efficiency, which could provide a better understanding of the variation present in RFI and reduce the costs associated with measuring feed efficiency.

Objectives

The objectives of this study were to evaluate the effects of residual feed intake classification on temperament, carcass composition, and feeding behavior traits in growing Santa Gertrudis heifers.

Materials and Methods

Animals and Experimental Design

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.

This study used 399 Santa Gertrudis heifers with initial BW of 275 ± 37.4 kg from the King Ranch in Kingsville, TX. Feed intake and behavior traits were collected for 4 groups of heifers during 4 consecutive yr at the Beef Cattle Systems Research Center in College Station, TX. Upon arrival, heifers were fitted with passive, half-duplex electronic identification (EID) transponder ear tags (Allflex, USA Inc., Dallas, TX) and randomly assigned into 1 of 4 pens (12 × 28 m) each equipped with 4 electronic feed bunks. The GrowSafe DAQ 4000E system was used during Trials 1 and 2, while Trials 3 and 4 used the GrowSafe DAQ 6000E (GrowSafe System Ltd., Airdrie, AB, Canada).

Heifers were allowed a 3 or 4 wk adaptation period to the GrowSafe bunks while consuming a forage-based diet (Table 2.1; 2.19 Mcal ME/kg, 11.2% CP on DM basis). The experiment diet consisting of 35% chopped alfalfa hay, 21.5% cottonseed hulls, 19.5% dry rolled corn, 15% alfalfa pellets, 7% molasses, and 2% mineral-vitamin premix was offered ad libitum twice daily (0800 and 1700) throughout the duration of the trials. Cattle were allowed ad libitum access to water.

The GrowSafe System

The GrowSafe DAQ 4000E system was used during trials 1 and 2, while trials 3 and 4 were conducted with the GrowSafe DAQ 6000E system. Software on the 4000E and 6000E system was capable of recording trough weights every second; however the two systems vary, such that on the 6000E system RFID ear tags were read every second, whereas on the 4000E system, RFID ear tags were read every 2 to 3 seconds. The passive electronic identification (EID) transponder tag wirelessly transmits data to a data-acquisition computer. Data transmitted includes EID number, feed bunk number, time stamp of each EID recording, and assigned feed. Load cells supporting feed bunks measure feed disappearance in grams continuously every second during each bunk visit (BV) event, which allows the user a live display of feed disappearance.

Data Collection

During the 70-d trials, BW were recorded at 14-d intervals, while exit velocity, ultrasound measurements of 12-th rib backfat thickness (BF), longissimus muscle (LM)

Table 2.1. Experimental diet ingredient and chemical composition summary for Santa Gertrudis heifers.

Item	
Ingredient	*As-fed basis %*
Dry rolled corn	19.5
Chopped alfalfa hay	35.0
Cottonseed hulls	21.5
Alfalfa pellets	15.0
Molasses	7.0
Premix[1]	2.0
Chemical Composition	*Dry matter basis*
Dry matter %	86.9
CP, %DM	11.2
NDF, %DM	53.9
ME, Mcal/kg DM	2.19

[1]Premix contained minimum 72.25% Dry rolled corn, 6.75% 9.1 KIU/kg Vit-E, 20% Salt, 1.0% Coop Beef TM contained minimum 19.0 ppm Zn, 7.0 ppm Mn, 1000 ppm Se, 500 ppm Co, 2300 ppm I, 4000 ppm Fe, and 4.5 ppm Cu.

area, and intramuscular fat (IMF) percentage were recorded at the start and end of each trial. A certified technician collected ultrasound measurements using an Aloka 500-V instrument with a 17-cm, 3.5-MHz transducer (Corometrics Medical Systems Inc., Wallingford, CT). Images collected were sent to the National Centralized Ultrasound Processing laboratory (Ames, IA) for estimation of 12th rib BF, LM area, and IMF.

Diet samples were collected every 14 d and composited by weight at the end of each trial for chemical analysis by an independent laboratory (Cumberland Valley Analytical Services, Hagerstown, MD). The moisture analysis for each trial was used to compute DMI.

Exit velocity (EV) was measured as the time in seconds for an animal to traverse a distance of 1.8 m (Burrow et al., 1988) after exiting a squeeze chute. The timing system featured 2 light beams focused on infrared sensors that activate the start and stop mechanism as the beams are broken. Exit velocity was calculated at rate (sec/m) to transverse the distance of 1.8m

A subroutine of the GrowSafe 4000E and 6000E, Process Feeding Intakes, was used to calculate feed intake and bunk visit data. All default settings as previously defined by GrowSafe (2009) were used in this study; however, parameter settings for the maximum duration of time between consecutive EID recordings to end an interrupted bunk visit event were set to 100 s based on recommendations from Mendes et al. (2011). Feed intake and feeding behavior were deleted for 13, 29, 9, and 3 d for trials 1, 2, 3, and 4, respectively. Factors contributing to data removal included system failure, power outage, EID transponder tag malfunction, pen average assigned feed disappearance

(AFD) less than 95%, or pen average assigned feed supply (AFS) less than 90%. An AFD percent close to 100% is desired as it ensures that feed is not disappearing without an EID associated with the feed disappearance. Similarly, an AFS percent close to 100% is desired, as it indicates that feed was available for consumption ad libitum. The average AFD for the remaining days was 98.3%, 97.6%, 99.4%, and 99.5%, while the average AFS was 98.3%, 97%, 96.6%, and 97.7% for Trial 1, 2, 3, and 4, respectively.

Feeding Behavior Analysis

Feeding behavior traits (Table 2.2) were evaluated for each individual animal on a daily basis for each trial. In this study, BV frequency was defined as the number of daily BV events regardless of whether or not feed was consumed. Bunk visit duration was determined as the summation of the lengths of time of all BV events during a 24 h period. Feeding bout (FB) frequency was defined as the number of bunk visits in a day with > 0 g feed consumed. Feeding bout duration was computed as the summation of time spent at the feed bunk with > 0 g feed consumed. Time to bunk (TTB) was calculated on an individual animal basis as the interval length between the feed truck dispensing the morning feed into each pen and the initial FB for each animal. Time to bunk was determined from the daily feed supply time and FB data using the R-script in the R statistical program.

The intervals between BV events when the animal was not at the feed bunks were defined as non-feeding intervals (NFI). The frequency and duration of NFI were computed from BV event data $\log_{10}$ transformed and plotted in a frequency distribution

Table 2.2 Definition of feeding behavior traits measured in this study.

Trait	Definition	Unit
Bunk visit (BV) frequency	Frequency of visits to the feed bunk on a daily basis	events/d
BV duration	Summation of time spent at the feed bunk per day	min/d
Feeding bout (FB) frequency	Frequency of visits to the feed bunk with > 0 g feed intake recorded on a daily basis	events/d
FB duration	Summation of time spent at the feed bunk with > 0 g feed intake recorded	min/d
Meal criterion	The longest interval between bunk visits that is still considered a meal	min/d
Meal frequency	Frequency of meal events per day	events/d
Meal duration	Summation of time consuming meals per day	min/d
Non-feeding interval (NFI) frequency	Frequency of non-feeding intervals per day	events/d
NFI duration	Summation of time between BV per day	min/d
Meal size	Average consumption per meal per day	kg/d
FB eating rate	Average DMI consumed per FB event	g/min
Meal eating rate	Average DMI consumed per meal event	g/min
Time to bunk (TTB)	Length of time between morning feed truck delivery and first bunk visit event with > 0 g feed consumed	min/event

graph using the Meal Criterion Calculation (MCC; http://nutritionmodels.tamu.edu) software in conjunction with the R statistical software (ver. 2.13.0; The R Foundation for Statistical Computing; http://www.r-project.org). Non-feeding intervals less than 2 s were removed prior to data analysis, which was similar to the approach used by Bailey et al. (2012). The Gaussian-Weibull distribution model was used in determining meal criterion for each animal based on several studies (Bailey et al., 2012; Yeates et al., 2002) concluding the Gaussian-Weibull model combination as the best approach in evaluating meal pattern behavioral traits in beef cattle. Meal criterion (MC) represents the longest interval between bunk visits that is still considered part of a meal. Moreover, MC serves as the foundation from which meal traits such as frequency and duration are derived from. Meal frequency was defined as the number of independent meal events recorded per day and meal duration was computed as the sum of all daily individual meal events.

Statistical Analysis

In this study each animal was considered the experimental unit for all the data analyzed. Model growth rates were generated by the PROC GLM procedure in SAS (SAS Inst. Inc. Cary, NC) for individual animals using linear regression of 14-d BW during the trial. Output regression coefficients were then used to calculate the initial and final BW, ADG, and mid-test $BW^{0.75}$ for individual animals. Dry matter intake for each animal was computed from recorded feed intake data and moisture analysis of composite diet samples. In the event of missing days, linear regression of daily feed intakes on day of trial was used to compute the values for missing days using the SAS PROC GLM procedure

Residual feed intake (RFI) was among the several traits (Table 2.3) analyzed in this study was computed as the difference between actual and expected DMI from linear regression of DMI, ADG, and mid-test $BW^{0.75}$ (Koch et al., 1963). Residual gain (RG) was computed from a linear regression of ADG on DMI and mid-test $BW^{0.75}$(Crowley et al., 2010; Koch et al., 1963) as the difference between actual and estimated gain. Residual intake and gain (RIG) was calculated as the sum of RFI × -1 and RG, while standardizing both to a variance of 1 (Berry and Crowley, 2012b). Standardizing RFI and RG ensures equal contribution when determining RIG. RFI is multiplied by -1 to account for efficient animals possessing a negative RFI number.

To further characterize RFI, RG, and RIG, heifers were classified using into low (< 0.50 SD), medium (± 0.5 SD), and high (> 0.50 SD) groups in the meta-analysis, and the PROC MIXED model was used to examine effect of RFI, RG, or RIG. Pen and trial were included in the model as random effects. Feed efficiency, performance, feeding behavior, exit velocity, and carcass ultrasound traits analyzed in this study were adjusted using the PROC MIXED procedure in SAS to remove the random effects of trial and pen within trial. Phenotypic Pearson correlation coefficients were computed with adjusted feed efficiency, feeding behavior, performance, temperament, and ultrasound traits using the PROC CORR command of SAS. Class comparisons (RFI, RG, and RIG) were analyzed with non-adjusted traits using the PROC GLIMMIX procedure of SAS, in which trial and pen within trial were fixed effects. Feed efficiency, feeding behavior,

Table 2.3. Description of feed efficiency traits measured in this study.

Trait	Description	Unit	Classification
Residual feed intake (RFI)	Difference between the actual and predicted intake based on regression of DMI on ADG and mid-test BW	Kg/d	Negative value indicates the animal is more efficient by consuming less than predicted feed
Gain to feed ratio (G:F)	Daily gain per DMI ratio	Ratio	Higher value is more efficient
Residual BW gain (R:G)	Difference between the actual and predicted gain based on regression of ADG on DMI and mid-test BW	Kg/d	Positive value indicates animals will gain more than expected
Residual intake and BW gain (RIG)	Combination of RFI and RG standardized to value of 1 to compensate for negative RFI value	No unit	Positive value indicates than an animal gains fast and has less than expected DMI

performance, temperament, and ultrasound traits were tested for normality using the Anderson-Darling test. For the 3 efficiency traits (RFI, RG, and RIG) classification models, ultrasound and feeding behavior traits that didn't have a normal distribution such as initial and final BF, initial and final IMF, meal criterion, meal frequency and duration, eat rate, BV frequency, FB frequency, FB eat rate, and TTB were analyzed using a Gamma distribution. Least squares means comparisons were generated for RFI, RG, and RIG using the Tukey post hoc test. Stepwise regression was determined with a significance level of 0.10 to determine the relationship of feeding behavior, ultrasound, exit velocity, and meal traits in the RFI base model that included ADG and MBW.

Trials were individually evaluated based on stringent criteria (e.g. chronic sick/treated) designed to remove heifers that were considered outliers. Prior to analysis, 2 heifers were removed due to death. Using BW R^2 determined from linear regression, heifers with a BW $R^2 < 0.75$ were removed (n = 9). Heifers were then assessed on ADG and DMI as percent BW, in which those animals outside of 2 standard deviations (SD) were considered outliers. Consequently, outliers were removed if they were chronically treated for illness (n = 16). Heifers outside of 2 SD of RFI were considered outliers and were removed if they received treatment for sickness and/or had an irregular intake pattern during the experimental trial (n = 3). Therefore applying these criteria to the study removed a total of 30 heifers (including 2 deceased heifers) from the final analysis, such that of the 399 heifers that started the trial, only 369 heifers were used for final analysis.

Results and Discussion

Means and standard deviations (SD) for the 4 performance trials are presented in Table 2.4. Average initial and final BW for the 4 trials were 275 ± 37.4 kg and 348 ± 41.4 kg, respectively. Across the 4 trials, ADG, DMI, and RFI for the heifers were 1.04 ± 0.18, 9.14 ± 1.32, and 0.00 ± 0.91 kg/d, respectively. Over all summary statistics are presented in Table 2.5 for performance feed efficiency, and over all feeding behavior traits.

Phenotypic Correlations Between Performance, Feed Intake, and Feed Efficiency Traits

The phenotypic correlations between growth and feed efficiency traits are presented in Table 2.6. Dry matter intake was strongly ($P < 0.05$) correlated positively with initial BW (0.48), ADG (0.58), and RFI (0.72), while negatively correlated with G:F (-0.33), and RIG (-0.42). Correlations of DMI with ADG and RFI from this study are comparable to those presented by Lancaster et al. (2009a) in Angus bulls, for DMI with ADG and RFI (0.57 and 0.70, respectively) and by Kelly et al. (2010b) in crossbred beef heifers (0.50 and 0.58, respectively). In contrast to results from the current study, Kelly et al. (2010b) found no a significant correlation between DMI and G:F (-0.06; P > 0.05).

As expected, RFI was found in this study to be independent of ADG and BW, but positively correlated with DMI, which is consistent with research presented in other studies (Arthur et al., 2001a; Herd and Bishop, 2000; Nkrumah et al., 2007a). The correlations between RFI with ADG, BW, and DMI are expected due to the linear regression used to calculate RFI, which influences RFI to be independent of ADG and

Table 2.4. Summary statistics (± SD) for performance, feed efficiency, ultrasound composition, feeding behavior, and exit velocity traits for Santa Gertrudis heifers in 4 trials.

Trait[a]	Trial 1	Trial 2	Trial 3	Trial 4
No. of Heifers	50	121	99	99
Performance traits				
Initial BW, kg	236.8 ± 30.4	273.5 ± 38.7	293.1 ± 32.7	279.1 ± 27.9
Final BW, kg	307.5 ± 33.4	347.4 ± 41.9	360.7 ± 38.2	358.1 ± 34.1
ADG, kg/d	1.01 ± 0.17	1.06 ± 0.19	0.97 ± 0.16	1.13 ± 0.20
DMI, kg/d	9.25 ± 1.41	9.15 ± 1.62	9.10 ± 1.20	9.00 ± 1.00
Feed efficiency traits				
G:F	0.11 ± 0.02	0.12 ± 0.02	0.11 ± 0.01	0.12 ± 0.02
RFI, kg/d	0.00 ± 1.09	0.00 ± 1.29	0.00 ± 0.71	0.00 ± 0.56
RG, kg/d	0.00 ± 0.14	0.00 ± 0.16	0.00 ± 0.12	0.00 ± 0.14
RIG	0.00 ± 1.80	0.00 ± 2.16	0.00 ± 1.34	0.00 ± 1.38
Carcass ultrasound traits				
Initial LM area, cm^2	44.06 ± 5.48	47.21 ± 7.10	51.70 ± 5.74	57.69 ± 6.41
Initial BF thickness, cm	0.21 ± 0.04	0.41 ± 0.13	0.38 ± 0.13	0.36 ± 0.15
Initial IMF, %	2.47 ± 0.43	2.37 ± 0.56	2.42 ± 0.69	2.16 ± 0.55
Final LM area, cm^2	55.57 ± 7.63	60.69 ± 7.42	64.05 ± 6.43	64.87 ± 6.65
Final BF thickness, cm	0.32 ± 0.10	0.57 ± 0.21	0.47 ± 0.19	0.53 ± 0.19
Final IMF, %	2.52 ± 0.48	2.21 ± 0.57	2.77 ± 0.68	2.29 ± 0.53
Bunk visit traits				
BV frequency, events/d	75.95 ± 13.18	71.89 ± 12.89	72.45 ± 15.57	70.36 ± 15.19
BV duration, min/d	89.4 ± 23.6	87.2 ± 27.9	119.4 ± 28.8	120.0 ± 25.2
FB frequency, events/d	68.71 ± 12.14	63.38 ± 11.43	65.01 ± 13.73	63.40 ± 13.28
FB duration, min/d	87.4 ± 23.6	84.9 ± 27.3	116.0 ± 27.5	117.4 ± 24.5
NFI frequency, events/d	74.44 ± 12.93	68.41 ± 12.36	70.86 ± 15.30	69.46 ± 14.82
NFI duration min/d	1333 ± 25.0	1353 ± 28.0	1300 ± 29.3	1321 ± 25.0
Time to bunk, min	44.10 ± 18.45	68.06 ± 30.39	60.45 ± 27.85	81.87 ± 34.27
Meal traits				
Meal criterion, min	10.03 ± 3.90	12.17 ± 4.70	7.82 ± 4.06	5.58 ± 2.49
Meal frequency, events/d	11.15 ± 2.38	10.32 ± 2.52	12.74 ± 3.50	13.16 ± 2.93
Meal duration, min/d	189.0 ± 31.5	180.7 ± 37.9	216.3 ± 49.6	180.0 ± 29.3
Meal length, min/event	17.93 ± 5.49	18.55 ± 6.25	18.61 ± 8.21	14.42 ± 4.23
Meal size, kg/event	0.86 ± 0.21	0.92 ± 0.23	0.77 ± 0.25	0.71 ± 0.18
Meal eating rate, g/min	49.77 ± 9.18	51.94 ± 10.34	43.33 ± 7.43	50.33 ± 6.67
FB eating rate, g/min	110.1 ± 21.9	115.5 ± 29.8	81.73 ± 17.2	78.59 ± 15.3
BV per meal, events/meal	7.05 ± 1.58	7.23 ± 1.80	5.99 ± 1.80	5.52 ± 1.41
Exit velocity traits				
Initial exit velocity, m/s	2.81 ± 0.73	3.56 ± 0.92	3.69 ± 1.10	3.48 ± 1.02
Final exit velocity, m/s	4.04 ± 1.50	n/a	3.98 ± 1.02	3.97 ± 1.14

[a]RFI = residual feed intake; RG = residual gain efficiency; RIG = residual intake and gain; LM = longissimus muscle; BF = 12th-rib fat thickness; IMF = intra muscular fat; BV = bunk visit; FB = Feeding bout; NFI = Non-feeding interval.

Table 2.5. Summary statistics for performance, feed efficiency, ultrasound composition, feeding behavior, and exit velocity traits in Santa Gertrudis heifers (n = 369).

Trait[a]	Mean	SD	Min	Max
Performance traits				
Initial BW, kg	275.3	37.4	165.9	381.8
Final BW, kg	348.4	41.4	222.5	464.1
ADG, kg/d	1.04	0.19	0.52	1.59
DMI, kg/d	9.10	1.34	4.81	14.58
Feed efficiency traits				
G:F	0.116	0.020	0.068	0.184
RFI, kg/d	0.00	0.96	-3.80	3.47
RG, kg/d	0.00	0.14	-0.41	0.43
RIG	0.00	1.72	-5.58	5.74
Carcass ultrasound traits				
Initial LM area, cm^2	50.63	7.93	27.74	70.32
Initial BF thickness, cm	0.363	0.142	0.102	0.991
Initial IMF, %	2.34	0.59	1.09	4.40
Final LM area, cm^2	61.98	7.62	40.65	81.94
Final BF thickness, cm	0.499	0.200	0.102	1.17
Final IMF, %	2.43	0.626	1.02	5.03
Bunk visit traits				
BV frequency, events/d	72.18	14.36	34.16	113.2
BV duration, min/d	105.0	31.2	31.6	220.8
FB frequency, events/d	64.55	12.75	30.28	104.7
FB duration, min/d	102.3	30.31	30.56	207.2
NFI frequency, events/d	70.17	14.03	33.32	112.3
NFI duration min/d	1327	34.24	1206	1413
Time to bunk, min	66.47	31.76	10.84	171.2
Meal traits				
Meal frequency, events/d	11.84	3.14	6.00	35.75
Meal duration, min/d	191.2	41.53	85.58	414.9
Meal criterion, min	8.94	4.71	1.79	25.87
Meal length, min/event	17.37	6.54	6.18	53.82
Meal size, kg/event	0.817	0.237	0.334	1.70
Meal eating rate, g/min	48.90	9.20	23.02	85.60
BV per meal, events/meal	6.41	1.82	2.76	13.80
Exit velocity traits				
Initial exit velocity m/s	3.47	1.01	0.419	6.67
Final exit velocity m/s	3.99	1.17	0.449	8.18

[a]RFI = residual feed intake; RG = residual gain efficiency; RIG = residual intake and gain; LM = longissimus muscle; BF = 12th-rib fat thickness; IMF = intra muscular fat; BV = bunk visit; FB = feeding bout; NFI = Non-feeding interval.

Table 2.6. Phenotypic correlations between performance, feed intake, and feed efficiency traits in Santa Gertrudis heifers (n = 369) fed a forage-based diet

Trait[a]	ADG	DMI	G:F	RG	RIG	RFI
Initial BW	0.187[b]	0.483[b]	-0.246[b]	-0.151[b]	-0.087	-0.001
ADG		0.578[b]	0.565[b]	0.796[b]	0.462[b]	0.00
DMI			-0.329[b]	0.00	-0.417[b]	0.720[b]
G:F				0.905[b]	0.942[b]	-0.720[b]
RG					0.862[b]	-0.486[b]
RIG						-0.862[b]

[a]RG = residual gain efficiency; RIG = Residual intake and BW gain; RFI = residual feed intake.
[b]Correlations are different from zero at $P < 0.05$.

BW, while the positive correlation suggests that favorable selection for RFI will result in lower DMI. Moderate to strong correlations ($P < 0.001$) between RFI with R:G and RIG (-0.49 and -0.86, respectively) were observed, such that heifers with lower RFI were more efficient in terms of having greater RG and RIG than high-RFI heifers. Moderate to strong correlations ($P < 0.001$) of G:F with ADG, DMI and RFI (0.57, -0.33 and -0.72 respectively) were found, such animals with greater G:F will have lower DMI and RFI but greater ADG. In addition, R:G was found positively ($P < 0.001$) correlated with G:F and ADG (0.91 and 0.80, respectively) suggesting that favorable RG selection may result in more efficient, faster gaining animals. Results from this study are in agreement with Berry and Crowley (2012a), where RG was found to be strongly correlated ($P < 0.02$) with ADG and F:G (0.70 and -0.71, respectively) and independent of DMI.

Residual intake and gain (RIG) was not phenotypically correlated ($P = 0.10$) with initial BW, while moderate to strong correlations ($P < 0.001$) were observed with ADG, DMI, and G:F were 0.46, -0.42, and 0.94, respectively. Favorable characteristics of RFI and RG is conveyed in RIG results found in this study, such that no differences were observed with BW, yet as RIG increased, DMI decreased and ADG increased. These results are comparable to those found by Berry and Crowley (2012a), in that high-RIG animals had greater ADG and lower DMI compared to low-RIG animals.

The heifers with low RFI (Table 2.7) consumed 21.5% less DMI compared to high-RFI heifers. These results are similar to the 21% difference reported by Carstens et al. (2002) in low-RFI steers and the 22.5% reported by Bingham et al. (2009) in low-RFI Brangus heifers. Collectively, these results are higher than the 15% difference reported by Lancaster et al. (2005b) in low-RFI calves when calves were separated based on ± 0.5 SD from mean RFI. Low-RFI heifers had a 30.6% greater ($P < 0.001$) G:F than high-RFI heifer groups. Results from this study are comparable to findings by Bingham et al. (2009) in which low-RFI heifers had a 30% greater G:F ratio than high-RFI heifers when consuming a roughage-based diet. Other studies have reported significantly lower differences including 9.4% (Basarab et al., 2003) and 13% (Baker et al., 2006) when comparing low-RFI to high-RFI groups, based on ± 0.5 SD from the RFI mean.

Classification of heifers by divergent phenotypes for RG revealed that high-RG heifers (Table 2.8) had a 37.1% higher G:F and lower RFI than low-RG heifers. Heifers that were classified as low RG were 5.0% heavier at the beginning of the trial, 2.9% lighter at the end of the trial, and gained 27.9% less ADG than high-RG heifers.

Results from this study indicated no significant differences in BW between low- and high-RIG heifers (Table 2.9), which is in contrast to other studies. Berry and Crowley (2012a) reported a difference of 2.1% in initial BW ($P < 0.001$) in favor of low-RIG bulls, yet a final BW difference of 2.3% in favor of the high-RIG bulls that consumed on average 5.5% less feed ($P < 0.001$) throughout the trial. As expected, RIG combined the favorable characteristics of RFI and RG by reducing DMI and increasing ADG of heifers with high-RIG phenotypes compared to those with low-RIG phenotypes. Compared to low-RIG heifers, the high-RIG heifers had 12.6% lower DMI and 22.8% higher ADG, which are similar to the 5.45% lower intakes and 24% higher ADG reported by Berry and Crowley (2012a) in high-RIG bulls.

In this study, high-RIG heifers were found to be more efficient with lower RFI

Table 2.7. Effects of RFI classification on performance and feed efficiency traits in Santa Gertrudis heifers.

Trait*	Low RFI	Med RFI	High RFI	SE	*P*-value
No. of heifers	101	168	100	-	-
Performance traits					
Initial BW, kg	271.0	269.5	273.0	12.3	0.732
Final BW, kg	345.3	341.2	346.0	12.7	0.541
ADG, kg/d	1.06	1.03	1.04	0.04	0.250
DMI, kg/d	8.06[a]	9.00[b]	10.27[c]	0.11	0.001
Feed efficiency traits					
G:F	0.132[a]	0.114[b]	0.101[c]	0.002	0.001
RFI, kg/d	-1.12[a]	0.002[b]	1.13[c]	0.049	0.001
RG, kg/d	0.096[a]	-0.007[b]	-0.085[c]	0.018	0.001
RIG	1.84[a]	-0.053[b]	-1.77[c]	0.110	0.001

*RFI = residual feed intake; RG = residual gain; RIG = residual intake and gain.
[a,b,c]Means within a row without a common superscript differ ($P < 0.05$).

Table 2.8. Effects of RG classification on performance and feed efficiency traits in Santa Gertrudis heifers.

Trait*	Low RG	Medium RG	High RG	SE	*P*-value
No. of heifers	113	132	124	-	-
Performance traits					
Initial BW, kg	275.3[a]	274.7[a]	262.3[b]	12.0	0.003
Final BW, kg	335.8[a]	348.4[b]	345.8[b]	12.3	0.027
ADG, kg/d	0.865[a]	1.05[b]	1.20[c]	0.04	0.001
DMI, kg/d	8.99	9.31	9.02	0.132	0.122
Feed efficiency traits					
G:F	0.097[a]	0.114[b]	0.133[c]	0.004	0.001
RFI, kg/d	0.466[a]	0.098[b]	-0.530[c]	0.082	0.001
RG, kg/d	-0.166[a]	-0.003[b]	0.155[c]	0.006	0.001
RIG	-1.65[a]	-0.117[b]	1.62[c]	0.093	0.001

*RFI = residual feed intake; RG = residual gain; RIG = residual intake and gain.
[a,b,c] Means within a row without a common superscript differ ($P < 0.05$).

Table 2.9. Effects of RIG classification on performance and feed efficiency traits in Santa Gertrudis heifers.

Trait*	Low RIG	Medium RIG	High RIG	SE	*P*-value
No. of heifers	104	158	107	-	-
Performance traits					
Initial BW, kg	274.0	271.0	267.5	12.2	0.364
Final BW, kg	339.0	344.3	347.2	12.6	0.272
ADG, kg/d	0.928[a]	1.05[b]	1.14[c]	0.04	0.001
DMI, kg/d	9.64[a]	9.17[b]	8.43[c]	0.12	0.001
Feed efficiency traits					
G:F	0.096[a]	0.114[b]	0.135[c]	0.004	0.001
RFI, kg/d	0.914[a]	0.056[b]	-0.976[c]	0.062	0.001
RG, kg/d	-0.152[a]	0.002[b]	0.144[c]	0.007	0.001
RIG	-2.01[a]	-0.043[b]	2.02[c]	0.079	0.001

*RFI = residual feed intake; RG = residual gain; RIG = residual intake and gain.

[a,b,c]Means within a row without a common superscript differ ($P < 0.05$).

values and higher G:F and R:G. Moderate heritability of RIG (0.36 ± 0.06) determined by Berry and Crowley (2012a), suggests retention of high-RIG heifers in the cow herd may lead to calves that are more feed efficient through higher daily gains with lesser feed consumptions. Although RIG is a fairly new trait in the beef industry, it has gained interest in other species including poultry. Willems et al. (2013) recently conducted a study with male turkeys and found that high-RIG toms were more efficient than low-RIG toms, such that high-RIG toms had 15.4% higher daily gains, consumed 7.6% less feed, and had 25.3% lower F:G.

Carcass Ultrasound Composition and RFI

Phenotypic correlations between RFI and initial and final BF thickness were not significant ($P < 0.05$) in this study. In purebred Angus steers, Baker et al. (2006) found no significant phenotypic correlations between RFI and initial and final BF thickness. Findings reported by Golden et al. (2008) also determined that BF thickness did not differ ($P > 0.10$) among efficient and inefficient Angus steers, which is also in agreement with Arthur et al. (2001a). While RFI classification had no effect on initial and final BF thickness (Table 2.10), it has been suggested that low RFI cattle may be leaner according to evidence of genetic and phenotypic relationships between RFI and BF thickness (Herd and Pitchford, 2011; Randel and Welsh, 2013). Phenotypic correlations reported by Nkrumah et al. (2004), Nkrumah et al. (2007a), and Lancaster et al. (2009a) between RFI and ultrasound BF thickness (r_p = 0.19, 0.25, and 0.20 respectively) provide evidence that low-RFI animals are leaner, such that animals

Table 2.10. Effects of RFI classification on carcass ultrasound traits in Santa Gertrudis heifers.

Trait*	Low RFI	Med RFI	High RFI	SE	*P*-value
No. of heifers	101	168	100	-	-
Carcass ultrasound traits					
Initial LM area, cm^2	50.60	50.21	49.65	2.99	0.554
Initial back fat depth, cm	0.345	0.345	0.332	0.045	0.691
Initial intramuscular fat, %	2.40	2.31	2.38	0.084	0.468
Final LM area, cm^2	61.89	60.90	61.39	2.18	0.542
Final back fat depth, cm	0.466	0.468	0.491	0.056	0.561
Final intramuscular fat, %	2.40	2.45	2.47	0.138	0.617

*LM = longissimus muscle; BF = 12th-rib fat thickness; IMF = intra muscular fat.
[a,b,c]Means within a row without a common superscript differ ($P < 0.05$).

classified as low RFI (P < 0.05) had 16.3, 16.1, and 11.9% lesser BF thickness than high-RFI animals, respectively. Although BF gain was found independent of RFI in this study, previous research by Nkrumah et al. (2004) and Lancaster et al. (2009a) determined weak phenotypic correlations (r_p = 0.20 and 0.30 respectively) between RFI and BF gain. Results presented by Lancaster et al. (2009a) and Nkrumah et al. (2007a) suggest less efficient animals are more likely to deposit greater amounts of BF, in that high-RFI animals had 52.4 and 31% greater BF gains, respectively. In the current study, the relationship between RFI and IMF was not significant, which corresponds with results from several studies (Basarab et al., 2003; Carstens et al., 2002; Nkrumah et al., 2004; Schenkel et al., 2004).

The associations of RFI with initial and final LM area, and LM area gain (P < 0.05) were not significant in this study. Likewise, Baker et al. (2006) found no significant correlations between RFI and initial and final LM area. Similarly, Golden et al. (2008) found that LM area did not differ among efficient and inefficient RFI Angus steers. Whereas, Lancaster et al. (2009a) found a weak phenotypic correlation between RFI and LM area gain (r_p = 0.17), which suggests that high-RFI animals had greater LM area gain, such that high-RFI bulls had 13.8% greater LM area gain. Although the relationship between RFI and marbling score was not evaluated in this study, reports by Nkrumah et al. (2004) on crossbred steers and bulls and concluded that RFI was independent of ultrasound-based marbling score. Although, Basarab et al. (2003) failed to detect a relationship between RFI and initial and final marbling score, a significant relationship was determined between RFI and gain in ultrasound marbling score (r = 0.22), such that low-RFI cattle had lower gain in marbling scores than high-RFI cattle.

As previously noted, RFI is a moderately heritable trait in beef cattle ($h^2 = 0.44$; Arthur et al., 1997), therefore, favorable selection for RFI will improve feed efficiency, and may also result in leaner animals. Richardson et al. (1998) examined the effect of postweaning selection for RFI,, and determined that progeny born to parents selected for low RFI had less BF thickness and smaller LM area for both initial and final measurements compared to progeny from high-RFI parents. Herd and Bishop (2000) reported negative genetic and phenotypic correlations between RFI and the expected lean content (r = -0.43 and -0.22 respectively) in Hereford cattle, demonstrating that low-RFI animals are leaner than high-RFI contemporaries. Phenotypic correlations reported by Nkrumah et al. (2007a) between RFI and carcass grade fat, lean meat yield, and carcass yield grade (0.23, -0.21, and 0.22; $P < 0.01$ respectively) in crossbred *B. taurus* cattle, suggests that low-RFI animals produce greater lean meat yields, in which low-RFI steers ($P < 0.001$) had 18.7% lesser carcass grade fat than high-RFI steers.

It has been suggested that leaner females reach puberty at older ages and calve later in the season, due to the strong influence of fat stores on estrus (Randel and Welsh, 2013). A weak negative correlation (-0.16; $P = 0.06$) was observed between RFI and age at puberty, determined from serum progesterone concentrations exceeding 1 ng/mL (Shaffer et al., 2011). It was determined by a linear association between RFI and age at puberty that a 1-unit increase in RFI resulted in reduction of 7.54 d age at puberty in *B. taurus* beef heifers (Shaffer et al., 2011). However, this relationship was not observed in

Bos indicus-influenced heifers (Randel and Welsh, 2013) suggesting there is genetic variation between breeds. Shaffer et al. (2011) determined that selection for low RFI was accompanied by indirect selection for later reproductive maturity, such that high-RFI females reached puberty 2 wk sooner than low-RFI females. However, Randel and Welsh (2013) determined that sexual maturity was not influenced by RFI phenotype. Shaffer et al. (2011) noted that selection for low RFI in beef cattle is unlikely to affect fertility, as there are large amounts of variation in age at puberty. Basarab et al. (2011) concluded that when RFI was adjusted for BF thickness and feeding behavior, no differences were observed in pregnancy rate, calving pattern and productivity in beef heifers. However, the authors noted when RFI was not adjusted for BF and feeding activities, selection for low RFI heifers may then contribute to reduced pregnancy rates. The differences in progeny results between low and high RFI heifers suggests further research is warranted in determining the effects of RFI in reproductive programs.

Residual gain was not correlated with initial and final LM area, initial and final BF thickness, or initial and final IMF, but was found weakly correlated with LM area gain and BF gain (0.14 and 0.11; $P < 0.05$ respectively). Classification of RG on carcass traits (Table. 2.11) determined that low-RG heifers possessed 5.35% larger initial LM area and 12.5% thicker initial BF, however no however no differences were observed for final LM area, BF thickness, and final IMF as *P*-values were 0.73, 0.25, and 0.49, respectively.

Phenotypic correlations between RIG and carcass ultrasound traits did not reach the significance level of $P < 0.05$. The effect of RIG classification on carcass ultrasound

Table 2.11. Effects of RG classification on carcass ultrasound traits in Santa Gertrudis heifers.

Trait[*]	Low RG	Medium RG	High RG	SE	P-value
No. of heifers	113	132	124	-	-
Carcass ultrasound traits					
Initial LM area, cm^2	51.40[a]	50.53[a]	48.67[b]	2.99	0.003
Initial BF thickness, cm	0.360[a]	0.352[a]	0.314[b]	0.045	0.012
Initial IMF, %	2.38	2.34	2.33	0.08	0.807
Final LM area, cm^2	61.59	61.53	60.95	2.15	0.734
Final BF thickness, cm	0.475	0.493	0.454	0.055	0.252
Final IMF, %	2.48	2.46	2.39	0.134	0.485

*LM = longissimus muscle; BF = 12^{th}-rib fat thickness; IMF = intra muscular fat.
[a,b,c] Means within a row without a common superscript differ ($P < 0.05$).

traits (Table 2.12) demonstrated similar results to the RFI results found in this study, such that no differences were observed between high and low-RIG heifers. Therefore, these results are in agreement with Berry and Crowley (2012a), such that RIG did not influence carcass characteristics.

Associations between Feeding Behavior and Feed Efficiency

It was determined that RFI was positively correlated with BV frequency and duration (0.45 and 0.35 respectively), but negatively correlated with NFI duration and MC (-0.32 and -0.25 respectively), such that heifers with low RFI had lower BV frequency and durations, but greater non-feeding durations and MC (Table 2.13). Similarly, Montanholi et al. (2009) determined that RFI was positively correlated with BV frequency and duration (0.35 and 0.24 respectively). Moreover, Nkrumah et al. (2007b) concluded that RFI was positively correlated with feeding frequency and duration, suggesting that high-RFI steers visited the feed bunks more often and for longer durations than low-RFI steers. The positive correlations found between RFI and eating rate, NFI frequency, and FB frequency (0.28, 0.44, and 0.49 respectively) suggests that high-RFI heifers consume feed at faster rates and have higher NFI frequencies attributed from high FB frequencies, which is similar to results presented by Kelly et al. (2010a). Low-RFI heifers visited the feed bunks 19.7% ($P < 0.001$) fewer times than high-RFI heifers; suggesting that low-RFI heifers expanded less energy walking to and from the feed bunks (Table 2.14). These findings are similar to differences reported by Golden et al. (2008) and Kelly et al. (2010a) who found 17.6%

Table 2.12. Effects of RIG classification on carcass ultrasound traits in Santa Gertrudis heifers.

Trait*	Low RIG	Medium RIG	High RIG	SE	*P*-value
No. of heifers	104	158	107	-	-
Carcass ultrasound traits					
Initial LM area, cm^2	51.00	49.89	49.87	3.02	0.353
Initial BF thickness, cm	0.355	0.341	0.330	0.045	0.386
Initial IMF, %	2.36	2.32	2.38	0.08	0.645
Final LM area, cm^2	62.13	60.75	61.79	2.20	0.304
Final BF thickness, cm	0.484	0.474	0.466	0.056	0.794
Final IMF, %	2.50	2.41	2.44	0.026	0.500

*LM = longissimus muscle; BF = 12th-rib fat thickness; IMF = intra muscular fat.

[a,b,c]Means within a row without a common superscript differ ($P < 0.05$).

Table 2.13. Phenotypic correlations between performance, feed efficiency, exit velocity, and feeding behavior traits in Santa Gertrudis heifers (n=369).

Traits[a]	ADG	DMI	G:F	RG	RIG	RFI
Bunk visit traits						
BV frequency, events/d	0.19[b]	0.35[b]	-0.13[b]	-0.02	-0.27[b]	0.45[b]
BV duration, min/d	0.40[b]	0.54[b]	-0.08	0.08	-0.16[b]	0.35[b]
FB frequency, events/d	0.18[b]	0.38[b]	-0.17[b]	-0.04	-0.31[b]	0.49[b]
FB duration, min/d	0.40[b]	0.55[b]	-0.10	0.08	-0.16[b]	0.35[b]
NFI frequency, events/d	0.19[b]	0.34[b]	-0.13[b]	-0.01	-0.27[b]	0.44[b]
NFI duration, min/d	0.28[b]	0.45[b]	-0.13[b]	-0.10	0.13[b]	-0.32[b]
Time to bunk, min	-0.35[b]	-0.40[b]	0.02	-0.12[b]	0.04	-0.19[b]
Exit Velocity traits						
Initial exit velocity, m/s	-0.18[b]	-0.27[b]	0.06	-0.02	0.03	-0.07
Meal traits						
Meal criterion, min/d	0.09	-0.06	0.19[b]	0.14[b]	0.22[b]	-0.25[b]
Meal frequency, events/d	-0.02	-0.01	-0.02	-0.01	-0.05	0.08
Meal duration, min/d	0.39[b]	0.49[b]	-0.02	0.12[b]	-0.11[b]	0.31[b]
Meal length, min/d	0.24[b]	0.30[b]	-0.01	0.07	-0.06	0.04
Meal size, kg/event	0.32[b]	0.55[b]	-0.17[b]	0.05	-0.19[b]	0.33[b]
Meal eating rate, g/min	0.02	0.29[b]	-0.29[b]	-0.16[b]	-0.25[b]	0.28[b]
BV per meal, events/meal	0.17[b]	0.28[b]	-0.08	0.00	-0.18[b]	0.30[b]

[a]RG = residual gain; RIG = residual intake and gain; RFI = residual feed intake; BV = bunk visit; FB = feeding bout; NFI = non-feeding interval.
[b]Correlations are different from zero at $P < 0.05$.

Table 2.14. Effects of RFI classification on feeding behavior and exit velocity traits in Santa Gertrudis heifers.

Trait*	Low RFI	Med RFI	High RFI	SE	*P*-value
No. of heifers	101	168	100	-	-
Bunk Visit traits					
BV frequency, events/d	64.69[a]	71.78[b]	80.56[c]	1.64	0.001
BV duration, min/d	95.7[a]	103.8[b]	113.4[c]	9.59	0.001
FB frequency, events/d	57.88[a]	64.82[b]	72.85[c]	1.43	0.001
FB duration, min/d	93.3[a]	101.2[b]	110.6[c]	3.49	0.001
NFI frequency, events/d	63.64[a]	70.32[b]	78.70[c]	1.65	0.001
NFI duration, min/d	1334[a]	1327[b]	1318[c]	11.66	0.001
Time to bunk, min	67.85[a]	61.57[ab]	58.28[b]	7.89	0.039
Meal traits					
Meal criterion, min	9.45[a]	8.24[b]	8.12[b]	1.39	0.015
Meal frequency, events/d	11.80	12.10	12.33	1.43	0.381
Meal duration, min/d	179.8[a]	188.2[b]	206.5[c]	8.90	0.001
Meal length, min/event	16.49[a]	17.02[a]	18.83[b]	1.17	0.017
Meal size, kg/event	0.732[a]	0.800[b]	0.910[c]	0.048	0.001
Meal eating rate, g/min	46.82[a]	49.87[b]	51.94[c]	2.05	0.001
FB eating rate, g/min	94.09	93.77	96.40	8.31	0.556
BV per meal, events/meal	5.84[a]	6.42[b]	7.12[c]	0.42	0.001
Exit Velocity Traits					
Initial exit velocity, m/s	3.37	3.47	3.30	0.21	0.396
Final exit velocity, m/s	3.86	4.03	4.07	0.16	0.557

*BV = bunk visit; FB= feeding bout; NFI = non-feeding interval; Meal data was derived from meal criterion calculated from individual data and applying a Gaussian-Weibull bimodal model.

[a,b,c]Means within a row without a common superscript differ (P < 0.05).

and 22% fewer daily bunk visits among efficient steers and heifers consuming a traditional high concentrate feedlot diet, respectively. Low-RFI heifers spent 15.6% less time at the feed bunk, consumed 19.6% smaller meals at a 9.9% slower rate while having a 16.4% longer MC than high-RFI heifers, respectively. These results suggest there is an increase in feeding-associated activities for high-RFI animals, while low-RFI animals may spend more time sedentary, and therefore utilize less energy for activity (Kelly et al., 2010a). Feeding behavior findings in this study are in agreement with other studies (Durunna et al., 2011; Kelly et al., 2010a; Nkrumah et al., 2007b; Nkrumah et al., 2006); however, results from Bingham et al. (2009) suggest otherwise such that efficient cattle spent a greater amount of time consuming feed at the feed bunk compared to inefficient cattle.

Residual gain was found weakly correlated with MC (0.14) and eating rate (-0.16), suggesting that high-RG heifers have greater MC and slower eating rates. The effect of RG on feeding behavior traits is depicted on Table 2.15. Bunk visit duration and FB duration results for low-RG heifers (99.14 and 96.7 respectively) and high-RG (105.0 and 102.1 respectively) determined that high-RG heifers had 6.0% more BV durations and 5.6% more FB durations than low-RG heifers. High-RG heifers were found to consume feed at a 5.6% slower rate than low-RG heifers, which is similar to RFI. It was determined that RIG, unlike RFI, was negatively correlated with BV frequency and duration (-0.27 and -0.16 respectively), suggesting that low-RIG animals visited the feed bunks more often and occupied them for longer durations than high-RIG heifers. Residual intake and BW gain was negatively correlated with NFI frequency

Table 2.15. Effects of RG classification on feeding behavior and exit velocity traits in Santa Gertrudis heifers.

Trait*	Low RG	Medium RG	High RG	SE	*P*-value
No. of heifers	113	132	124	-	-
Bunk visit traits					
BV frequency, events/d	72.17	72.52	71.89	1.65	0.943
BV duration, min/d	99.14[a]	108.0[b]	105.0[ab]	9.14	0.032
FB frequency, events/min	64.87	65.03	63.91	1.49	0.742
FB duration, min/d	96.67[a]	105.4[b]	102.1[ab]	8.91	0.030
NFI frequency, events/d	70.17	70.60	69.98	1.70	0.934
NFI duration, min/d	1332[a]	1323[b]	1325[b]	11.26	0.039
Time to bunk, min	67.73[a]	59.65[b]	60.23[b]	7.88	0.044
Meal traits					
Meal criterion, min	7.93	8.68	8.94	1.35	0.074
Meal frequency, events/d	12.73	12.25	13.40	34.03	0.408
Meal duration, min/d	184.6[a]	196.0[b]	196.2[b]	9.15	0.022
Meal length, min/event	16.56	17.68	17.80	1.58	0.235
Meal size, kg/event	0.789	0.836	0.806	0.05	0.241
Meal eating rate, g/min	50.05[a]	48.75[ab]	47.28[b]	1.93	0.038
FB eating rate, g/min	96.37	93.14	94.49	8.30	0.436
BV per meal, events/meal	6.34	6.49	6.47	0.04	0.742
Exit velocity traits					
Initial exit velocity, m/s	3.39	3.42	3.37	0.20	0.920
Final exit velocity, m/s	4.24	3.95	3.78	0.16	0.084

*BV = bunk visit; FB = feeding bout; NFI = non-feeding interval; Meal data was derived from meal criterion calculated from individual data and applying a Gaussian-Weibull bimodal model.

[a,b,c]Means within a row without a common superscript differ ($P < 0.05$).

(-0.27) but positively correlated with NFI duration (0.13), such that heifers with low RIG had greater NFI frequencies consequently from greater BV frequencies and shorter NFI durations. Moreover, the positive correlation between RIG and MC (0.25) suggests that high-RIG heifers, like low RFI, took longer to initiate a subsequent meal compared to low-RIG heifers. Results from this study indicate that low-RIG heifers visited the feed bunks on average 12.6% more often and occupied feed bunks 7.7% longer than high-RIG heifers, which is similar to RFI results from this study (Table 2.16). In addition, low-RIG heifers consumed 11.6% smaller meals at an 8.1% slower eating rate than high-RIG heifers, which are similar to RFI results.

Associations of Temperament and RFI

To examine whether or not animal variation in aggressiveness of feeding behavior contributed to differences in performance and feed efficiency, time to bunk (TTB) was measured as the interval length between the initial feed truck delivery of feed to each pen in the morning and the initial FB event for each animal. It is believed that TTB may provide additional information to characterize inter-animal variation in temperament. The means ± SD of TTB for trials 1, 2, 3, and 4 were 44.1 ± 18.5, 68.1 ± 30.4, 60.5 ± 27.9, and 81.9 ± 34.3, respectively. Preliminary analysis found that TTB was negatively correlated with feed supply time (-0.27) and pen average empty bunk time (-0.06), such that TTB decreased as animals were fed later in the day or as length of empty bunk time increased. Consequently, data for days in which feed was delivered after 1100 (2, 5, 8, and 0 days) were deleted for trials 1, 2, 3, and 4, respectively.

Table 2.16. Effects of RIG classification on feeding behavior and exit velocity traits in Santa Gertrudis heifers.

Trait*	Low RIG	Medium RIG	High RIG	SE	*P*-value
No. of heifers	104	158	107	-	-
Bunk Visit traits					
BV frequency, events/d	77.18[a]	72.14[b]	67.48[c]	1.62	0.001
BV duration, min/d	105.7[a]	107.8[a]	97.61[b]	9.12	0.007
FB frequency, events/d	69.52[a]	64.52[b]	60.00[c]	1.71	0.001
FB duration, min/d	103.0[a]	105.1[a]	95.20[b]	1.75	0.007
NFI frequency, events/d	74.89[a]	70.26[b]	65.80[c]	12.74	0.001
NFI duration, min/d	1326[ab]	1322[a]	1332[b]	11.16	0.012
Time to bunk, min	60.44	63.36	62.80	7.29	0.682
Meal traits					
Meal criterion, min	7.82[a]	8.49[ab]	9.29[b]	1.38	0.012
Meal frequency, events/d	11.86	11.84	11.63	0.63	0.781
Meal duration, min/d	194.1	193.0	185.1	8.01	0.136
Meal length, min/event	17.52	17.55	16.97	1.18	0.722
Meal size, kg/event	0.861[a]	0.824[a]	0.762[b]	0.05	0.004
Meal eating rate, g/min	51.68[a]	49.70[a]	47.45[b]	2.08	0.001
FB eating rate, g/min	96.54	92.50	95.78	8.26	0.202
BV per meal, events/meal	6.74[a]	6.37[ab]	6.03[b]	0.437	0.004
Exit Velocity Traits					
Initial exit velocity, m/s	3.34	3.46	3.36	0.20	0.559
Final exit velocity, m/s	4.20	4.02	3.73	0.15	0.066

*BV = bunk visit; FB = feeding bout; NFI = non-feeding interval; Meal data was derived from meal criterion calculated from individual data and applying a Gaussian-Weibull bimodal model.

[a,b,c]Means within a row without a common superscript differ ($P < 0.05$).

Time to bunk was moderately correlated with (0.36) initial exit velocity (IEV), indicating that animals with more excitable temperaments took longer to initiate their first FB event following morning feed delivery than animals with more calm temperaments (Table 2.17). Time to bunk was negatively correlated with BV frequency and BV duration (-0.25 and -0.32 respectively), such that heifers that took longer to initiate their first FB event also had lower BV frequency and BV durations. Time to bunk was found to be moderately correlated in a negative manner with ADG and DMI (-0.35 and -0.40 respectively), but weakly correlated with RG and RFI (-0.12 and -0.19 respectively). The weak but significant correlations between TTB, RG, and RFI were primarily due to results from 1 of 4 trials. Therefore, the meta-analysis correlation results between TTB with RFI and RG are biologically questionable. Initial EV was also found negatively correlated with ADG and DMI (-0.18 and -0.27 respectively), such that heifers with greater EV had lower daily gains and consumed less feed. Initial EV appeared to have a greater impact on DMI than ADG, such that in all 4 trials concluded significant correlations between EV and DMI, whereas EV was significantly related to ADG in 2 of the 4 trials. Greater EV has typically been associated with cattle that are more easily excitable and less productive (Burdick et al., 2011; Burrow et al., 1988; Nkrumah et al., 2007b). Voisinet et al. (1997) concluded that cattle that became more agitated, as assessed by subjective chute scores, during handling had 14% low BW gains when compared to cattle with calm temperaments. In the current study, it was determined that TTB was negatively correlated ($P < 0.001$) with initial and final BW (-0.23 and -0.32 respectively) indicating that lighter BW heifers were more likely to

Table 2.17. Phenotypic correlations between feeding behavior, time to bunk, and exit velocity traits in Santa Gertrudis heifers.

Trait[a]	BVD	Eat Rate	MC	MF	MD	TTB	IEV
BV frequency	0.15[b]	-0.14[b]	-0.24[b]	0.32[b]	0.39[b]	-0.25[b]	-0.05
BV duration		-0.29[b]	0.41	-0.10	0.70[b]	-0.32[b]	-0.17[b]
Eating rate			-0.61[b]	0.32[b]	-0.65[b]	0.01	-0.02
Meal criterion				-0.64[b]	0.51[b]	-0.02	-0.08
Meal frequency					-0.28[b]	-0.20[b]	-0.03
Meal duration						-0.33[b]	-0.18[b]
Time to bunk							0.36[b]

[a]BV = Bunk visit; IEV = initial exit velocity
[b]Correlations are different from zero at $P < 0.05$.

approach the feed bunks later for their initial daily feeding. Similarly, IEV was negatively correlated with initial and final BW (-0.32 and -0.34 respectively), suggesting more excitable heifers had lower BW than calm heifers. Low-RFI heifers took 9.6 min longer ($P < 0.05$) to initiate their first FB event compared to heifers with high RFI. However, RFI classification had no effect on EV, which is in agreement with previous studies (Brown, 2005; Fox et al., 2004; Nkrumah et al., 2007b). These results suggest that slower growth rates of cattle with aggressive temperaments assessed by EV are a function of decreased DMI not decreased feed efficiency. However, the negative relationship between RFI and TTB suggests TTB may be a more sensitive form of measuring temperament compared to EV.

It is known that cattle are social animals that typically express their dominant hierarchies at the feed bunks (Grant and Albright, 1995). In addition, social dominance is associated with age, body size, and seniority in the herd, which can alter feeding behavior patterns and influence DMI (Barroso et al., 2000; Grant and Albright, 1995; Tolkamp et al., 2000). Therefore, results from this study suggest that TTB may help explain some of the associated differences of RFI and feeding behavior and therefore warrant further investigation.

RFI Base Model Variation

Variation in the RFI base model is represented on Table 2.18. The RFI base model (ADG and $BW^{0.75}$) R^2 was 0.475. The inclusion of BF thickness gain and feeding behavior traits (BV frequency and duration, MC, meal frequency and duration, and TTB)

Table 2.18. Variation in residual feed intake (RFI) base model (BM) R^2 including partial R^2 in feeding behavior traits for Santa Gertrudis heifers.

Trait*	Partial R^2	Model R^2	*P*-value
ADG	0.328	0.328	< 0.001
MBW	0.147	0.475	< 0.001
RFIp base model (BM; ADG and MBW)	0.475		
Bunk visit frequency	0.113	0.588	< 0.001
Bunk visit duration	0.054	0.642	< 0.001
Meal criterion	0.011	0.653	< 0.001
Meal duration	0.011	0.664	< 0.001
Meal frequency	0.014	0.678	< 0.001
Backfat gain	0.006	0.684	0.009
Time to bunk	0.004	0.688	0.045

*Meal data was derived from meal criterion calculated from individual data and applying a Gaussian-Weibull bimodal model.

increased the R^2 from 0.475 to 0.688. It was determined that BF thickness and feeding behavior activities account for 41% of the variation in DMI not explained by ADG, and MBW. Based on the partial R^2, BV frequency appeared to contribute the largest form of variation (0.113), suggesting that a portion of variation in RFI is related to energy expended to and from the feeding bunk. It has been suggested that variation in energy expenses related with physical activity such as lying vs. standing and locomotion may also contribute inter-animal variation in RFI (Carstens and Kerley, 2009; Lancaster et al., 2009a). Bunk visit duration appeared to contribute the second largest partial R^2 amount (0.054) suggesting that the amount of time spent at the feed bunk also contributes to the variation in RFI.

Results from this discussion are in agreement with previous studies (Durunna et al., 2011; Lancaster et al., 2009a), which determined that feeding behavior traits, such as meal frequency and duration, accounted for a substantial proportion of between-animal variation in DMI beyond that attributed to variances due to BW and production. Results presented in the current study were somewhat different than those reported by Lancaster et al. (2009a), such that when feeding behavior activities (head down duration, meal frequency, and duration) were incorporated in the carcass-adjusted model, feeding behavior explained an additional 35% of the variation in DMI. Durunna et al., (2011) determined that feeding behavior (head down duration and feeding duration) accounted for 17% of the variation in RFI not explained by ADG, mid-test $BW^{0.75}$ and ultrasound BF thickness.

The costs to measure feed intake and determine RFI remains expensive. Therefore, the relationships between RFI and feeding behavior have been investigated to determine their value as indicator traits that would be predictive of RFI. Feeding behavior activities in this discussion demonstrated that more efficient (low-RFI) animals attended the feed bunks less often and spent lesser amounts of time at the bunks, and consequently had shorter meal durations and smaller meal sizes compared to less efficient (high-RFI) animals. Results from this study suggest that selection based on RFI will favorably improve feed efficiency as RFI is inherently independent of BW and therefore will not indirectly increase mature BW. In addition, selecting animals with low RFI is more environmental favored as illustrated by results from Nkrumah et al. (2006) demonstrating that low-RFI animals had lesser methane and heat production, and greater retained energy compared to high-RFI animals. Therefore, favorable selection for RFI has the potential to mitigate greenhouse gas emissions and reduce the carbon footprint of beef cattle production systems.

CHAPTER III

SUMMARY AND CONCLUSIONS

Traditional methods of measuring feed efficiency, such as G:F, have limited value for use in breeding programs due to high genetic correlations with growth traits, such that favorable selection for G:F will lead to increases in mature BW of breeding females. Feed cost has been determined to be the largest variable associated with beef production. Therefore, in order to improve profitability beef production systems, the inputs (i.e., feed cost) must be reduced relative to the outputs. Favorable selection for RFI identifies animals with lower DMI while having minimal influences on productivity or mature size. Arthur et al. (2001c) determined that selection for RFI results in improvement in postweaning efficiency of feed utilization while minimally affecting growth. While other studies have reported negative phenotypic correlations between RFI and age at puberty (Shaffer et al. (2011), Basarab et al. (2007) found that adjusting RFI for variances in BF thickness and feeding behavior traits can minimize or reduce this association. Although there is currently considerable interest in the use of intake-measurement technologies to select for improve feed efficiency in seedstock cattle, the expense of measuring individual feed intake in beef cattle remains cost prohibitive for many producers. More research is warranted to discover genetic markers, and indicator traits for RFI that can be more cost effectively measured (e.g., feeding behavior traits).

Researchers have investigated the relationships of feeding behavior activities associated with RFI and other feed efficiency traits in attempts of identifying alternative cost-efficient forms of determining efficiency. Results from this study validate previous findings for low to moderate correlations found between feeding behavior traits (e.g., BV frequency and duration) and RFI, which suggests there is a relationship between intake and biological mechanisms that control satiety. Results from this study reveal that low-RFI animals expended lesser amounts of energy as they recorded fewer bunk visits and spent shorter time durations at the feed bunk. The examination of TTB revealed moderate negative correlations with DMI and ADG (-0.35 and -0.40 respectively) but weak correlations with RFI and RG (-0.19 and -0.12 respectively) such that heifers that were approaching the feed bunks sooner for the initial daily FB event, had greater DMI, ADG, RG, and RFI. Time to bunk was positively correlated with (0.36) EV, suggesting that animals with excitable temperaments had greater TTB. Exit velocity was found to be negatively correlated with ADG and DMI (-0.18 and -0.27 respectively), but not correlated with G:F, RFI, RG, and RIG. These results suggest that heifers with slower growth rates and aggressive temperaments, as determined by EV, are a function of decreased DMI but not necessarily decreased feed efficiency. Therefore, it may be suggested that TTB may be a more sensitive form of measuring temperament. In contrast to RFI, TTB was found to be lower in high-RG heifers and was not found to be significant in the classification of RIG. Further investigation of TTB is needed in identifying its relationship with temperament and feed efficiency.

High-RG heifers were found to have a 38.7% higher ADG, 37.1% higher G:F, and no differences found between DMI compared to low-RG heifers such that selection based on improved RG would improve gain while not affecting DMI. It was determined that animals favorable in RIG had lower DMI and greater ADG. Phenotypic correlations in this study demonstrate that selection based on RIG will have minimal effects on BW (-0.09; $P > 0.05$), improve ADG (0.78; $P < 0.05$), and reduce DMI (-0.42; $P < 0.05$). High-RIG heifers were found to have a 22.8% higher ADG consuming 12.6% less feed, which subsequently resulted in a 40.6% higher G:F than low-RIG heifers. High-RIG heifers were also found to initiate fewer trips and spend less time at the bunks while consuming smaller meal sizes. Results from this study provide additional evidence that validate previous studies suggesting that selection based on RFI, RG, and/or RIG can improve profitability and maximize feed efficiency in the beef industry.

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