RESIDUAL FEED INTAKE IN BEEF CATTLE;
IN RELATION TO BREED, SELECTION, AND BEHAVIOR

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

with a

Major in Animal Physiology

in the

College of Graduate Studies

University of Idaho

by

Marcus McGee

June 2014

Major Professor: Rodney A. Hill, PhD.

AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Marcus McGee, submitted for the degree of Doctorate of Philosophy with a Major in Animal Physiology and titled “Residual Feed Intake in Beef Cattle; in Relation to Breed, Selection, and, Behavior,” has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduated Studies for approval.

Major Professor: ________________________________ Date: ____________
Rodney A. Hill, Ph.D.

Committee
Members: ________________________________ Date: ____________
Gordon K. Murdoch, Ph.D.

________________________________ Date: ____________
John B. Hall, Ph.D.

________________________________ Date: ____________
Phillip Watson, Ph.D.

Departmental
Administrator: ________________________________ Date: ____________
Mark A. McGuire, Ph.D.

Discipline’s
College Dean: ________________________________ Date: ____________
Larry D. Makus, Ph.D.

Final Approval and Acceptance

Dean of the College
Of Graduate Students: ________________________________ Date: ____________
Jie Chen, Ph.D.

ABSTRACT

Feed efficiency is a necessary factor in beef production systems due to rising feed ingredient costs, population growth, and beef supply demands. With this known, it is important for researchers to delve into mechanisms involved in efficiency to provide producers with a knowledge base for future selection and breeding programs. Though the use of residual feed intake (RFI) is fairly well know, traditional traits are often considered more desirable due to costs associated with testing. However, previous research has provided evidence of benefits using a less biased measurement (RFI) in comparison with its counterparts (e.g. ADG, FCR, F:G etc…) Though RFI does provide indication of efficiency status, there are underlying mechanisms that also play a role in these measurements that are not completely understood. One attribute of efficiency often overlooked is feeding behavior, in which this body of work attempts to interpret via relationships with RFI. Previous research has provided has examined relationships between these two parameters, however further studies are necessary to gain a more solid foundation. Research within this dissertation will add to this knowledge base using two breeds of cattle examined for behavior traits (bunk visit frequency, bunk visit duration, feed bout frequency, feed bout duration, meal frequency, meal duration, and average meal intake) during the course of RFI evaluation. Niche breeds of beef cattle (e.g. Japanese Black Cattle) are often excluded from feed efficiency examinations, due to focuses of output, carcass quality traits, and increased specialty market value. However, the recent rise of feed ingredient costs are universal, and producers of niche breeds may benefit as well. Within this body of work, 3 cohorts of Wagyu cattle were evaluated for feeding behavior parameters with some insight towards relationships with efficiency. Red Angus cattle were also evaluated over both growing and finishing phase RFI to clarify feeding behaviors' role in efficiency. Results from these studies provide researchers with additional tools for elucidating these relationships as well as identifying specific feeding behaviors that contribute to efficiency status in beef cattle.

ACKNOWLEDGEMENTS

During the course of my Ph.D. career, I have encountered several people who have become mentors in my life. These people are as deserving of this degree as I am. Without their help, none of this would have been possible.

First, I would like to thank my mother Mildred McGee for supporting me throughout this journey. You have always been there for me through the hills and valleys of my life. Without your encouragement and blessings, I would have never made it this far. Even at my lowest, you have always pointed towards the stars. I love you and hope that you are proud of your son.

Thanks are due to AgriBeef Genetics, as they provided the incentive to do this research. I greatly appreciate the assistance of Wade Small and Garrett Tschida in their efforts to make me successful in my career.

I would like to acknowledge my committee members, Drs. Gordon Murdoch, John Hall, and Phillip Watson. You all have been there for me at each step of the long road travelled. I whole-heartedly appreciate your assist and hope to make you all proud in the near future. I am forever indebted to you all.

Special thanks are due to the Murdoch family including Drs. Gordon and Brenda Murdoch, Xavier, and Breanna. You invited me into your home and hearts. I value our friendship and will forever be in close contact. You are the family that I hope to have one day. Thank you for your inspiration.

In addition, I would like to thank the staff at the NMCREEC ranch including Chad Stevenson, Heber Stokes, Jeremy Drake, Allen Petrick, Sabas Ayala, Wayne Smith, Judy Skinner, and others I met along the way. I arrived there during the first semester of my program, and you all made it memorable. Thank you for the help, guidance, and support provided. Without you my research program would not have been possible. Also, thanks are due to Richard Ambrosek and

Heath Wells. You guys became my brothers over that summer, and created a friendship that will forever be appreciated.

The AVS department has become my second home. I appreciate the assistance of faculty and staff members that made this all possible. You are a great group of people. I will miss you all and hope to come back to see the department even more fruitful.

I would also like to thank all of my fellow graduate students including Cassie Welch, Kara Thornton, Suresh Acharya, Kalyan Chapalamadugu, Katherine Hunt, Brittany Casperson and others. We became a family over the last few years. I have thoroughly enjoyed my time here at U of I, and you made it possible. Though far away from home, I have always felt as though family was right around the corner. I will forever cherish our time together.

Finally, I would like to thank my major professor Dr. Rodney Hill. You provided me with the opportunity to become proficient in my area and consistently pushed me towards success. I applaud you for your efforts and hope to have your compassion towards research and mentorship in the future.

DEDICATION

I wholeheartedly dedicate this dissertation to several people who have provided me with drive and perseverance to reach my goals.

Firstly, I would like to dedicate this body of work to my mother Mildred McGee, who has always provided positivity throughout my life, as well as my academic career. She is always there to open my eyes and view the world from different perspectives. Her calming words always provide me with the strength to move forward through troubling times.

I would also like to dedicate this dissertation to my 3 brothers, Theaortres McGee Jr., Mose McGee, and Robert Von McGee. Without them, I would not be who I am today. Through comfort, challenges, and even arguments, you have molded me into a more positive and courageous person who is unafraid to push boundaries if need be. I thank you all.

I dedicate this research to Cassie Welch. We have been by each other's sides throughout this entire process; lifting each other from the pitfalls and enjoying the view from the peaks. This is another journey that has fortified our relationship, and I know that we will embark upon many more during our lifetime together.

Lastly, I would like to dedicate this body of work to my late father, Theaortres McGee Sr. Though our time together was brief, the impact you've made on my life will last forever. I know that you are watching me from above and hope that I make you proud.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

Introduction and Literature Review

Introduction

Due to substantial increases in the cost of feed and cattle production (since 2006), feed efficiency has become an important performance evaluator within many beef production systems. In previous years, profit has been driven by the US cattle inventory where supply and demand influenced cattle prices, with producers being more profitable when cattle inventory was low and less profitable when inventory was high. This was considered a stable occurrence until 2008, when financial losses were attributed more so to elevated input costs than beef demand (Ahola and Hill, 2012). However, the increased price of corn and hay (nearing $5.00/ bushel and $140/ ton, respectively) has encouraged producers to seek new outlets for improved profitability (Ahola and Hill, 2012; USDA, 2014). Residual feed intake (RFI) was first introduced by Koch et al. (1963) as a means to categorize cattle performance using less biased measurements that were independent of body size and rate of gain. Residual feed intake is defined as the difference between actual and predicted feed intake required for an observed rate of gain (Koch et al., 1963) and allows for the identification of feed efficient cattle that produce similar gains (as their inefficient contemporaries) while consuming less feed. It is well documented within the literature that feed cost is one of the largest, variable (or non-fixed) expenses that occur in livestock production (Archer et al., 1999; Miller et al., 2001; Basarab et al., 2007; Lancaster et al., 2008). Therefore, profit margins can be increased by minimizing input costs associated with production and maximizing (or at least maintaining) desired marketable products or outputs. Before feed costs became significantly elevated and market trends became much more volatile, it was estimated that a 10% improvement in feed efficiency would increase profits by 44% (Fox, 2001). In contrast, Fox et al. (2001) noted that a 10% improvement in ADG would only increase profits by 20%. Therefore, improving feed efficiency provides producers an opportunity to minimize input costs while enhancing production efficiency. It is important to note increasing ADG is more easily attained by adjusting nutrition and/ or management practices. In turn, profit generating theories based on ADG fail to account for the volatility of feed costs, therein providing an unstable method to predict revenue. Similarly, this is a "short term" enhancement that does not benefit future generations of cattle. However, improving efficiency is a substantial process in which genetic progression enhances efficiency. This leads to an overall improvement of herd characteristics in long term production efficiency.

Beef cattle occupy a special niche within the animal kingdom by utilizing poor quality feeds towards growth and performance. However, they are less efficient at converting feed to protein than other market animals; therefore more expensive to produce. This in turn supports the need to identify and utilize beef cattle that are feed efficient. Through the use of genetic selection programs, the incorporation of feed efficient animals may offer producers the potential of generating highly productive animals and creating a sustainable beef market, while lowering input costs (Crews, 2005). Genetic improvements (i.e. growth, carcass quality, reproduction) have been selected for within common commercial beef breeds (i.e. Angus, Hereford, Charolais, etc.) for several years. However, niche market breeds (i.e. Hanwoo, Japanese Black, etc.) have not faced selection pressures to the same extent as their large-market counterparts. Additionally, limited research has been performed examining feed efficiency of Japanese Black cattle (Hoque et al., 2006; Okanishi et al., 2008; Inoue et al., 2010). However, there are potential impacts for the use of feed efficiency in niche market breeds to generate maximal profit for producers, as well as decreasing end-product costs for consumers (Hoque et al., 2006; Hoque et al., 2007). The costs associated with measuring feed efficiency via RFI are expensive; therefore, measuring alternative or assisting indicators may provide an added value to cattle performance evaluation that is more economically attainable (Kahi and Hirooka, 2007).

Health status, well-being, and reproductive status can impede or enhance feeding behavior and thus cattle performance. Due to selection pressures, large-market cattle (e.g. Angus) have been bred in an effort to increase intake, producing greater gains that result in larger product quantities over a defined period of time (Bonsma et al., 1940). It is known that an increased rate of consumption and frequency of meals alters the feeding behavior of cattle (Nkrumah et al., 2007b). However, very few studies have investigated feeding behavior and its impact on production performance of beef cattle (Weary et al., 2009), especially in the context of feed efficiency. With this known, it is important to examine factors that influence intake parameters, not only as a means to gain greater insight into feed efficiency, but also to improve overall efficiency status. In past endeavors, the observation and recording of feeding behavior of individual animals was often compromised by excessive handling and feeding methodology (i.e., open bunk/ feedlot bunk systems). However, new technologies (e.g. radio frequency identification systems) are more readily accessible for research purposes and can improve methods of investigation by measuring individual feed intakes and evaluating feeding behavior in a simulated feedlot-bunk system (e.g. GrowSafe Systems) with limited human interaction.

The relationship of feed efficiency and feeding behavior has been observed with varying conclusions (Schwartzkopf-Genswein, 2003; Golden et al., 2008; Kelly et al., 2010). Herd et al. (2004) stated feeding patterns only account for approximately 2% of the variation in RFI (Figure 1.1). However, within the same review, the researchers also noted that stress, along with protein turnover and tissue metabolism, account for approximately 37% of the variation in RFI. Knowing this, it can be assumed that stress plays an important role in this variation, and it has been noted that stress can often influence feeding patterns (Lindstrom et al., 2001; Montanholi et al., 2010; Gomes et al., 2013). For example, the introduction of animals into a new environment creates a stressful situation that can often depress intake patterns (Samuels and Hen, 2011). Additionally, co-mingling of new animals with others often induces stress and shifts feeding patterns until a new social hierarchy is established (Grant and Albright, 2001). Previous methods of observing feeding behavior, such as separating animals from the herd (i.e. single-animal pen intake evaluations), have also resulted in the skewing of animal feeding patterns and a reduction in feed intake. With new monitoring systems (e.g., GrowSafe Systems, Inc.), animals are able to maintain herd companionship, while being individually assessed for intake evaluations. To this end, feeding patterns are not static and can change due to several physiological and psychological instances, potentially impeding the goal of linear gain in growing animals. Therefore, it is possible that stressors can influence feeding patterns and produce greater variation in feed efficiency than the percentage (2%) estimated by Herd et al. (2004), further necessitating the need for research investigating the relationship between feed efficiency and feeding behavior.

Japanese Black (Wagyu) Cattle

History

During the time period of 1635 to1854, Wagyu cattle were separated by geographical areas in Japan, known as prefectures. Consequently, populations of the breed were isolated, which prevented the introduction of new genetics and resulted in an increase of inbreeding (Namikawa, 1992). Due to these circumstances, most Wagyu cattle can be classified as descendants of the five oldest strains or populations of cattle (Table 1.1), which were originally founded on maternal lines (Namikawa, 1992). Until about 1960, Wagyu cattle were primarily used as draft animals due to religious restraints. Buddhism was a prominent religion in the area and therefore limited the consumption of meat. For this reason, Wagyu were often crossed with a continental breed of cattle in order to produce a heartier animal that had a greater ability to perform labor. Since the consumption of meat products has only been practiced in Japan for approximately 140 years and has recently become more widespread (within the last 50 years), beef programs aimed at the improvement of end-product quality in Japanese beef cattle were not initiated until around 1950, but have become more utilized in recent years (Obata, 1996).

Genetic Lines

As previously mentioned, each prefecture or geographical area resulted in a strain or population of Wagyu cattle. The Shimane strain of Wagyu are medium-framed, with an average growth rate, good quality meat, and are well suited for crossbreeding with Angus cattle (Table 1.1).

The Tajima strain of Wagyu, which originated from the Hyogo prefecture, was used for intense farm-labor purposes, thus developing large forequarters and subsequently smaller hindquarters. Generally smaller-framed, the Tajima Wagyu exhibit excellent meat quality, with a large ribeye and superior marbling and are thought to be ideal for the production of F1 cattle for slaughter. The Tottori strain of Wagyu were used as pack animals in the grain industry, being larger-framed with straight, strong backlines and fair growth rates, but variable meat quality (Namikawa, 1992).

In 1976, the United States began to import Wagyu cattle from three prefectures; Hyogo, Okayama, and Tottori. Later, in 1993 and 1994, several more Wagyu cattle, from different prefectures, were imported to America and Australia, supplying greater genetic diversity in the newly formed populations (Namikawa, 1992). Wagyu cattle soon sparked the attention of many producers due to their high propensity for increased marbling in crossbred cattle (Radunz et al., 2009). This began an influx of Wagyu-influenced herds in both countries, as well as creating an "American" purebred herd and Wagyu-Angus crosses.

Management Practices

Various breeding and feeding techniques were employed in order to ensure meat quality of the native cattle within each of the Japan prefectures. Since there was a lack of pasture land available for grazing, a concentrate diet was used to produce proper marbling during the fattening period (Obata, 1996). Japanese fattening ideology differs from many other countries, in that steers are fattened for an average of 20.2 months post-weaning and finished at approximately 696 kg. This unconventional method is not rational for survival in high volume markets, yet is seen as profitable due to a strong demand for top quality beef (Obata, 1996). Additionally, Wagyu farmers followed traditional methods of feeding, care, and general production. Management practices included scheduled massages using oils or sake, feeding beer and other foods designated to stimulate the appetite of animals, and limited exercise which was thought to prevent muscle toughness (Longworth, 1983). Using these intensive management practices, producers could only manage a relatively small herd size, thus limiting production volume.

American Wagyu cattle within feedlots are managed similarly to other commercial beef breeds, but with some exceptions. Due to slow maturation, Wagyu are fed using several high-energy, “step-up diets” during the finishing phase, which are similar to those used in Japan, as well as being finished over a longer period of time to achieve proper marbling scores (Mir et al., 1999). Continental and/ or European breeds of cattle with Wagyu influence have the propensity to exhibit highly marbled carcasses (Lunt et al., 1993), and producers will often choose to add Wagyu influence to their herd instead of raising full blood or purebred animals (Mir et al., 1999). Research by Mir et. al., (1999) suggests that 50% Wagyu-Angus cattle exhibit extensive marbling traits with a decreased finishing time, when compared to full blood and purebred Wagyu cattle. Additionally, these “percentage” cattle are often finished around 18 mo of age and with a greater degree of marbling when compared to other notable continental beef breeds, but with smaller carcass size (Mir et al., 1999). If American Wagyu producers would like to continue to be competitive in the international market, they must develop economical strategies to incorporate into production systems, which would support the production of consistent, high quality, and safe products (Obata, 1996). Furthermore, proper genetic improvement via breeding methods should be examined for use in Japanese cattle. Research by Sasaki et al., (2006) show benefits using BLUP (Best Linear Unbiased Prediction) towards predictions of expected progeny values of carcass traits in Japanese Black and Brown cattle. To this end, there is a need to improve genetics of Wagyu cattle in efforts to generate more productivity within commercial markets.

Carcass and Palatability

Wagyu-influenced cattle have exceptional marbling scores along with many superior carcass traits, when compared to continental breeds of beef cattle. Contrasting these benefits, Wagyu-influenced cattle have also been noted as having decreased feedlot performance and red meat yield (Mir et al., 1999). However, since marbling score is considered to be the most important aspect of carcass classification using the Japanese Meat Grading Association system, the carcasses of Wagyu cattle retail at a premium value. Highly marbled beef has a sweet, fatty aroma that is preferred in

Japan (Ueda et al., 2007), and Wagyu carcasses are generally sought after by the Japanese population due to their increased content of “soft” fat. This type of fat occurs when there is a greater ratio of mono-unsaturated fatty acids (MUFAs) to saturated fatty acids. When comparing Wagyu cattle with other continental breeds, carcass composition of Wagyu cattle display significantly higher ratios of MUFAs (Ueda et al., 2007), which results in an increased marbling score and a grade considered to be above prime. Because of this, Wagyu carcasses are classically graded using the Japan Meat Grading Association system, which produces a more accurately scored carcass when compared to that of the USDA grading system (Radunz et al., 2009). In an ideal scenario, producing cattle with high yielding carcasses and extreme marbling in a small period of time would be desirable; however, this is nearly impossible due to maturation of beef cattle and the physiological processes associated with the deposition of intramuscular and subcutaneous fat. Carcass grades (i.e., quality and yield) are partially based on the amount of fat deposition (Geary et al., 2003), which is an expensive attribute in terms of required energy input. Thus, it is possible that pursuing marbling may be less profitable, due to increased input (feed) costs associated with fat deposition in Wagyu cattle.

Studies have been conducted to examine methods of finishing Wagyu with fewer days on feed, while promoting superior meat quality. Radunz et al.(2009) performed a study to evaluate the effects of early weaning management with Angus- vs. Wagyu- sired cattle on feedlot performance, carcass yield, and quality grade, using the USDA and Japan Meat Grading Association systems. Conclusions from the study revealed Wagyu- sired cattle produce higher IMF, as well as increased LMA, when compared to Angus- sired cattle. Early weaning management of Wagyu- sired calves may increase carcass numbers within USDA Choice and Prime grades; however, the additional cost of days on feed (77 d) when compared to Angus- sired calves may limit producer profit.

Furthermore, aiming to achieve greater product quality via nutritional value and flavor, Calles et al., (2000) examined the effects of various Wagyu sires on carcass quality traits, as well as palatability attributes of cooked ribeye steaks. The Wagyu sires used in this study include “Old” and “New”, which are defined by the chronological order in which they were imported into North

America. “Old” sires were imported into the United States and Canada from 1974 to 1976, while “New” sires were imported in 1993. Results from carcass data concluded that increased marbling score, ribeye area, younger maturity scores, brighter/ firmer texture of lean, and more desirable fat luster were produced in “New” Wagyu-sired calves. “New” and “Old” sired progeny did not differ in growth rate. However, overall results reveal “New” Wagyu lines superior to “Old” sire genetics. Additionally, sensory taste panel results revealed “New” sire progeny steaks to be more palatable when compared to those of “Old” sire progeny. Examination of this study illustrates genetic superiority of “New” Wagyu bloodlines in producing progeny with decreased external fat and shear force, while increasing ribeye area and marbling in comparison to “Old” Wagyu lines. To this end, it can be noted that Japanese producers have made great genetic improvement over the last 20 years in the breed of Wagyu cattle.

Importance of Feed Efficiency within the Beef Industry

Within any production system, it is important to maximize quality and quantity without sacrificing profitability. To this end, one must efficiently manage large marginal costs in order to generate profit. Beef cattle improvement is often based on output (performance) traits and often fails to account for intake parameters (Lancaster et al., 2009). A fact sheet generated by Massey (1993) detailed producer’s concentration on performance traits, in which results show a lack in analogous profit surge over time in association with the growth of intense selection for performance traits. Additionally, the beef cattle market has been unpredictable with volatility of both input and output components over the past several years. Growth of the biofuel industry and increased ethanol production has resulted in competition for grains (i.e., corn) and land resources that have traditionally been utilized for production of crops for both human consumption and livestock production (Westcott, 2007). Furthermore, natural causes such as weather and disease may influence crop yields, contributing to the variability of agriculture. With limited land to produce protein sources for human consumption, as well as grains being used for animal feed, human food, and ethanol production, it is expected that beef operations will foresee a large increase in production costs (Ahola and Hill, 2012). This generates great concern for the future, as the world population is expected to exceed 8.3 billion over the next 15 years (FAO, 2002).

Rising feed costs have proved to be fiscal challenges for large and small producers alike. Estimations as high as 75% of total costs have been associated with beef cattle feeding (NRC, 2000). Poultry and swine operations have acknowledged these issues and have made significant progress towards improvement in feed efficiency and production over many years (Luiting, 1991). Due to the inherently inefficient conversion of feed to product by ruminants, only 5% of total life cycle energy is converted to protein, while monogastric animals use between 14 - 22% (Ritchie, 2000). Selection for feed efficient cattle is noted as an option to reduce these costs, improving producer revenue to further their operations and increasing market stability. These economic impacts are beneficial to producers, and efforts will produce a “trickle down” effect to consumers. This will give rise to reduced end-product cost with the possibility of increased product availability. Previously, research has only focused on F:G and feed intake measures as selection criterion for efficient cattle (Herd and Bishop, 2000; Arthur et al., 2001). However, the use of F:G as a selection parameter has been found to increase mature cow size in breeding herds (Crews, 2005; Moore et al., 2009). Independent of growth traits, using the feed efficiency measurement of RFI allows producers to select for feed efficient animals without increasing costs associated with maintaining the breeding herd (Herd et al., 2003a). Gibb and McAllister (1999) estimated that a 5% increase in feed efficiency could possibly yield a four-fold higher result than a comparable improvement in ADG traits. Estimations such as these present scientific evidence for the need to improve production practices and implement profit management strategies associated with beef cattle production.

Furthermore, previous research states that there is individual animal variation associated with feed intake beyond maintenance requirements (Herd et al., 2003a, b), and the use of RFI is perceived as a method in which these variances can be accounted for without sacrificing other aspects of production (Tedeschi et al., 2006). Herd et al. (2003a) report RFI as being moderately heritable, with h^2 ranging from 0.16 to 0.43, which provides an opportunity to select for feed efficiency without significantly altering other performance attributes. Residual feed intake has been evaluated using several European breeds (Basarab et al., 2003; Nkrumah et al., 2007a; Lancaster et al., 2009; Welch et al., 2012). However, literature lacks RFI studies exclusively performed on Wagyu cattle (Hoque and Oikawa, 2004). Because Wagyu are such a slow maturing breed, reducing the amount feed used throughout their finishing period, while achieving high quality carcass traits is of immense value (Okanishi et al., 2008).

Biological Variations in Feed Efficiency of Beef Cattle

It is important to gain a complete understanding of underlying mechanisms driving inter-animal variation associated with feed efficiency of cattle. Animals classified as less efficient consume as much as 20% more energy than efficient counterparts with similar growth and composition (Nkrumah et al.., 2004; Brown, 2005). Thus, there are underlying physiological mechanisms driving changes in the efficiency levels of animals. Richardson and Herd (2004) explained some plausible causes of this variation, such as digestion, heat increment of feeding, and body composition. Within their analysis (Figure 1.1), approximately 27% of underlying drivers of variation in RFI were not detailed (i.e., labeled as other), with the remainder characterized as variation in body composition (10%), feeding patterns (2%), protein turnover ,tissue metabolism, and stress (37%), heat increment of fermentation (9%), digestibility (10%), and activity (10%). Though these are simply estimates, ratios between parameters may provide some insight into possible physiological variation. As researchers, it is important to note overlap and discrepancies within these proposed categories.

Correlations between intake and feed efficiency have been noted in the literature. To this end, there is no doubt that intake is an integral component that influences efficiency. Ferrell and Jenkins (1998) found that an inefficiency in the conversion of nutrients to mass can influence intake. Heat increment of feeding plays a role in energy expenditure from all animals. Heat increment of feeding can increase body temperatures significantly above tolerable levels for animals, thereby reducing intake (Blaxter, 1989). Heat loss has also been examined as an indicator of efficiency, with high RFI (inefficient) animals having 10% greater heat loss than efficient contemporaries (Basarab et al., 2003). However, increased feed intake of inefficient animals may generate greater heat loss. Feeding behavior may provide elucidation by observing both feed consumption as well as activity associated with feeding. Research has shown feed intake accounts for as much as a third of total heat production in swine (Robinson and Oddy, 2004). This can be seen in cattle as well due to heat increments of feeding during rumination and the associated energy costs of grazing (activity in pasture based management systems). Feedlot animals are managed in which activity levels are lessened due to confinement and centrally located feed. In this context, literature has provided insight that RFI-efficient animals were less active than their inefficient counterparts (Richardson et al., 1998; Robinson and Oddy, 1999, 2004). The degree of activity difference between RFI-efficient and RFI-inefficient animals is not well defined, and more research is needed to accurately describe the role of animal activity in driving differences in RFI.

It is agreed that as much as 25% of energy expenditure is from proton leak and turnover (Rolfe and Brown, 1997; Richardson and Herd, 2004; Lancaster et al., 2008). A large amount (> 90%) of ATP is produced via oxidative phosphorylation that is associated with mitochondrial electron transport (Bottje and Carstens, 2012). The backflow of protons during transport dissipates motive force and causes a short circuit of ATP synthesis. In these situations, up to 50% of oxygen consumption has been noted in muscle (Rolfe and Brown, 1997). Uncoupling proteins (UCPs) have been shown to be culprits, creating a dissipation of oxidation energy as heat (Erlanson-Albertsson, 2003; Rousset et al., 2004). Present in skeletal muscle, UCP3 targeted disruption provided no effect on whole body energy metabolism, but gave rise to more coupled transport (Erlanson-Albertsson, 2003). To this end, there is a strong possibility that inter-animal variation in proton motive force may play a role in driving phenotypic differences among efficiency groups.

Ion pumps maintain cellular homeostasis, ion transport and membrane potential (Milligan and McBride, 1985). These processes have high energy utilization, with reports of 50% or more energy expenditure in animal tissues (Kelly and McBride, 1990). The Na+, K+-ATPase pump can be influenced by the concentration of extracellular amino acids available for transport across the plasma membrane and their eventual use in cellular metabolism. This suggests Na+, K+-ATPase function can be directly related to protein synthesis. Levels of feed intake have also been noted as influencing Na+, K+- transport (Flier et al., 1981; McBride and Milligan, 1985). Results by Gill et al. (1989) show the gastrointestinal tract and liver in growing lambs are high sources of Na+, K+- transport. Increased Na+, K+- activity indicates increased energy expenditure, therein decreasing efficiency. This suggests variation in ion pumping may play a role in driving physiological variation in animal efficiency.

Skeletal Muscle and Adipose Tissue

Skeletal muscle accounts for as much as 30% of total oxygen consumption in the resting state (Zurlo et al., 1990), and a large portion of energy expenditure is used to maintain muscle mass at normal activity levels. With heavier muscled animals, this quotient is quite large and can account for a considerable amount of increased intake. Some physiological processes that may account for variation in energy utilization are ion pumping, thyroid hormones, lipid metabolism enzymes, protein turnover, sympathetic activity, and proton leak (Johnson et al., 2003). “Proton leak” is defined as inefficiency associated with the promotive force of ATP production, with protons entering the mitochondrial matrix and generating heat instead of energy substrate. This phenomenon is responsible for approximately 26% of variation in basal energy expenditure within animals (Harper et al 2002). Therein, proton leak is a contributor driving overall efficiency. However, research has determined that RFI- divergent lines of animals have differing capacities for oxygen consumption. Bottje et al. (2002) examined mitochondria from breast and leg muscles of divergently selected broilers based on G:F phenotype. Results indicate that efficient animals had greater respiratory chain coupling than their counterparts. However, further studies from the isolated mitochondria indicate that both phenotypes have a similar ability to carry out oxidative phosphorylation (Bottje et al., 2002). Similar studies were performed in steers confirming that respiratory chain coupling is greater in efficient animals when compared to their divergent pen-mates (Lancaster et al., 2008). These results provide insight into underlying mechanism at the cellular level between efficient and inefficient animals that deserve further elucidation.

Body composition may contribute to variation in RFI due to the energetic costs of lean and fat deposition (1.24 vs. 9.39 kcal/g, respectively) (Carstens and Kerley, 2009). Feedlot cattle are often fed high-grain finishing diets that enhance the propensity to deposit intramuscular fat (i.e., marbling), which improves quality grade scores at harvest. However, there is a substantial cost associated with providing these diets. Improving the lean to fat deposition ratio can lower feed costs for producers and coincides with the reduction and control of subcutaneous fat deposition (Nkrumah et al., 2004). Variation in depots, adipocyte size, and animal physiology all indicate that the energy dynamics of metabolism differ as animals fluctuate in adiposity across depots. Thus, variation in fat depots is a potential difference at the tissue level contributing to variation in maintenance requirements and efficiency.

Accretion of fat occurs when lipogenesis surpasses lipolysis (Figure 1.2). This process is mitigated by hormonal control with insulin having a key role in short term regulation. Insulin inhibits lipolysis, stimulates fatty acid synthesis and glucose utilization in adipocytes among other physiological activities (Vernon et al., 1981). Long term regulation is influenced by growth hormone depressing lipogenesis, and in turn, stimulating lipolysis (Vernon et al., 2001). These activators are not solely responsible for fat accretion, as a cascade of signals may modulate lipolysis, including thyroid hormones, glucocorticoids, progesterone and testosterone. Fat deposition in cattle occurs overall several phases. Early research by Hammond et al. (1955) reveals that depots are generated in the following order: perirenal, intermuscular, subcutaneous, and intramuscular. Though listed as phases, there is a degree of overlap during adipocyte growth with different rates and mechanisms (hypertrophy and hyperplasia), and the asynchronous development of fat depots is not well characterized. Research by Adams et al. (1992) found isolated preadipocytes from various depots of sheep at different ages grew at a similar rates. Results from this study suggest that there are no intrinsic changes in these cells accounting for the differential developmental properties in live animals. However, Van der Walt (1984) found that various adipose tissue depots in ruminants are not uniformly, metabolically active, with 2-7 fold higher activity in backfat than mesenteric fat. These metabolic activities may be influenced by age and nutritional plane as well as other physiological attributes. Furthermore, intramuscular fat is highly valued by producers and the beef industry, as it provides an excellent indicator of meat palatability. Thus, high intramuscular fat levels indicate a higher quality product. As noted above, there is a considerable energetic price associated with producing a high quality product with high intramuscular fat levels. Intramuscular fat is late developing relative to other depots (Van der Walt, 1984). As mentioned previously, fat is deposited at a greater rate than lean tissue in mature animals, which leads to greater intramuscular fat deposition in finishing phase animals. Marbling increases over time, along with age, declining activity levels, and increased consumption (Scanes, 2003). Researchers Robinson and Oddy (2004) noted a positive genetic correlation between RFI and rib (0.48) and rump fat (0.72) in finishing steers. Similarly, Schenekel et al. (2004) observed a weak, positive correlation between RFI and carcass fat when evaluating growing bulls. However, adipocyte accretion is constant, with fat depots growing in similar proportions as animals fatten (Johnson et al., 1972; Pugh et al., 2005). Though intramuscular fat depots are enhanced during maturity, other depots of less desirable fat are increased as well. Previous research has suggested a period of nominal intramuscular fat change in young animals with a linear increase from 200- 400 kg carcass weight in crossbreed cattle (Aoki et al., 1999; Pethick, 2005; Pugh et al., 2005). Changes in adiposity are therefore relative to the initial cell number and lipogenic proteins. With this known, there is the possibility of identifying early markers for fat deposition as adipocyte development is somewhat predetermined during early development.

Mobilization of body tissue occurs when an animal’s nutritional intake does not meet the requirement for maintenance capacity (Moe et al., 1971). When in this negative energy balance, animals rely on body fat reserves as an energy source. The release of fatty acids from stored lipid provides a source of energy for oxidation (Trayhurn and Beattie, 2001).

Each depot of adipose tissue differs in its metabolic regulation. Trayhurn and Beattie (2001) reported in human preadipocytes isolated from different fat depots that the omental depot has a higher lipid flux than the subcutaneous depot. The rate of triglyceride mobilization is also greater within visceral as opposed to omental fat depots. Furthermore, omental preadipocytes have a higher glucocorticoid receptor (GR) density, LPL activity, adenylyl cyclase activity, and apoptotic properties than subcutaneous adipose tissue.

Subcutaneous adipocytes have been shown to have higher levels of GLUT 4, glycogen synthase, and insulin receptors, as well as a higher rate of differentiation when compared to omental adipocytes (Niesler et al., 2001). These authors also reported that omental cells expressed higher levels of cellular inhibitor of apoptosis protein (cIAP), an antiapoptotic protein, than subcutaneous adipocytes. This suggests that cells from different depots show inherent differences that account for the observed physiological variation between adipocytes isolated from different locations (Niesler et al., 2001). Intramuscular fat deposition is regulated by different factors than those regulating deposition in other tissue depots. Thus, there are metabolic differences between intramuscular and subcutaneous fat depots (Miller et al., 1991). Both this study and others (May et al., 1994; Eguinoa et al., 2003) reported that in cattle, intramuscular adipocytes are smaller than subcutaneous fat cells. Additionally, activities of the glycolytic enzymes hexokinase and phosphofructokinase were higher in intramuscular depots. Subcutaneous fat depots had higher levels of the lipogenic enzymes: NADP-malate dehydrogenase, 6-phosphogluconate dehydrogenase, and glucose 6-phosphate dehydrogenase.

Intermuscular fat depots have similar characteristics to intramuscular fat depots. Eguinoa et al. (2003) reported that in cattle, the intermuscular fat depot had the smallest adipocyte size when compared to omental, perirenal, and subcutaneous depots. The intermuscular depot additionally had a lower level of lipogenic enzyme activity than other depots, as was the case in intramuscular fat depots. However, when adjusting for adipocyte size, subcutaneous and intermuscular fat depots had higher enzyme activity than the other depots. This indicates a potential role of other factors such as blood flow and lipolytic activity as determinants of depot differences observed.

Vasculature development precedes adipose tissue growth, and adipose tissue has the ability to grow throughout the lifetime of the animal. Hutley et al.(2001) hypothesized that microvascular endothelial cells may secrete location-specific factors that regulate adipose tissue growth. These factors may play a role in depot differences seen in adipose tissue. These researchers also found that endothelial cells stimulated preadipocyte proliferation, but there were negligible differences in differentiation observed between different depots (Hutley et al., 2001). Researchers have compared adipogenic factors from cells isolated from subcutaneous abdominal, omental, and mesenteric fat depots (Montague et al., 1997; Van Harmelen et al., 2002). Subcutaneous preadipocytes developed the most, mesenteric cells were intermediate, and omental cells had the lowest levels of lipid, GDPH activity, and adipocyte FABP (aP2). Levels of the transcription factors peroxisome proliferator activated receptor-γ (PPAR-γ) and CAAT/enhancer-binding protein-α (C/EBP-α) followed the same order of expression. There appears to be higher leptin mRNA levels in subcutaneous than omental fat depots, but this may be due to adipocyte volume, as it has been reported that leptin is correlated to adipocyte volume, and subcutaneous adipocytes are larger than omental adipocytes (Zhang et al., 2001; Kokta et al., 2004).

This variation in fat depot metabolism, adipocyte size, and physiological dynamics indicates that as animals vary in the relative proportions of fat that is accumulated across different depots, the energetic dynamics of their overall metabolism will vary. Thus, variation in fat depots is a potential difference at tissue level that can contribute to variation in maintenance requirements and feed efficiency.

Carcass quality is extremely important in beef production systems. Evidence in the feed efficiency literature suggests that it is important to consider the potential antagonism in selecting for RFI that may lead to inadvertent selection for leaner animals. The identification of feed efficient cattle is important; however, it should be noted that selection for single traits can have negative effects within the herd. Residual feed intake is reported to be independent of other performance traits; however, it has been observed that low RFI animals (efficient) tend to have a leaner carcass (Herd et al., 2003b; Lefaucheur et al., 2011). Some niche market breeds are prized for high intramuscular fat content (i.e. Wagyu, Hanwoo), and a decrease in carcass quality would damage profit margins. Correlations of fatness are not the same for all depots (Egarr et al., 2009), and in a recent study (Richardson et al., 2001), carcasses from RFI- divergent cattle had no problems meeting market specifications with fatness. A further review of literature provides details of studies in which selection for low post-weaning RFI animals did not compromise product quality (Herd et al., 1997; Richardson et al., 1998; Arthur et al., 1999; Exton et al., 2004; Baker et al., 2006; Welch et al., 2012). Many researchers include ultrasound backfat thickness in the model used to predict RFI to warrant against selection of lean animals. Schenkel et al. (2004) provided evidence of low genetic and phenotypic correlations of RFI and rib fat ($r_p = 0.14$, $r_g = 0.09$) and rump fat ($r_p = 0.11$, $r_g = 0.06$). However, Jensen et al. (1992) found a positive genetic correlation (r = 0.17) between carcass lean percentage and RFI. Basarab et al (2007) evaluated 90 calves (of five different strains) over 2 consecutive years for RFI including body composition, using the comparative slaughter approach described by Lofgreen and Garrett (1968). Observation revealed that 6.8% of variation in RFI was explained by gain of empty body fat (Basarab et al., 2003). When adjusted for independence of live weight gain (i.e. adding ultrasound backfat thickness and marbling traits), results indicate efficient animals as consuming less feed with similar growth traits and wholesale cuts as their inefficient counterparts. These researchers attributed a portion of the greater energetic differentiation in high RFI (inefficient) animals was accounted for by chemical composition of gain and heat production, due to diet-associated metabolic actions at high intake levels (Basarab et al., 2007). However, their study did reveal that high RFI animals retained more energy as waste fat (intermuscular, body cavity, and trim fat) (Basarab et al., 2007). This study aids in the addition of ultrasound fat measurements to prevent co- selection of lean animals. Additionally, RFI evaluation including ultrasound fat measurements must be conducted following guidelines established by the Beef Improvement Federation for validation by the National Cattle Evaluation program (Crews and Carstens, 2012). As evidenced from the selection of lean animals in swine, correlations between immune traits and adiposity were found to be detrimental (Clapperton et al., 2006). It is clear from this and other examples that caution must be observed when performing single trait selection (Richardson et al., 2001). One of the great advantages of using RFI as a feed efficiency trait in genetic selection programs is its independence from many other production parameters. Thus, it can be potentially combined into more complex selection indices without biasing other performance traits. This illustrates the importance of fat deposition and the need for enhancements and further studies of its relationship with RFI.

Feed Efficiency and Reproduction

Producing a healthy calf each year is the principal goal of seedstock operations. Nutritional feedback from the periphery to the hypothalamus influences bodyweight, appetite, and reproductive status of animals. However, nutrient availability and energy utilization are shared among several biological processes during pregnancy (Basarab et al., 2012). Therefore, body fat reserves are important in generating a balance in nutrient utilization at conception and during pregnancy.

It is important for an animal to attain adequate body energy reserves prior to calving. Nutrition therefore provides a link of body condition and reproductive status. Puberty can be defined as the first behavioral estrus in which a corpus luteum is formed, followed by subsequent estrus intervals. The endocrinology of estrus onset is driven by the release of gonadotropin releasing hormone (GnRH) from the hypothalamus with subsequent release of downstream hormonal regulators, luteinizing hormone (LH) and estradiol (Basarab et al., 2012). Low energy reserves in heifers has been shown to delay the onset of puberty, reduce conception rates, and increase pregnancy losses (Lemenager et al., 1980; Basarab et al., 2003). Energy restriction on prepubertal heifers show altered LH release from the anterior pituitary by reducing GnRH (Short and Adams, 1988). This may be due in part to the theorized priority of resource allocation in which estrous cyclicity and initiation of pregnancy are lowest in the hierarchy of growing animals (Short and Adams, 1988). It has been shown that concentrations of LH and follicle stimulating hormone (FSH) in the pituitary are affected by nutritional status, while GnRH receptors remain similar (Downing and Scaramuzzi, 1997). Increased concentrations of NEFA and β- hydroxybutyrate are released from adipose during feed restriction and have been negatively correlated to RFI in heifers (Kelly 2010). However, researchers Ciccioli et al. (2003) found no correlation of NEFA and reproductive performance in primiparous beef cows. These results indicate that nutrition plays a role at the hypothalamic level in controlling reproduction.

Similarly, an increased energy demand is required to maintain a growing fetus. It is known that nutritional restriction has little to no effect on very early fetal development(Palsson, 1955). However, the greatest demands are placed during late fetal development (Palsson, 1955). At this point, energy reserves are often mobilized due to a negative energy balance caused by fetal development. A study by Fitzsimmons et al. (2014) examined body condition of pregnant beef cows characterized as high, medium, or low RFI feed a silage based diet. Results suggest pregnant cows classified as low RFI were mobilizing more body fat to offset the nutritional debt caused by fetal development, than high RFI contemporaries. These results indicate a higher demand of nutrient utilization in low RFI cows. Herd et al. (2005) reported high RFI cows had greater backfat than low RFI contemporaries during mating season, suggesting that these animals would have a better body condition score after calving. The relationship of RFI and the onset of puberty has been examined in relation to feed efficiency of progeny of RFI –divergent cows (Basarab et al., 2007). In this study, RFI selection was performed on parents prior to breeding, with high RFI pairs and low RFI pairs bred to generate divergent lines. Their study show low RFI cows gave birth to calves 5-6 days later than their high RFI counterparts. Speculation of this occurrence has led the researchers to believe that it is due to longer anestrus periods and possibly a delay of puberty in heifers (Basarab et al., 2007). These results are in accordance with Johnston et al. (2009), suggesting that high RFI heifers reached onset of puberty earlier due to increased feed consumption and greater fat stores.

Additionally, Basarab et al. (2007) noted a tendency of high RFI cows having greater calving ease. These results disagree with those of Crowley et al. (2011), which suggest selecting for improved RFI would not be accompanied by increased calving difficulty. This provides insight towards careful management practices as selection against RFI may prove related to reproductive performance in the future.

Feed Efficiency and Digestion

Energy utilization during feed digestion may also contribute to feed efficiency. In a study by Krueger et al (2009), results show low RFI Brangus heifers fed a roughage based diet had higher digestibility (3%) than their high RFI counterparts, accounting for approximately 19% of variation in RFI. Similarly, Richardson et al (1996) found 1% higher digestibility in low RFI calves consuming a pelleted roughage-based diet, accounting for 14% of variation in RFI. However, these studies disagree with those in monogastric species, which found no associations of RFI and digestibility (de Haer et al., 1993). This discrepancy provides insight of biological differences between species in mechanisms driving variation in RFI.

Implications for feeding behavior analysis in context of feed efficiency.

Previous research has identified relationships between feeding behavior traits and feed efficiency in several species including poultry (Luiting, 1991), swine (de Haer et al., 1993), and beef cattle (Archer et al., 1999; Robinson and Oddy, 2004). Feeding behavior has been correlated with social status and temperament, as well as a predictors of animal health and well-being (Schwartzkopf-Genswein, 2003; Gonzalez et al., 2009). New technology has made it more economical as well as more practical to examine individual animal feeding behavior of animals towards selection possibilities (Eradus, 1999). Studies have more recently noted correlations between feeding duration and feeding frequency traits with feed efficiency (Nkrumah et al., 2007b; Bingham et al., 2009; Lancaster et al., 2009). In a study of beef cattle sired by Angus, Charolais, or hybrid bulls, Nkrumah et al. (2007a) found positive correlations ($P < 0.01$) between feeding behavior traits (feeding duration, head down duration, and feeding frequency) and RFI. Schwartzkopf-Genswein et al. (2002) reported a positive association of DMI and meal duration, indicating efficient animals spend less total time at the feed bunk. Furthermore, Lancaster et al. (2009) noted feeding behavior variation can account for as much as 35% of variation in animal performance and ultrasound traits. In swine studies, Haer et al. (1993) noted that feeding behavior accounted for 44% of variation in RFI, using early behavior measurement techniques. However, Richardson and Herd (2004) noted that feeding patterns only account for 2% of variation in RFI in cattle studies. Results are conflicting; however, this reinforces the need for more detailed studies of feeding behavior towards increasing efficiency.

Researchers often focus on meal data alone to examine feeding behaviors (Tolkamp et al., 1998; Tolkamp and Kyriazakis, 1999). However, meal criterion is often user defined rather than standardized, resulting in a difficulty to compare multiple studies. Examining other factors (i.e. bunk visits, head up and head down durations, feed bouts, etc) is paramount to identifying relationships between efficiency and feeding behavior. Meal data combines feeding bouts which negates the individual occurrences of intake. Given that energy is expended during feed consumption, it is important to examine each aspect of feeding behavior to elucidate drivers of efficiency. Ingestion rates and durations are well known factors that suggest the energy cost of eating (Adam et al., 1984). These are all variables that must be fully examined for a more comprehensive analysis of feeding behavior.

Physiological Mechanisms Regulating Intake

Identifying underlying physiological mechanisms that regulate feed intake in the context of production efficiency and energy regulation is important to reduce economic losses associated with cattle production (Wertz-Lutz, 2006). Feeding behavior can be influenced by a several factors including palatability and sensory cues (Baile and Della-Fera, 1981). Also, there are a wide variety of hormones and associated neurotransmitters that partake in appetite control (Matteri, 2001). Notably, leptin and ghrelin are well known as regulators that influence feed consumption and cessation. Ghrelin has been examined in several ruminant species including sheep, dairy, and beef

(Wertz-Lutz, 2006; Harrison et al., 2008; Roche et al., 2008). However, most studies have examined the effect of ghrelin on DMI only. Similarly, research shows relationships of leptin and RFI that may lead to elucidation of leptin as a marker for animal fatness (Wegner et al 2001). There is a need to further examine physiological roles of hormones and neurotransmitters, as they may provide insight into animal performance in the context of feed efficiency.

Orexic Hormones

From a behavioral standpoint, feed deprivation can be defined as “a lack of access to feed in high capacity pens with inadequate spacing, or a reduction in high quality concentrates due to sorting by more dominant animals.” This produces a feeding response stimulated by orexins such as ghrelin. Ghrelin is a potent growth hormone secretagogue synthesized by gastrointestinal tissues. Researchers Hayashirda et al. (2001) noted ghrelin to exist in the bovine oxyntic glands of the abomasum. Feed deprivation increases ghrelin concentrations in cattle (Wertz-Lutz, 2006), and fluctuations in blood ghrelin concentrations are known to impact feeding behavior in many species (Date, 2000; Hayashida et al., 2001; Sugino et al., 2002). Ghrelin is responsible for stimulating intake via neuropeptide Y and agouti- related proteins located in feeding centers of the brain (Shintani et al., 2001). Regulation of ghrelin, along with other associated hormones (i.e. growth hormone, insulin, leptin, etc.) requires meticulous coordination between peripheral nutrient sensing molecules and central regulatory systems (Hahn, 1998). Ghrelin is inversely correlated with blood glucose concentrations and is sensitive to the nutritional content of meals (Erdmann et al., 2003). Therefore, insulin and ghrelin share a direct relationship regulating intake via glucose concentrations, as both increase in concentration post-prandial (Greenman et al., 2004). Meals consisting of high fat content have been shown to decrease ghrelin concentrations (Greenman et al., 2004). It is also known that exogenous growth hormone decreases plasma concentration of ghrelin, suggesting a feedback regulation associated with ghrelin production in the stomach (or abomasum). As well, there is a pulsatile effect of both ghrelin and growth hormone, demonstrating that these hormones are simultaneously regulated (Koutkia et al., 2004).

Anorexic Hormones

Leptin is considered a long term regulator of nutritional status and energy balance. Leptin assists in meal size control and generally provides a steady pace for gastrointestinal passage. Without this mechanism, it is possible that meal sizes would be too large and overburden the absorptive processes occurring during digestion (Guyton, 2010). These hormones not only ensure proper metabolic processes of the animal, but also play roles in maintaining proper energy stores. Leptin is primarily produced by adipose tissue, maintaining control of adiposity and regulating adaptive changes relevant to nutritional modifications (Valassi et al., 2008). Leptin is thought to be an afferent signal that translates information about energy stores, as well as efferent regulation of appetite (Delavaud et al., 2002). Inversely related to ghrelin, leptin functions by inhibiting intake, therein defeating the effects of ghrelin on feeding centers in the brain (Klok et al., 2007). Mature animals have a greater amount of adipose tissue, as this is a major factor in finishing animals for market weight (Hood, 1982). Increases of adiposity produces an increase in circulating leptin concentrations (Geary et al., 2003), and leptin has a strong, positive correlation to adipocyte size (Delavaud et al., 2002). Modification of leptin release regulates negative and positive energy balances, as well as meal size due to expenditure (Schwartz, 2000). Diet and feeding times have been correlated with circulating levels of leptin (Daniel et al., 2002), whereby fasting decreases circulating levels and overfeeding increases levels. It is known that well-fed ruminants have decreased intake with a central administration of leptin (Morrison et al., 2001); however, there are discrepancies concerning correlations between circulating leptin concentration and feed efficiency. In swine studies, Hoque et al (2009) reported a genetic correlation of circulating leptin concentrations with RFI. Within this study, Duroc pigs over seven generations were examined for RFI and serum leptin concentration levels at 8wks of age and 105 kg body weight. Results indicate that serum leptin concentrations are more strongly associated with RFI than daily feed intake (Hoque et al., 2009). However, Nkrumah et al. (2007c) observed a moderate relationship of circulating leptin concentration and RFI in feedlot cattle. These researchers examined 464 crossbred steers with results suggesting daily DMI, RFI, and ultrasound backfat were greater for animals with elevated leptin concentrations. Additionally, Richardson et al. (2004) noted a significantly positive relationship between RFI and serum leptin concentration within a study using 33 first generation progeny from parents previously selected for low or high post weaning RFI. The observed differences in relationships between the various studies may be due to species dependence (Hoque et al., 2009). As cattle mature, more fat is deposited, allowing greater concentrations of leptin production. Cattle in the previously mentioned study may have differed in maturity level, thereby providing different correlations between leptin and RFI. As well, differing breeds have a different propensity to deposit fat, leading to variation within these studies. Wenger et al. (2001) noted plasma leptin concentrations increased in relation to the percentage (0, 50, and 75%) of Wagyu influence in animals within their study. As Wagyu animals deposit greater intramuscular fat when compared to other breeds, it was expected that the increase of leptin concentration would follow suit. Interestingly, Wenger et al. (2001) found no differences in fat characteristics of 50% and 75% Wagyu cattle, but noted a linear increase of leptin with breed influence. These results indicate that breed does in fact play a role in fat deposition and consequently leptin concentration or resistance.

Another hormone regulating feed intake is cholecystokinin (CCK), a part of the humoral satiety system. Cholecystokinin acts upon the gallbladder, initiating the release of bile via contraction and stimulating pancreatic secretions (Polak, 1977). Cholecystokinin has also been reported as a potent satiety factor in small ruminants (Baile and Della-Fera, 1981), thus regulating feed intake . These actions are preceded by the breakdown of dietary fat and proteins, which stimulate CCK release from cells of the small intestine (Figure 1.3). Researchers have found a negative correlation between circulating concentrations of CCK and insulin, and positive associations between CCK and pancreatic polypeptide (Choi et al., 2000). Based on ration formulation and feed ingredients, fat content may vary, thus affecting concentrations of CCK and the regulation of intake. It is well known that high levels of fat in a diet can affect feeding patterns and possibly depress intake (Choi et al., 2000). However, researchers did not observe an increase in post-feeding plasma CCK concentrations, when 60g of fat per kg diet (dry matter) was fed to dairy cattle (Choi et al., 2000). Results were verified by monitoring NEFA and triacylglycerol concentrations post-prandial. Interestingly, these researchers found an early surge in plasma CCK concentrations at approximately 30 minutes post-prandial (Choi et al., 2000). Reasoning behind this occurrence is unknown and needs further elucidation. It can be assumed that diet content may play a role in this surge of CCK, with high fat diets generally stimulating its release. Cholecystokinin receptor blockade studies have been also been performed with results indicating increased intake with a variety of species (Reidelberger and O'Rourke, 1989; Reidelberger, 1994). In these studies, lateral ventricular administration of CCK antisera was administered in sheep and rats, acting upon type A receptors in several regions of the brain (lateral and ventromedial hypothalamus, medial pontic area, and caudal hindbrain regions) inhibiting feed intake (Schick et al., 1990). Therefore, there is evidence suggesting that CCK is a physiological appetite control regulator; however, more studies are needed to determine the exact role of CKK in the regulation of intake.

Furthermore, there are several neuro-hormones involved in the regulation of appetite control in animals. These include Neuropeptide Y (NPY), Agouti-related protein (AGRP), Melanin-concentrating hormone (MCH), and orexins (ORX) as stimulants, while α- Melanocyte stimulating hormone and cocaine and amphetamine-regulated transcript (CART) act in a suppressant role (Matteri, 2001). These regulators act in a direct role to modulate intake at the hypothalamic pituitary axis, by activating their respective central nervous system (CNS) receptors and initiating a cascade of downstream regulatory processes (Figure 1.4) Neuropeptide Y is upregulated when an animal is undernourished, and decreased in the presence of leptin (Schwartz et al., 1996). Agouti- related protein increases appetite by antagonizing the effects of α- Melanocyte stimulating hormone via binding to type 4 melanocortin receptor (Fan et al., 1997). Cocaine and amphetamine-regulated transcript suppresses normal intake with expression downregulated by food deprivation (Kristensen et al., 1998). Direct sites of interest are the ventromedial nucleus, paraventricular nucleus and dorsomedial nucleus of the hypothalamus. Lesions from these sites produce uncontrollable hunger and weight gain as noted by researchers Kalra et al (1999). However, lesions of the lateral hypothalamus defeat the desire to consume feed (Matteri, 2001). In livestock, studies of appetite suppression have been based around cDNA clones and sequence data towards interpreting polymorphisms for marker assisted selection programs (Montaldo and Meza-Herrera, 1998). Further study of these mechanisms will likely provide better insight of appetite control, as well as generate more physiologically comparative measures of feeding behavior.

Other Factors Contributing to Variation in Feeding Behavior

Often unaccounted for in feeding behavior studies, parameters such as daylight hours, precipitation, temperature, seasonality, and fluctuating weather condition can alter how and when animals consume feed. In early studies, cattle were observed as “grouping” together to turn away from strong winds during thunderstorms (Hafez, 1969; Stricklin et al., 1976). In doing so, animals may not consume feed during these periods, disrupting the otherwise rhythmic patterns observed during periods of typical weather conditions. Thus, systematic calculation and observation of feeding behavior traits may be associated with high incidence of error, depending on experimental conditions that are often uncontrollable.

Daylight hours and seasonality also play a role in feeding behavior. Most studies describing these factors have focused on grazing animals; however, some elements may be readily applied to feedlot cattle. Effects of day-length change (daylight hours) on cattle intake have observed in several studies (Dudzínski, 1979; Low et al., 1981b, c, a). Low et al (1981b) noted increased grazing with longer daylight hours in Shorthorn cows continuously observed over 24 hr periods. Their findings also indicate some seasonal differences in feeding behaviors, with supplemental feeding periods observed in the non -summer months. Dudzinski (1979) found that the duration of grazing in a given day was influenced by the time of dawn or dusk, and temperature in Border Leicester x Merino sheep. However, in grazing animals, seasonality plays a secondary role to that of feeding behavior by also altering the quality of forage available (Provenza, 1997). Furthermore, feeding behavior in ruminants may also be modulated by changes in humidity and temperature (Dudzínski, 1979).

During periods of increased humidity, animals are prone to graze in early morning and late evening as reported by Arnold (1982). However, animal performance is improved with night grazing during high heat days, unless supplements are provided (Ayantunde et al., 2000). Seasonal variations in animal performance are thought to be caused by differences in adaptation and efficiency of energy utilization in response to the requisite demands (Mujibi et al., 2010). Ayantunde et al. (2000) observed 64 Azawak (*Bos indicus*) male calves over 70 days with 4 treatments (0,2,4, and 6 h) of night grazing periods, as well as 2 levels (0 and 608g DM) of feed supplementation of supplementation. Results showed no differences of time spent eating of supplemented and un-supplemented animals; however, animals without night grazing spent less time (~ 2hrs) consuming feed per day. Increased night time grazing was also correlated with lower weight loss during the dry season, providing animals with better performance (Ayantunde et al., 2000). Results from these studies and others like it generate a desire to examine seasonal factors that may play a role in feeding behavior.

Animals may also experience food aversions if the feed offered is unsuitable. For example, extremely wet feed (i.e. associated with snowfall or heavy rain) may become less palatable due to excess fermentation (Provenza, 1997). Grazing animals also have specific feed preferences for more palatable feeds (Armstrong et al., 1997) and have memories (up to three years) of food that provided negative or positive consequences (Hughes, 1993). With this known, it is important to keep feed fresh to prevent an unintentional aversion, during both intake evaluations and in general production practices.

Stress and Temperament

Feed efficiency is directly related to energy expenditure from a variety of sources. These sources include stress noted in cattle, other production animals, and fish (Campbell et al., 1977; Fuquay, 1981; Martins et al., 2011). Stress is defined as any shift from a homeostatic state, including a threat or fear and physical or psychological disruptions. However, all stress is not the same. Acute stress is characterized by temporary influence in the stress response, while chronic stress is a long term response to constant stressors. Stress is however, not inherently bad for the animal. As stated by Moberg and Mench (2000) the fundamental differences between stress and distress is the biological cost associated with the event. When there are insufficient reserves that can be replenished after a stressful event, these costs can be high and reduce animal performance. Changes in environment, temperature, and social status can all be considered stressors. Due to production demands associated with livestock (i.e. lean weight gain, milk production, and wool production), it is conceivable that some animals enter into a stressed state by means such as handling procedures, intense selection and other management practices. This in turn leads to decreased production from their respective standpoints and a loss of product. When this occurs, energy expenditure is shifted away from production toward increased maintenance as an animal's energy reserves become depleted (Figure 1.5).

It is important to minimize stressors as well as select for animals that provide generous yield, without interfering with quality or increasing cost. It has been observed in many species that animals in distress perform poorly in comparison to their counterparts. Measurements of stress (e.g. chute score, pen score, flight speed etc.) have been correlated with efficiency status in animals. Efficient cattle had lower flight speeds (Nkrumah et al., 2007b). Additionally, Sue et al., (2006) noted that selection against feather picking provided more efficient hens. These results suggest that animals considered stressed (high flight speed, increased feather picking) suffer from excess energy usage, yielding poor performance when compared to less stressed counterparts. Induction of stress has been found to reduce feed intake in animals. Voisinet et al. (1997) determined that feedlot cattle with calm temperaments showed higher ADG than cattle considered temperamental. In feedlot operations, pen size can be seen as a stressor that can be deleterious to cattle performance. In a scenario in which animals have reduced access to the feed bunk due to competition, additional stress can be generated and reflected by cortisol levels (Voisinet, 1997). Cortisol is an andrenocortical steroid produced from the adrenal cortex that elevates during moments of stress strain (Strain, 2004). Chronic increases in cortisol are detrimental to animal performance due to an increase in catabolic processes and metabolic rate (Bassett, 1968; Brockman, 1986). Increased cortisol concentrations increase heart rate and raise blood glucose in efforts to provide animals the appropriate blood circulation and available energy for "fight or flight" responses. This diverts energy away from animal performance (e.g. meat, milk, wool), and generates an increased caloric intake to replenish the deficit caused by stressors. Also, stressors cause mobilization of energy stores (i.e. lipid), that can prevent desirable carcass characteristics. Knott et al (2010) found correlations of increased cortisol responses and feed efficiency status in rams. In this study, efficient animals were discovered to have higher cortisol levels and lessened fat tissue content (Knott et al., 2010). Though this study was performed in sheep, there may be implications to further examine this phenomenon in bovine species. However, it is important to note that highly efficient animals may not be able to cope with common stressors as well as their counterparts. A negative correlation was observed between feed efficiency and adrenal response to adrenocorticotropic hormone (ACTH) in swine (Hennessy et al., 1988). Knott et al., (2008) noted RFI a positive association of cortisol release following ACTH infusion in sheep. This is further elucidated by Richardson and Herd (2004), observing evidence of high RFI animals being more susceptible to stress. Noted by Moberg (2000), stress initiates a shift in physiological resources, depleting some energy stores for immediate use. With this known, it is important to take into account the validity of energy stores of inefficient animals towards coping with stress.

Hierarchy

Recently, animal production systems have limited animal space (increased stocking density) due in part to bunk feeding management practices. This in turn creates competition for animals when feed is provided. It is believed that social competition is controlled through dominance relationships (Drews, 1993). Social dominance in cattle was initially described by Schein and Fohrman (1955), elucidating that one animal of a pair could intimidate the other via unidirectional aggression. These researchers also concluded that a transitive effect could be observed among the dominance patterns (Schein and Fohrman, 1955). Though dominance might be thought as negative, it plays important roles in relationships among the herd. However, this does not negate the fact that dominance can impede animals from attaining access to important resources (i.e. food and water) (Grant and Albright, 2001).

Competition for feed has been examined in several studies and observed as greatest during the initial delivery of fresh feed to feed bunks (DeVries and von Keyserlingk, 2005; Val-Laillet et al., 2008). However, it is also noted that dominant animals are actually displaced from feeders by animals deemed subordinate without clear, logical explanations (Val-Laillet et al., 2008). Results such as these suggest a bi-directional displacement mechanism, which digresses from the single dominant- subordinate relationship noticed in earlier research (Beilharz and Zeeb, 1982; Wierenga, 1990; Val-Laillet et al., 2008). Early research also noted results in which increased competition and bunk pressure has the potential decrease aggressive behaviors. Wagnon (1966) observed that range cows, allotted excess bunk space when supplemented, spent more time defending than consuming feed. This relationship was reversed when space was reduced, with animals having fewer interactions (Wagnon, 1966). To this end, classification of animals by social hierarchy plays a role in feeding behavior; however, displacement of dominant animals by their subordinate counterparts is not uncommon and should be examined carefully during experimentation. By negating the impact of dominant animal displacement, researchers may fail to properly categorize rank order, thereby confounding results.

Feed competition can also play a different role in eating behavior. Prawl et al. (1997), reported a study in which animals were not limit fed, but had limited access to feed of 1.5, 3, 6, 9 or 24 h per day. Cattle with access to feed for 9 h per day had higher intake, improved F:G , and more desirable carcass composition than those with unlimited feed access. Results from this study suggest that increased competition, or limited availability to feed access, can in fact stimulate appetite.

Herd Behavior

In the past, feeding behavior was often analyzed using a single stall methodology due to limited technology. This can often inhibit the natural feeding pattern, neglecting the herd mentality of cattle. Cattle have been known to eat more when fed as a group versus individually (Coppock, 1972; Warnick, 1977; Phipps, 1983). Gonyou and Stricklin (1981) performed analysis of feeding behavior in groups of 15 feedlot beef cattle from single stalls and trough systems. Analyses showed a difference in stall fed cattle having a greater rate of intake as well as a differing diurnal feeding pattern than trough feed counterparts (Gonyou and Stricklin, 1981). In a similar situation, Corkum et al. (1994) examined changes in feeding behavior associated with the reduction of feeder space by a maximum of three-quarters. These methods increase feed competition and this is thought to reduce subordinate animal feeding events. Results from the study yield an increase in feeding events in animals with reduced feed space; however, there was no difference in feed intake between groups. The study also measured circulating cortisol and leukocytes as indicators of stress, and no differences were observed among the groups. Results from Corkum et al. (1994) suggest that reduction in feed space did not influence weight gains nor stress response. However, it must be noted that there was a change in feed consumption patterns when space became limited, and could therefore skew natural patterns when analyzing for other parameters. This in turn plays into competitive actions of feeding behavior via social hierarchy (dominance or subordination) within a given population.

Feed Delivery

Feed delivery also plays a role in driving variation in feeding behavior of animals. Typically, cattle exhibit a somewhat diurnal feeding regimen, with intake greatest during daylight hours (Hafez, 1975; Haley, 2000). Pen-fed animals are routinely offered a total mixed ration (TMR) that includes all ingredients that can be easily dispensed in a single feeding. Borland and Kesler (1979) reported that feeding a TMR to all cattle would provide balanced nutrient intake while lessening the occurrence of sorting due to individual animal preference, as well as preventing some adverse feeding behaviors. Though TMR are well mixed, animals consistently compete to gain access to the concentrate components of rations during initial feed delivery (Gonzalez et al., 2009). During competition, high ranking animals have greater access to the better quality feed ingredients. If the feed is sorted by high ranking cattle, this may change the diets composition as post-delivery time increases (DeVries and von Keyserlingk, 2005). This in turn can alter the feeding patterns of pen-mates notionally by restricting availability of higher quality feed, leading to their consumption of lower quality, less palatable feed. However, researchers must be aware of changes in consumption rates to accurately analyze these changes and understand nutritional and behavioral effects (Val-Laillet et al., 2008).

Dairy cows are often fed post milking to stimulate consumption as well as deter lying behaviors to prevent the occurrence of mastitis (Johansson, 1999). DeVries and von Key (2005) noted that daily feeding patterns of group housed cattle is mainly influenced by time of delivery of fresh feed. To this end, changes in feed delivery can alter animal feeding behavior. The delay of feed delivery has also been shown to alter aggression and displacement at the feed bunk in dairy cattle (DeVries et al., 2004; DeVries and von Keyserlingk, 2005).

Other Implications of Feeding Behavior Analysis

Feeding behavior analysis can be linked to several different attributes in animal welfare. Of note, monogastric animal behavior analysis has been performed to detect the onset of estrus of individual sows using electronic sow feeding systems. It has been found that onset of estrus reduces feed intake of sows in the weeks prior to successive estrus (Friend, 1973). The onset of estrus has an effect on appetite due to estrogen hormone elevation (Forbes, 1995). Cornou et al. (2008), examined estrus in sows with a sensitivity level of detection (using depressed daily feed intake) between 59 and 75% using 3 herds of animals. However, these researchers also mentioned a high incidence of false-positives (Cornou et al., 2008). Although there was not a perfect correlation between depressed feed intake and onset of estrus, results from this study yield a high likelihood of early estrus detection via monitoring feeding behavior, without the need to physically examine animals or use other detection equipment. This study also characterized health associated issues (i.e. lameness) with sensitivity of detection varying from 41-70% (Cornou et al., 2008). Animals exhibited decreased intake over periods of poorer health. With findings such as these, it can be suggested that feeding behavior may be used as a predictor of animal health status, as well as for DMI or feed efficiency.

In the feedlot, ruminal acidosis is a digestive disease with potential for financial losses, as well as animal death (Galyean and Rivera, 2003). Diets high in grains typically fed to finishing cattle are implicated as a primary factor (Stock et al., 1995). A reduction or severe fluctuation in intake is often associated with acidosis, and can be easily detected in real time using feeding systems such as the GrowSafe Feed Intake system.

Overall, there are a variety of factors that contribute to feed efficiency and feeding behavior. The use of feeding behavior has the potential to non-invasively monitor a myriad of conditions including efficiency, health, and well-being. The use of RFI examination in Wagyu cattle may provide a wealth of knowledge to producers in this niche breed. Research within this dissertation aims to provide insight of efficiency status in a niche breed of cattle as well as elucidate some correlations with feeding behavior.

Research Objectives and Hypotheses

Focus of research

Originating as a draft animal, Wagyu cattle provide excellent genetic increases towards carcass qualities in American beef cattle. Both purebred and “percentage” Wagyu cattle have been proven to contain higher instances of marbling when compared to continental breeds of beef cattle. This superior quality comes at a premium; for both producers and consumers. Despite the great carcass quality and marbling, Wagyu cattle are associated with slow maturation, poor feed efficiency, and often decreased yield of red meat. Therefore, research efforts should aim to develop better feeding programs, genetic selection techniques, as well as breeding protocols to develop high quality beef for the American market.

Research within this dissertation examined the efficiency status of a niche breed of cattle (Japanese Black) with aims of providing insight into links of feeding behavior and feed efficiency. Though there is considerable variation among methods used to examine feeding behavior, the current studies use a RFID-based technology (GrowSafe Systems) to examine feeding behavior of cattle on test, providing quantifiable behavioral measurements. It is possible that this technology and approach may enhance currently accepted protocols to estimate ADG, DMI and RFI. For example, if an algorithm including feeding behaviors was as accurate as weighing of feed in estimating daily DMI, it would be possible to eliminate the use of expensive weighing equipment and simply use electronic means to record individual animal feeding behavior. Parts 2 and 3 of this research program provide some steps towards discovering the potential of feeding behavior as a predictive tool for DMI and other production measurements. With the current knowledge of efficiency of beef cattle, the following hypotheses are proposed:

Development of Hypothesis I (relevant to Chapter 2)

The use of efficient animals in Wagyu production could greatly improve production efforts as well as improve profitability in Wagyu operations. Residual feed intake is a means by which individual animals can be identified by efficiency status, for selection of improved feed efficiency in various populations. Residual feed intake has not been extensively evaluated in Wagyu cattle. As well, within this niche breed it is important to maintain excellent carcass composition. To this end, it is important that selection for efficient animals does not inhibit the highly desirable IMF characteristics of Wagyu beef products. Therefore it was hypothesized that Wagyu bulls have physiological variation in efficiency that can be identified using RFI.

Development of Hypothesis II (relevant to Chapters 3 and 4)

There are aspects of feed efficiency that are not fully understood in beef cattle. Identifying these unknown attributes can provide some elucidation of underlying physiological drivers in variation of efficiency. Examining feeding behavior may provide some insight into differences in efficiency status of animals. To the author’s current knowledge, feeding behavior has not been evaluated in Wagyu cattle. Understanding the relationships of feeding behavior and feed efficiency may assist in management practices, as well as, add to the growing knowledgebase of feed efficiency.

Maintenance requirements of cattle are a large portion of caloric use. Reducing maintenance energy requirements of cattle may be possible through selection processes. Considered a major contributor to animal variation in feed utilization, favorable selection for maintenance energy may provide an accompanying asset towards reducing input costs, improving profitability, and maintaining a sustainable beef industry. The relationships of maintenance energy and feeding behavior have not been thoroughly evaluated, and could provide a deeper understanding of efficiency in beef cattle. To this end, it was hypothesized that 1) Dry matter intake and efficiency status of Wagyu and British cattle can be predicted using feeding behavior measurements during a standard RFI test, 2) there is a relationship between time at the feed bunk and efficiency, and 3) sire maintenance energy EPD plays a role in progeny feeding behavior.

Summary of dissertation hypotheses

The following chapters provide information regarding the experimental design, testing, and conclusions associated with the following hypotheses:

1) It is possible for efficient animals to attain superb marbling and marketable carcasses in Japanese Black Cattle.
2) Dry matter intake and efficiency status of Wagyu and Red Angus cattle can be predicted using feeding behavior measurements during a standard RFI test.
3) There is a relationship between time at the feed bunk and efficiency.
4) Sire maintenance energy EPD plays a role in progeny feeding behavior.

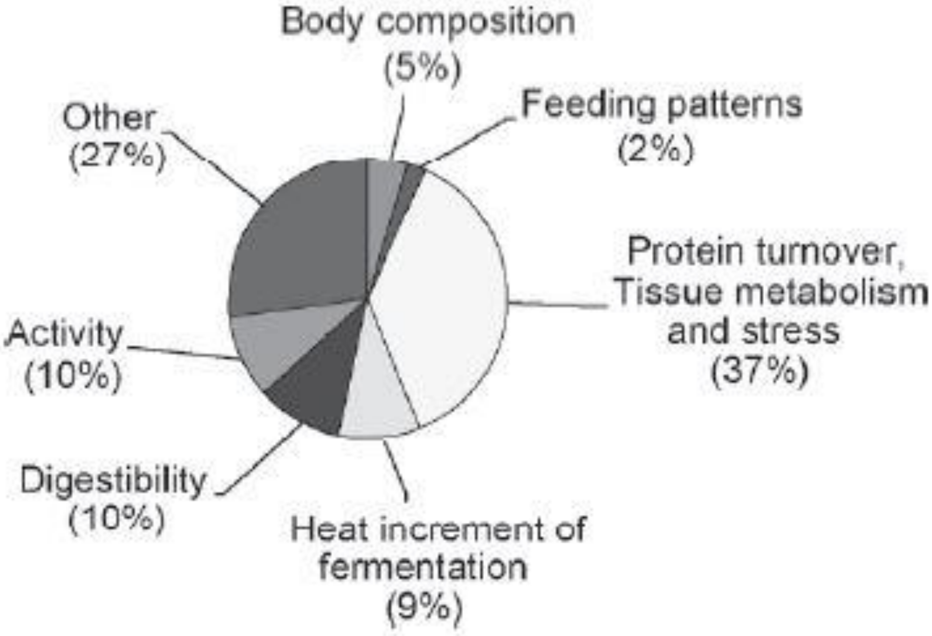

Fig 1.1. Contributions of biological mechanisms to variation in RFI from divergently selected cattle (Richardson and Herd, 2004). Permission to reprint obtained from Journal of Animal Science on May 27, 2014.

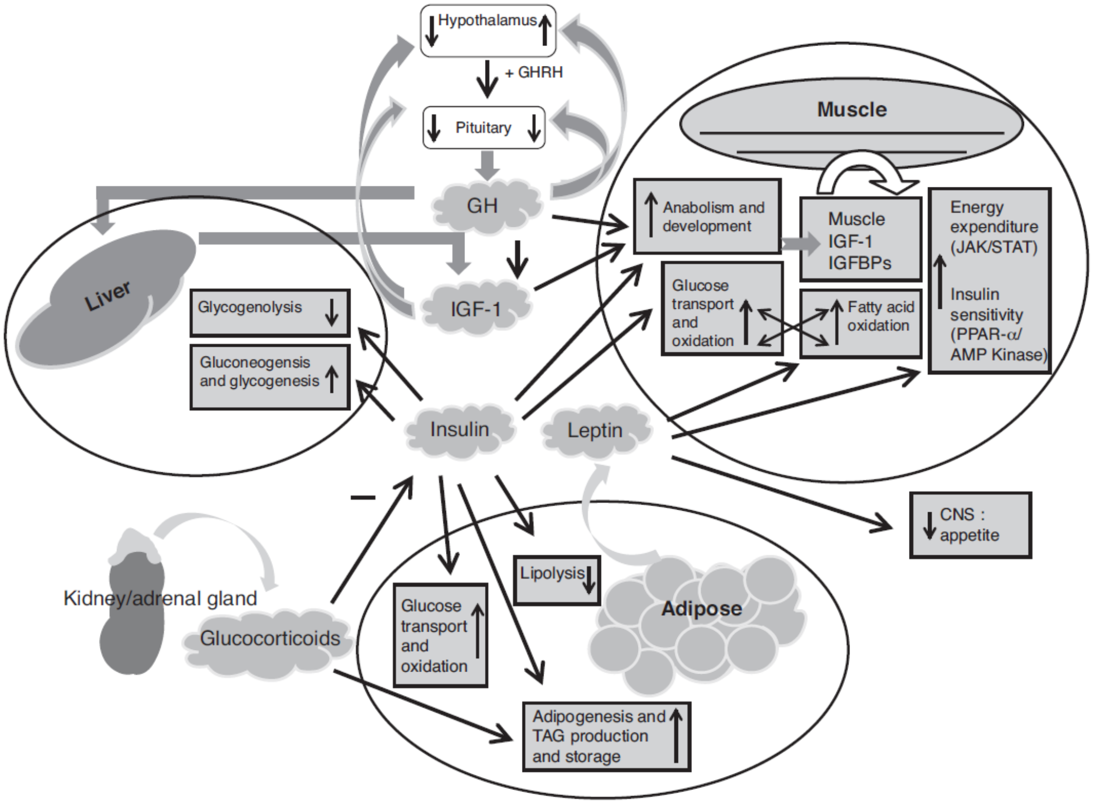

Figure 1.2 A brief overview of the pathways and processes that link muscle and adipose tissues with potential to contribute to variation in energetic (feed) efficiency. Some endocrine pathways have been suggested to play a role in these interactions. *Note*: The pathways depicted are shown in the case of positive energy balance. The factors involved include growth hormone (GH), insulin-like growth factor-1 (IGF-1), insulin, leptin, and glucocorticoids. *Figure key*: the main tissues of focus are shown along with tissue-specific processes (grey boxes). Broad, grey arrows link tissues to endocrine factors and endocrine feedback loops. Heavy, black arrows link endocrine signals to tissue-specific processes. Black arrows within process boxes indicate either upregulation or downregulation responses. Within muscle, some additional processes are depicted. The crossed arrows indicate the competing interactions of insulin and leptin that stimulate glucose oxidation and fatty acid oxidation, respectively. Interactions of these pathways can repartition oxidation between these two substrates. Each pathway may also inhibit the action of the other. The broad white arrow indicates that stimulation of locally produced IGF-1 and IGF-binding proteins (IGFBPs) results in autocrine/paracrine signaling that also regulates anabolic processes in muscle. (Hill 2012) Permission to reprint obtained from Wiley-Blackwell Publishing on May 27, 2014

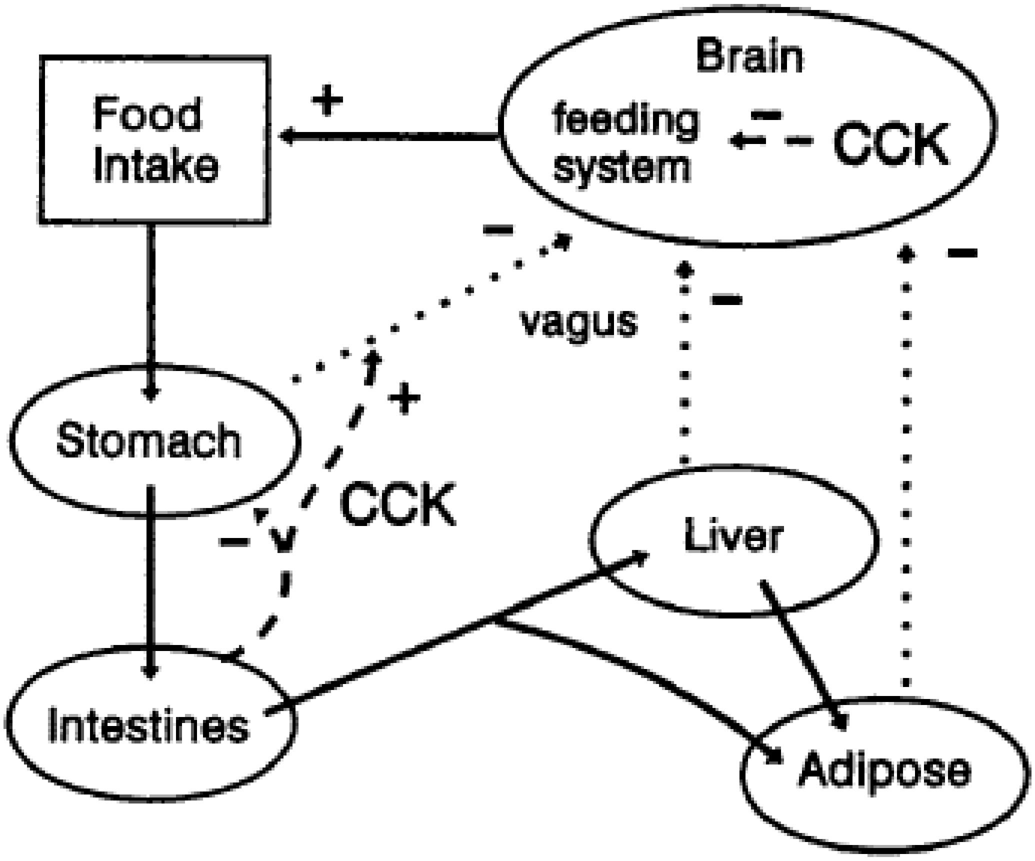

Figure 1.3. Schematic diagram of putative cholecystokinin (CCK) satiety mechanisms based primarily on studies of the effects of exogenous CCK on food intake. Solid lines represent direction of nutrient flux. Broken lines represent putative regulatory feedback mechanisms to suppress feeding (Reidelberger, 1994). Permission to reprint obtained from The Journal of Nutrition on May 27 2014.

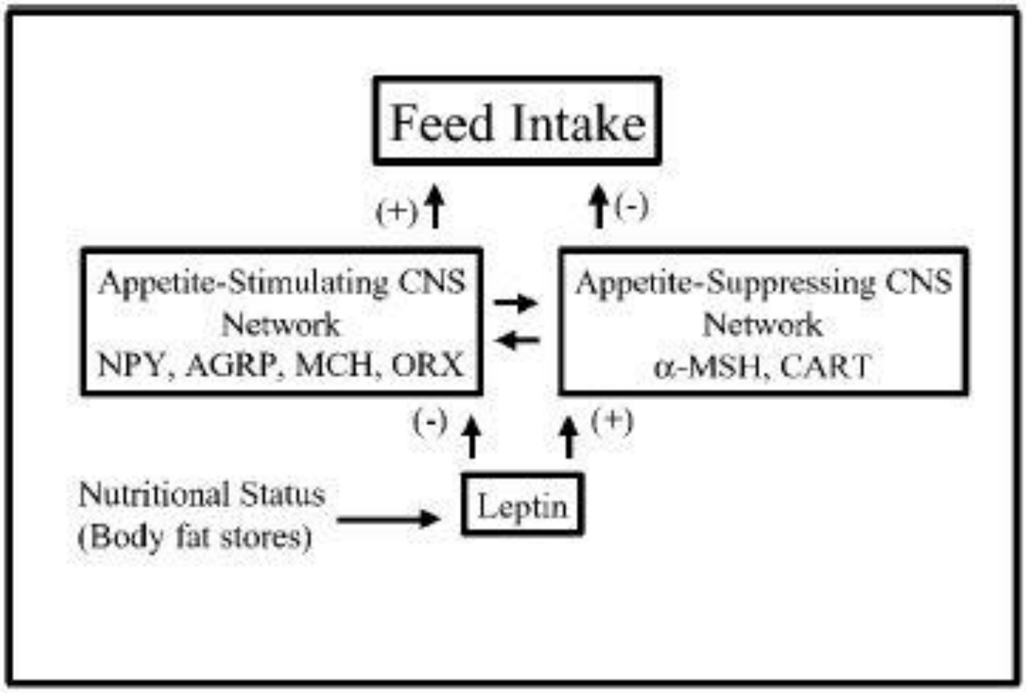

Fig 1.4. Conceptual diagram depicting feed intake modulation and appetite control via signaling factors of the central nervous system and leptin. NPY = neuropeptide Y; AGRP = agouti-related protein; MCH = melanin-concentrating hormone; ORX = orexin; *α*-MSH = *α*-melanocyte stimulating hormone; CART = cocaine and amphetamine regulated transcript (Matteri, 2001). Permission to reprint obtained from American Society of Animal Science on May 27, 2014.

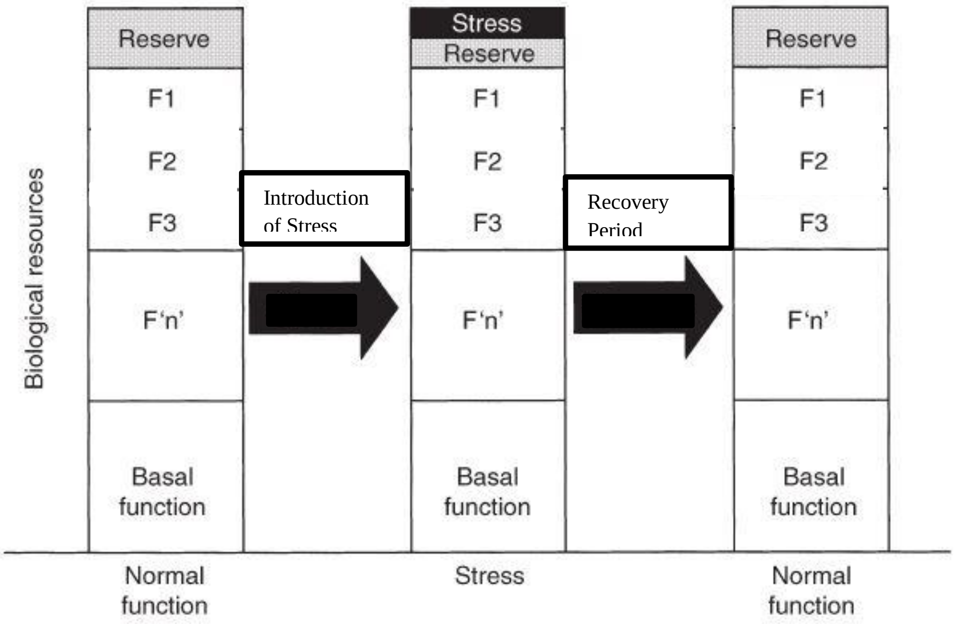

Fig 1.5. Hypothetical scheme of how mild stress redirects resources during the stress response. Biological functions are assigned F1-F'n'. In mild stress, only reserved resources are diverted to contend with the proposed stressor. Adapted from (Moberg and Mench, 2000).

Table 1.1. Oldest inbred strains of Japanese Black cattle.

Strain	Region	Year Established	Range	Characteristics of Strain
Takenotan-zuru	Atetsu, Okayama	1830	Atetu, Okayama Hino, Tottori Nita, Shimane Nogi, Shimane	Large build, soundness, serial reproduction, strong backline and loin, fullness of hind.
Bakura-zuru	Nita, Shimane	1855	Nita, Shimane	Similar to Takenotani-zuru; due to branch strain.
Iwakura-zuru	Hiba, Hiroshima	1843	Hiba, Hiroshima	Mild disposition, longevity superior reproduction, good udder development, good body conformation.
Shusuke-zuru	Mikata, Hyogo	1845	Mikata, Hyogo	Longevity, serial reproduction, Soundness, quality.

Adapted from (Namikawa, 1992).

LITERATURE CITED

Adam, I., B. A. Young, A. M. Nicol, and A. A. Degen. 1984. Energy cost of eating in cattle given diets of different form. Animal Science 38: 53-56.

Adams, K., D. J. Flint, and R. G. Vernon. 1992. Hanna research institute yearbook, Ayr, Scotland.

Ahola, J. K., and R. A. Hill. 2012. Input factors affecting feed intake and utilization in growing cattle. In: R. A. Hill (ed.) Feed efficiency in the beef industry. p 7-20. Wiley-Blackwell, Ames, IA.

Aoki, N., M. Kawamura, and T. Matsuda. 1999. Lactation-dependent down regulation of leptin production in mouse mammary gland. Biochimica Et Biophysica Acta 1427: 298-306.

Archer, J. A., E. C. Richardson, R. M. Herd, and P. F. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: A review. Australian Journal of Agricultural Research 50: 147-161.

Armstrong, R. H., S. A. Grant, T. G. Common, and M. M. Beattie. 1997. Controlled grazing studies on nardus grassland: Effects of between-tussock sward height and species of grazer on diet selection and intake. Grass and Forage Science 52: 219-231.

Arnold, G. W. 1982. Some factors affecting the grazing behaviour of sheep in winter in new south wales. Appl. Anim. Ethol. 8: 119–125.

Arthur, P. F., J. A. Archer, R. M. Herd, E. C. Richardson, S. C. Exton, C. Oswin, K. C. P. Dibley, and D. A. Burton. 1999. Relationship between postweaning growth, net feed intake and cow performance. Proceedings of the Thirteenth Conference Association for the Advancement of Animal Breeding and Genetics: 484-487.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in angus cattle. Journal of Animal Science 79: 2805-2811.

Ayantunde, A. A., Fernandez-Reivera, S.. Hiernaux, Fernandez-Reivera, H. S., V. K. P.H.Y., U. H., and C. H.M.J. 2000. Effect of nocturnal grazing and supplementation on diet selection, eating time, forage intake and weight changes in cattle. Anim. Sci. 71: 333–340.

Baile, C. A., and M. A. Della-Fera. 1981. Nature of hunger and satiety control systems in ruminants. Journal of dairy science 64: 1140-1152.

Baker, S. D., J. I. Szasz, T. A. Klein, P. S. Kuber, C. W. Hunt, J. B. Glaze, Jr., D. Falk, R. Richard, J. C. Miller, R. A. Battaglia, and R. A. Hill. 2006. Residual feed intake of purebred angus steers: Effects on meat quality and palatability. J Anim Sci 84: 938-945.

Basarab, J., D. McCartney, E. K. Okine, and V. S. Baron. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87: 489-502.

Basarab, J. A., C. Fitzsimmons, S. C. Whisnant, and R. P. Wetteman. 2012. Interactions with other traits: Reproduction and fertility. In: R. Hill (ed.) Feed efficiency in the beef industry p123-144. Wiley-Blackwell, Ames, IA.

Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Canadian Journal of Animal Science 83: 189-204.

Bassett, J. M. 1968. The relation of fat and protein catabolic actions of cortisol to glucose homeostasis in fasting sheep. Metabolism 17: 644-652.

Beilharz, R. G., and K. Zeeb. 1982. Social dominance in dairy cattle. Applied Animal Ethology 8: 79-97.

Bingham, G. M., T. H. Friend, P. A. Lancaster, and G. E. Carstens. 2009. Relationship between feeding behavior and residual feed intake in growing brangus heifers. Journal of Animal Science 87: 2685-2689.

Blaxter, K. L. 1989. Energy metabolism in animals and man. Cambridge University Press.

Bonsma, J. C., G. D. J. Scholtz, and F. J. G. Badenhorst. 1940. The influence of climate on cattle. Fertility and hardiness of certain breeds. Farming 15: 7-12 ; 16.

Borland, K., and E. M. Kesler. 1979. Complete rations for holstein calves 8 to 18 weeks of age1. Journal of dairy science 62: 304-309.

Bottje, W., and G. E. Carstens. 2012. Variation in metabolism: Biological efficiency of energy production and utilization that affects feed efficiency. In: R. A. Hill (ed.) Feed efficiency in the beef industry. p 251-274. Wiley-Blackwell, Ames, IA.

Bottje, W., M. Iqbal, Z. X. Tang, D. Cawthon, R. Okimoto, T. Wing, and M. Cooper. 2002. Association of mitochondrial function with feed efficiency within a single genetic line of male broilers. Poultry Science 81: 546-555.

Brockman, R. P., Laarveld, B. 1986. Hormonal regulation of metabolism in ruminants: A review. Livestock Production Science 14: 313-334.

Calles, J. A. E., Gaskins, C. T., Busboom, J. R., Duckett, S. K., Cronrath, J. D., Reeves, J. J., Wright, Jr., R. W. . 2000. Differences among wagyu sires for usda carcass traits and palatability attributes of cooked ribeye steaks. . Journal of Animal Sciences 78: 1710-1715.

Campbell, J. B., R. G. White, J. E. Wright, R. Crookshank, and D. C. Clanton. 1977. Effects of stable flies on weight gains and feed efficiency of calves on growing or finishing rations. Journal of Economic Entomology 70: 592-594.

Carstens, G. E., and M. S. Kerley. 2009. Biological basis for variation in energetic efficiency of beef cattle Proceedings of the Beef Improvement Federation 41st Annual Research Symposium, Sacramento, CA.

Choi, B. R., D. L. Palmquist, and M. S. Allen. 2000. Cholecystokinin mediates depression of feed intake in dairy cattle fed high fat dietsâ˜†1 1 â˜†salaries and research support provided by state and federal funds appropriated to the ohio agricultural research and development center. Domestic Animal Endocrinology 19: 159-175.

Ciccioli, N. H., R. P. Wettemann, L. J. Spicer, C. A. Lents, F. J. White, and D. H. Keisler. 2003. Influence of body condition at calving and postpartum nutrition on endocrine function and reproductive performance of primiparous beef cows. J Anim Sci 81: 3107-3120.

Clapperton, M., S. C. Bishop, and E. J. Glass. 2006. Selection for lean growth and food intake leads to correlated changes in innate immune traits in large white pigs. Animal Science 82: 867-876.

Coppock, C. E., C. H. Noller, S. A. Wolfe, C. J. Callaghan, and J. S. Baker. 1972. Effect of forage - concentrate ratio in complete feeds fed ad libitum on feed intake prepartum and the occurrence of abomasal displacement in dairy cows. J. Dairy Sci. 55: 783-789.

Corkum, M. J., L. A. Bate, T. Tennessen, and A. Lirette. 1994. Consequences of reduction of number of individual feeders on feeding behaviour and stress level of feedlot steers. Applied Animal Behaviour Science 41: 27-35.

Cornou, C. c., J. Vinther, and A. R. Kristensen. 2008. Automatic detection of oestrus and health disorders using data from electronic sow feeders. Livestock Science 118: 262-271.

Crews, D. H., and G. E. Carstens. 2012. Measuring individual feed intake and utilization in growing cattle. In: R. Hill (ed.) Feed efficiency in the beef industry. p 21-28. Wiley-Blackwell, Ames, IA.

Crews, D. H., Jr. 2005. Genetics of efficient feed utilization and national cattle evaluation: A review. Genet Mol Res 4: 152-165.

Crowley, J. J., R. D. Evans, N. Mc Hugh, D. A. Kenny, M. McGee, D. H. Crews, and D. P. Berry. 2011. Genetic relationships between feed efficiency in growing males and beef cow performance. Journal of Animal Science 89: 3372-3381.

Daniel, J. A., B. K. Whitlock, J. A. Baker, B. Steele, C. D. Morrison, D. H. Keisler, and J. L. Sartin. 2002. Effect of body fat mass and nutritional status on 24-hour leptin profiles in ewes. J Anim Sci 80: 1083-1089.

Date, Y. M., Mondal, M.S., Matsukura, Ueta, Y, Yamashita, H., Kaiya, H., Kangawa, K. Nakazato, M. 2000. Distribution of orexin//hypocretin in the rat median eminence and pituitary. Brain Res. Mol. 76: 1-6.

de Haer, L. C. M., P. Luiting, and H. L. M. Aarts. 1993. Relations among individual (residual) feed intake, growth performance and feed intake pattern of growing pigs in group housing. Livestock Production Science 36: 233-253.

Delavaud, C., A. Ferlay, Y. Faulconnier, F. Bocquier, G. Kann, and Y. Chilliard. 2002. Plasma leptin concentration in adult cattle: Effects of breed, adiposity, feeding level, and meal intake. Journal of Animal Science 80: 1317-1328.

DeVries, T. J., and M. A. G. von Keyserlingk. 2005. Time of feed delivery affects the feeding and lying patterns of dairy cows. Journal of dairy science 88: 625-631.

DeVries, T. J., M. A. G. von Keyserlingk, and D. M. Weary. 2004. Effect of feeding space on the inter-cow distance, aggression, and feeding behavior of free-stall housed lactating dairy cows. Journal of dairy science 87: 1432-1438.

Downing, J. A., and R. J. Scaramuzzi. 1997. The effect of the infusion of insulin during the luteal phase of the estrous cycle on the ovulation rate and on plasma concentrations of lh, fsh and glucose in ewes. Theriogenology 47: 747-759.

Drews, C. 1993. The concept and definition of dominance in animal behaviour. Behaviour 125: 283-313.

Dudzínski, M. L. a. A., G.W. 1979. Factors influencing the grazing behaviour of sheep in a mediterranean climate Appl. Anim. Ethol.: 125–144.

Egarr, A. R., W. S. Pitchford, M. J. Bottema, R. M. Herd, J. P. Siddell, J. M. Thompson, and C. D. K. Bottema. 2009. Fat distribution in angus steers is related to residual feed intake estimated breeding value. 536-539.

Eguinoa, P., S. Brocklehurst, A. Arana, J. A. Mendizabal, R. G. Vernon, and A. Purroy. 2003. Lipogenic enzyme activities in different adipose depots of pirenaican and holstein bulls and heifers taking into account adipocyte size. J. Anim Sci 81: 432-440.

Eradus, W. J., and M. B. Jansen. 1999. Animal identification and monitoring. Comp. Elect. Agr. 24: 91-98.

Erdmann, J., F. Lippl, and V. Schusdziarra. 2003. Differential effect of protein and fat on plasma ghrelin levels in man. Regulatory Peptides 116: 101-107.

Erlanson-Albertsson, C. 2003. The role of uncoupling proteins in the regulation of metabolism. Acta Physiologica Scandinavica 178: 405-412.

Exton, S. C., R. M. Herd, and P. F. Arthur. 2004. Identifying bulls superior for net feed intake, intramuscular fat and subcutaneous fat. Animal Production in Australia 25: 57-60.

Fan, W., B. A. Boston, R. A. Kesterson, V. J. Hruby, and R. D. Cone. 1997. Role of melanocortinergic neurons in feeding and the agouti obesity syndrome. Nature 385: 165-168.

FAO. 2002. World agriculture 2030: Main findings.

Ferrell, C. L., and T. G. Jenkins. 1998. Body composition and energy utilization by steers of diverse genotypes fed a high-concentrate diet during the finishing period: Ii. Angus, boran, brahman, hereford, and tuli sires. Journal of Animal Science 76: 647-657.

Fitzsimons, C., D. A. Kenny, A. G. Fahey, and M. McGee. 2014. Feeding behavior, ruminal fermentation, and performance of pregnant beef cows differing in phenotypic residual feed intake offered grass silage. Journal of Animal Science 92: 2170-2181.

Flier, J. S., P. Usher, and M. Deluise. 1981. Effects of sucrose overfeeding on na,k-atpase mediated mrb uptake in normal and ob/ob mice. Diabetes 975-978.

Forbes, J. 1995. Voluntary food intake and diet selection in farms animals CAB international, Wallingford, Oxon OX10DE, UK.

Fox, D. G., L.O. Tedeschi, and P.J. Guiroy. 2001. A decision support system for individual cattle management: Proceedings of the cornell nutrition conference for feed manufacturers pp. 64-76

Friend, D. W. 1973. Self-selection of feeds and water by unbred gilts. J Anim Sci 37: 1137-1141.

Fuquay, J. W. 1981. Heat stress as it affects animal production. Journal of Animal Science 52: 164-174.

Galyean, M. L., and J. D. Rivera. 2003. Nutritionally related disorders affecting feedlot cattle. Canadian Journal of Animal Science 83: 13-20.

Geary, T. W., E. L. McFadin, M. D. Macneil, E. E. Grings, R. E. Short, R. N. Funston, and D. H. Keisler. 2003. Leptin as a predictor of carcass composition in beef cattle. Journal of Animal Science 81: 1-8.

Gibb, D. J., and T. A. McAllister. 1999. The impact of feed intake and feeding behaviour of cattle on feedlot and feedbunk management. 20th Western Nutrition Conference on Marketing to the 21st Century Proc. p 102-116.

Gill, M., J. France, M. Summers, B. W. McBride, and L. P. Milligan. 1989. Simulation of the energy costs associated with protein turnover and na+,k+-transport in growing lambs. J Nutr 119: 1287-1299.

Golden, J. W., M. S. Kerley, and W. H. Kolath. 2008. The relationship of feeding behavior to residual feed intake in crossbred angus steers fed traditional and no-roughage diets. J Anim Sci 86: 180-186.

Gomes, R. d. C., R. D. Sainz, and P. R. Leme. 2013. Protein metabolism, feed energy partitioning, behavior patterns and plasma cortisol in nellore steers with high and low residual feed intake. Revista Brasileira de Zootecnia 42: 44-50.

Gonyou, H. W., and W. R. Stricklin. 1981. Eating behavior of beef cattle groups fed from a single stall or trough. Applied Animal Ethology 7: 123-133.

Gonzalez, L. A., L. B. Correa, A. Ferret, X. Manteca, J. L. RuÃz-de-la-Torre, and S. Calsamiglia. 2009. Intake, water consumption, ruminal fermentation, and stress response of beef heifers fed after different lengths of delays in the daily feed delivery time. Journal of Animal Science 87: 2709-2718.

Grant, R. J., and J. L. Albright. 2001. Effect of animal grouping on feeding behavior and intake of dairy cattle. Journal of dairy science 84: E156-E163.

Greenman, Y., N. Golani, S. Gilad, M. Yaron, R. Limor, and N. Stern. 2004. Ghrelin secretion is modulated in a nutrient- and gender-specific manner. Clinical Endocrinology 60: 382-388.

Guyton, A. C., Hall, John E. 2010. Guyton and hall textbook of medical physiology. twelfth ed. Saunders.

Hafez, E. S. E., and M. F. Bouissou. 1975. The behaviour of domestic animals. 3rd ed. Bailliere Tindall, London.

Hafez, E. S. E., M. W. Schein and R. Ewbank. 1969. The behavior of cattle In: E. S. E. Hafez (ed.) The behavior of domestic animals The Williams and Wilkins Co Baltimore, MD.

Hahn, T. M., Breininger, J.F., Baskin, D.G., Schwartz, M.W. 1998. Coexpression of agrp and npy in fasting-activated hypothalamic neurons. Nature Neuroscience 1: 271-272.

Haley, D. B., Rushen, J. de Passille, A.M. 2000. Behavioral indicators of cow comfort: Activity and resting behaviour of dairy cows housed in two types of housing. Canadian Journal of Animal Science: 257-263.

Hammond, W. H. 1955. Measurement and interpretation of subcutaneous fat, with norms for children and young adult males. Br J Prev Soc Med 9: 201-211.

Harrison, J. L., D. W. Miller, P. A. Findlay, and C. L. Adam. 2008. Photoperiod influences the central effects of ghrelin on food intake, gh and lh secretion in sheep. Neuroendocrinology 87: 182-192.

Hayashida, T., K. Murakami, K. Mogi, M. Nishihara, M. Nakazato, M. S. Mondal, Y. Horii, M. Kojima, K. Kangawa, and N. Murakami. 2001. Ghrelin in domestic animals: Distribution in stomach and its possible role. Domestic Animal Endocrinology 21: 17-24.

Hennessy, D. P., T. Stelmasiak, N. E. Johnston, P. N. Jackson, and K. H. Outch. 1988. Consistent capacity for adrenocortical response to acth administration in pigs. Am J Vet Res 49: 1276-1283.

Herd, R. M., J. A. Archer, and P. F. Arthur. 2003a. Reducing the cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application. Journal of Animal Science 81(E Suppl. 1): E9-E17.

Herd, R. M., J. A. Archer, and P. F. Arthur. 2003b. Selection for low postweaning residual feed intake improves feed efficiency of steers in the feedlot 50 years of DNA: Proceedings of the Fifteenth Conference, Association for the Advancement of Animal Breeding and Genetics, Melbourne, Australia, 7-11 July 2003.

Herd, R. M., J. A. Archer, P. F. Arthur, E. C. Richardson, J. H. Wright, K. C. P. Dibley, and D. A. Burton. 1997. Performance of progeny of high vs. Low net feed conversion efficiency cattle. In: Association for the Advancement of Animal Breeding and Genetics. Proceedings of the Twelfth Conference. p 742-745.

Herd, R. M., P. F. Arthur, and S. C. Exton. 2005. Breeding for improved feed efficiency - key results from crc feed efficiency research Moving from research to industry adoption. NSW Department of Primary Industries and CRC for Cattle and Beef Quality Conference, Quality Resort Nautilus, Coffs Harbour, New South Wales, 3-5 May 2005.

Herd, R. M., and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in british hereford cattle. Livestock Production Science 63: 111-119.

Herd, R. M., V. H. Oddy, and E. C. Richardson. 2004. Biological basis for variation in residual feed intake in beef cattle. 1. Review of potential mechanisms. Australian Journal of Experimental Agriculture 44: 423-430.

Hood, R. L. 1982. Relationships among growth, adipose cell size, and lipid metabolism in ruminant adipose tissue. Proceedings Federation of American Societies for Experimental Biology 41: 2555-2561.

Hoque, A., and T. Oikawa. 2004. Comparison and relation among different estimates of residual feed intake for japanese black (wagyu) bulls. Animal Science Journal 75: 201-205.

Hoque, M. A., P. F. Arthur, K. Hiramoto, and T. Oikawa. 2006. Genetic relationship between different measures of feed efficiency and its component traits in japanese black (wagyu) bulls. Livestock Science 99: 111-118.

Hoque, M. A., K. Katoh, and K. Suzuki. 2009. Genetic associations of residual feed intake with serum insulin-like growth factor-i and leptin concentrations, meat quality, and carcass cross sectional fat area ratios in duroc pigs. Journal of Animal Science 87: 3069-3075.

Hoque, M. A., K. Suzuki, and T. Oikawa. 2007. Estimation of genetic gain on growth and carcass traits over direct and index selection for growth and feed efficiency of japanese black cattle by computer simulation. Tohoku Journal of Agricultural Research 58: 31-41.

Hughes, R. N. 1993 Diet selection Blackwell Scientific publication, Oxford.

Hutley, L. J., A. C. Herington, W. Shurety, C. Cheung, D. A. Vesey, D. P. Cameron, and J. B. Prins. 2001. Human adipose tissue endothelial cells promote preadipocyte proliferation. Am J Physiol Endocrinol Metab 281: E1037-E1044.

Inoue, K., M. Kobayashi, N. Shoji, and K. Kato. 2010. Genetic parameters for fatty acid composition and feed efficiency traits in japanese black cattle. animal 5: 987-994.

Jensen, M. D. 1992. Research techniques for body composition assessment. J Am Diet Assoc 92: 454-460.

Johansson, B., Redbo, I., Svennersten-Sjaunja, K. 1999. Effect of feeding before, during and after milking on dairy cow behaviour and the hormone cortisol. Animal Science 68: 597- 604.

Johnson, B. J., M. E. White, M. R. Hathaway, and W. R. Dayton. 2003. Effect of differentiation on levels of insulin-like growth factor binding protein mrnas in cultured porcine embryonic myogenic cells. Domestic Animal Endocrinology 24: 81-93.

Johnson, M. E. M., M. E. Das, N. Mamota, F. R. Butcher, and J. N. Fain. 1972. The regulation of gluconeogenesis in isolated rat liver cells by glucagon, insulin, dibutyryl cyclic adenosine monophosphate, and fatty acids. Journal of Biological Chemistry 247: 3229-3235.

Johnston, D. J., S. A. Barwick, N. J. Corbet, G. Fordyce, R. G. Holroyd, P. J. Williams, and H. M. Burrow. 2009. Genetics of heifer puberty in two tropical beef genotypes in northern australia and associations with heifer- and steer-production traits. Animal Production Science 49: 399-412.

Kahi, A. K., and H. Hirooka. 2007. Effect of direct and indirect selection criteria for efficiency of gain on profitability of japanese black cattle selection strategies. J Anim Sci 85: 2401-2412.

Kalra, S. P., M. G. Dube, S. Pu, B. Xu, T. L. Horvath, and P. S. Kalra. 1999. Interacting appetite-regulating pathways in the hypothalamic regulation of body weight. Endocrine Reviews 20: 68-100.

Kelly, A. K., M. McGee, D. H. Crews, Jr., A. G. Fahey, A. R. Wylie, and D. A. Kenny. 2010. Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables, and body composition traits in growing beef heifers. Journal of Animal Science 88: 109-123.

Kelly, J. M., and B. W. McBride. 1990. The sodium pump and other mechanisms of thermogenesis in selected tissues. Proc Nutr Soc 49: 185-202.

Klok, M. D., S. Jakobsdottir, and M. L. Drent. 2007. The role of leptin and ghrelin in the regulation of food intake and body weight in humans: A review. Obesity Reviews 8: 21-34.

Knott, S. A., L. J. Cummins, F. R. Dunshea, and B. J. Leury. 2008. Rams with poor feed efficiency are highly responsive to an exogenous adrenocorticotropin hormone (acth) challenge. Domestic Animal Endocrinology 34: 261-268.

Knott, S. A., L. J. Cummins, F. R. Dunshea, and B. J. Leury. 2010. Feed efficiency and body composition are related to cortisol response to adrenocorticotropin hormone and insulin-induced hypoglycemia in rams. Domest Anim Endocrinol 39: 137-146.

Koch, R. M., D. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. Journal of Animal Science 22: 486-494.

Kokta, T. A., M. V. Dodson, A. Gertler, and R. A. Hill. 2004. Intercellular signaling between adipose tissue and muscle tissue. Domest Anim Endocrinol 27: 303-331.

Koutkia, P., B. Canavan, J. Breu, M. L. Johnson, and S. K. Grinspoon. 2004. Nocturnal ghrelin pulsatility and response to growth hormone secretagogues in healthy men. American Journal of Physiology - Endocrinology and Metabolism 287: E506-E512.

Kristensen, P., M. Judge, L. Thim, U. Ribel, K. N. Christjansen, B. S. Wulff, J. T. Clausen, P. B. Jensen, O. D. Madsen, N. Vrang, P. J. Larsen, and S. Hastrup. 1998. Hypothalamic cart is a new anorectic peptide regulated by leptin. Nature 393: 72-76.

Lancaster, P. A., G. E. Carstens, F. R. Ribeiro, M. E. Davis, J. G. Lyons, and T. H. Welsh, Jr. 2008. Effects of divergent selection for serum insulin-like growth factor-i concentration on performance, feed efficiency, and ultrasound measures of carcass composition traits in angus bulls and heifers. J Anim Sci 86: 2862-2871.

Lancaster, P. A., G. E. Carstens, F. R. B. Ribeiro, L. O. Tedeschi, and D. H. Crews. 2009. Characterization of feed efficiency traits and relationships with feeding behavior and ultrasound carcass traits in growing bulls. Journal of Animal Science 87: 1528-1539.

Lefaucheur, L., B. Lebret, P. Ecolan, I. Louveau, M. Damon, A. Prunier, Y. Billon, P. Sellier, and H. Gilbert. 2011. Muscle characteristics and meat quality traits are affected by divergent selection on residual feed intake in pigs. Journal of Animal Science 89: 996-1010.

Lemenager, R. P., W. H. Smith, T. G. Martin, W. L. Singleton, and J. R. Hodges. 1980. Effects of winter and summer energy levels on heifer growth and reproductive performance. Journal of Animal Science 51: 837-842.

Lindstrom, T., I. Redbo, and K. UvnÃ¤s-Moberg. 2001. Plasma oxytocin and cortisol concentrations in dairy cows in relation to feeding duration and rumen fill. Physiology & Behavior 72: 73-81.

Lofgreen, G. P., and W. N. Garrett. 1968. A system for expressing net energy requirements and feed values for growing and finishing beef cattle. Journal of Animal Science 27: 793-806.

Longworth, J. W. 1983. Beef in japan: Politics, production, marketing & trade. University of Queensland Press.

Low, W. A., R. L. Tweedie, C. B. H. Edwards, R. M. Hodder, K. W. J. Malafant, and R. B. Cunningham. 1981a. Detailed analysis of sequential behaviour patterns and integrated discussion. Appl. Anim. Ethol. 7: 39-56.

Low, W. A., R. L. Tweedie, C. B. H. Edwards, R. M. Hodder, K. W. J. Malafant, and R. B. Cunningham. 1981b. The influence of environment on daily maintenance behaviour of free-ranging shorthorn cows in central australia. I. General introduction and descriptive analysis of day-long activities. Applied Animal Ethology 7: 11-26.

Low, W. A., R. L. Tweedie, C. B. H. Edwards, R. M. Hodder, K. W. J. Malafant, and R. B. Cunningham. 1981c. Multivariate analysis of duration and incidence of activities Appl. Anim. Ethol. 7: 27–38.

Luiting, P. 1991. The value of feed consumption data for breeding in laying hens, Wageningen Agricultural University, The Netherlands.

Lunt, D. K., R. R. Riley, and S. B. Smith. 1993. Growth and carcass characteristics of angus and american wagyu steers. Meat Science 34: 327-334.

Martins, C. I. M., L. E. C. Conceicao, and J. W. Schrama. 2011. Feeding behavior and stress response explain individual differences in feed efficiency in juveniles of nile tilapia oreochromis niloticus. Aquaculture 312: 192-197.

Massey, J. 1993. The systems concept of beef production: Bif fact sheet g2037. University of missouri extension.

Matteri, R. L. 2001. Overview of central targets for appetite regulation. Journal of Animal Science 79: E148-E158.

May, S. G., J. W. Savell, D. K. Lunt, J. J. Wilson, J. C. Laurenz, and S. B. Smith. 1994. Evidence for preadipocyte proliferation during culture of subcutaneous and intramuscular adipose tissues from angus and wagyu crossbred steers. J Anim Sci 72: 3110-3117.

McBride, B. W., and L. P. Milligan. 1985. Influence of feed intake and starvation on the magnitude of na+,k+-atpase(ec 3.6.1.3)-dependent respiration in duodenal mucosa of sheep. Br J Nutr 53: 605-614.

Miller, A. J., D. B. Faulkner, R. K. Knipe, D. R. Strohbehn, D. F. Parrett, and L. L. Berger. 2001. Critical control points for profitability in the cow-calf enterprise. The Professional Animal Scientist 17: 295-302.

Miller, M. F., H. R. Cross, D. K. Lunt, and S. B. Smith. 1991. Lipogenesis in acute and 48-hour cultures of bovine intramuscular and subcutaneous adipose tissue explants. J Anim Sci 69: 162-170.

Milligan, L. P., and B. W. McBride. 1985. Energy costs of ion pumping by animal tissues. The Journal of Nutrition 115: 1374-1382.

Mir, P. S., D. R. C. Bailey, Z. Mir, T. Entz, S. D. M. Jones, W. M. R. Tson, R. J. Weselake, and F. J. Lozeman. 1999. Growth, carcass and meat quality characteristics of beef cattle with 0, 50 and 75 percent wagyu genetic influence. Canadian Journal of Animal Science 79: 129-137.

Moberg, G., and J. Mench. 2000. The biology of animal stress: Basic principles and implications for animals welfare. CAB International, New York.

Moe, P. W., H. F. Tyrrell, and W. P. Flatt. 1971. Energetics of body tissue mobilization. J. Dairy Sci.: 548-553.

Montague, C. T., J. B. Prins, L. Sanders, J. E. Digby, and S. O' Rahilly. 1997. Depot- and sex-specific differences in human leptin leptin mrna expression: Implications for the control of regional fat distribution. Diabetes 46: 342-347.

Montaldo, H. H., and C. A. Meza-Herrera. 1998. Use of molecular markers in major genes in the genetic improvement of livestock. Elect. J. Biotech.

Montanholi, Y. R., K. C. Swanson, R. Palme, F. S. Schenkel, B. W. McBride, D. Lu, and S. P. Miller. 2010. Assessing feed efficiency in beef steers through feeding behavior, infrared thermography and glucocorticoids. animal 4: 692-701.

Moore, S. S., F. D. Mujibi, and E. L. Sherman. 2009. Molecular basis for residual feed intake in beef cattle. J Anim Sci 87: E41-47.

Morrison, C. D., J. A. Daniel, B. J. Holmberg, J. Djiane, N. Raver, A. Gertler, and D. H. Keisler. 2001. Central infusion of leptin into well-fed and undernourished ewe lambs: Effects on feed intake and serum concentrations of growth hormone and luteinizing hormone. Journal of Endocrinology 168: 317-324.

Mujibi, F. D. N., S. S. Moore, D. J. Nkrumah, Z. Wang, and J. A. Basarab. 2010. Season of testing and its effect on feed intake and efficiency in growing beef cattle. Journal of Animal Science 88: 3789-3799.

Namikawa, K. 1992. Breeding history of japanese beef cattle and preservation of genetic resources as economic farm animals: Wagyu. . Wagyu Registry Association, Kyoto, Japan. .

Niesler, C. U., J. B. Prins, S. O' Rahilly, K. Siddle, and C. T. Montague. 2001. Adipose depot-specific expression of ciap2 in human preadipocytes and modulation of expression by serum factos and tnfa. International Journal of Obesity 25: 1027-1033.

Nkrumah, J. D., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, D. H. Crews, Jr., and S. S. Moore. 2007a. Genetic and phenotypic relationships of feed intake and measures of efficiency with growth and carcass merit of beef cattle. J Anim Sci 85: 2711-2720.

Nkrumah, J. D., D. H. Crews, Jr., J. A. Basarab, M. A. Price, E. K. Okine, Z. Wang, C. Li, and S. S. Moore. 2007b. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J Anim Sci 85: 2382-2390.

Nkrumah, J. D., D. H. Keisler, D. H. Crews, Jr., J. A. Basarab, Z. Wang, C. Li, M. A. Price, E. K. Okine, and S. S. Moore. 2007c. Genetic and phenotypic relationships of serum leptin concentration with performance, efficiency of gain, and carcass merit of feedlot cattle. J Anim Sci 85: 2147-2155.

NRC (Editor), 2000. Nutrient requirements of beef cattle: Update 2000 National Academy Press, Washington, DC.

Obata, T., Takeda, H., Satoh, M., Wada, Y. . 1996. Progress in breeding techniques for effective beef cattle production in japan. . JARQ 30: 203-211.

Okanishi, T., M. Shojo, T. Katsuta, K. Oyama, and F. Mukai. 2008. Genetic analysis of residual feed intakes and other performance test traits of japanese black cattle from revised protocol. Animal Science Journal 79: 291-296.

Palsson, H. 1955. Conformation and body composition Progress in the physiology of farm animals No. II, Butterworths, London.

Pethick, D. W. D. S., D.N.; Dunshea, F.R.; Harper, G.S. 2005. Fat metabolism and regional distribution in ruminants and pigs - influences of genetics and nutrition Recent Advances in Animal Nutrition in Austrailia. p 39. University of New England Publications Unit, University of New England, Armidale, NSW.

Phipps, R. H., J. A. Bines, and A. Cooper. 1983. A preliminary study to compare individual feeding through calan electronic feeding gates to group feeding. Anim. Prod. (Abstr.) 36.

Polak, J. M., Bloom, S.R., Rayford, P.L., Pearse, A.G., Buchan, A.M., Thompson, J.C. 1977. Identification of cholecystokinin-secreting cells. Lancet 2: 1016.

Prawl, Z. I., W. J. Hill, F. N. Owens, D. R. Gill, R. L. Ball and R. Porter. . 1997. Effects of limited access time to feed on feedlot performance and carcass characteristics. J. Anim. Sci. 75 (Suppl 1): 239.

Provenza, F. D. 1997 Feeding behavior of herbivores in response to plant toxicants. Handbook of Plant and Fungal Toxicants. : 231–242.

Pugh, A. K., B. McIntyre, D. W. Pethick, and G. Tudor. 2005. Understanding the effect of gender and age on the pattern of fat deposition in cattle. In: J. F. Hocquette and S. Gigli (eds.) Indicators of milk and beef quality. p 405-408. Wageningen Academic Publishers, Wageningen, Netherlands.

Radunz, A. E., S. C. Loerch, G. D. Lowe, F. L. Fluharty, and H. N. Zerby. 2009. Effect of wagyu- versus angus-sired calves on feedlot performance, carcass characteristics, and tenderness. Journal of Animal Science 87: 2971-2976.

Reidelberger, R. D. 1994. Cholecystokinin and control of food intake. The Journal of Nutrition 124: 1327S-1333S.

Reidelberger, R. D., and M. F. O'Rourke. 1989. Potent cholecystokinin antagonist l 364718 stimulates food intake in rats. American Journal of Physiology - Regulatory, Integrative and Comparative Physiology 257: R1512-R1518.

Richardson, E. C., and R. M. Herd. 2004. Biological basis for variation in residual feed intake in beef cattle. 2. Synthesis of results following divergent selection. Australian Journal of Experimental Agriculture 44: 431-440.

Richardson, E. C., R. M. Herd, J. A. Archer, and P. F. Arthur. 2004. Metabolic differences in angus steers divergently selected for residual feed intake. Australian Journal of Experimental Agriculture 44: 441-452.

Richardson, E. C., R. M. Herd, J. A. Archer, R. T. Woodgate, and P. F. Arthur. 1998. Steers bred for improved net feed efficiency eat less for the same feedlot performance. Animal Production in Australia. Proceedings of the Australian Society of Animal Production 22: 213-216.

Richardson, E. C., R. M. Herd, V. H. Oddy, J. M. Thompson, J. A. Archer, and P. F. Arthur. 2001. Body composition and implications for heat production of angus steer progeny of parents selected for and against residual feed intake. Australian Journal of Experimental Agriculture 41: 1065-1072.

Ritchie, H. D. 2000. Why is efficiency so important to the beef industry? Feedstuffs February 21: 12-27.

Robinson, D. L., and V. H. Oddy. 1999. Modelling feed intake and efficiency in feedlot cattle. 496-499.

Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. Livestock Production Science 90: 255-270.

Roche, J. R., A. J. Sheahan, L. M. Chagas, and R. C. Boston. 2008. Short communication: Change in plasma ghrelin in dairy cows following an intravenous glucose challenge. Journal of dairy science 91: 1005-1010.

Rolfe, D. F., and G. C. Brown. 1997. Cellular energy utilization and molecular origin of standard metabolic rate in mammals. Physiol Rev 77: 731-758.

Rousset, S., M.-C. Alves-Guerra, J. Mozo, B. Miroux, A.-M. Cassard-Doulcier, F. d. r. Bouillaud, and D. Ricquier. 2004. The biology of mitochondrial uncoupling proteins. Diabetes 53: S130-S135.

Samuels, B. A., and R. Hen. 2011. Novelty-suppressed feeding in the mouse # T mood and anxiety related phenotypes in mice. Neuromethods No. 63. p 107-121.

Sasaki, Y., T. Miyake, C. Gaillard, T. Oguni, M. Matsumoto, M. Ito, T. Kurahara, Y. Sasae, K. Fujinaka, S. Ohtagaki, and T. Dougo. 2006. Comparison of genetic gains per year for carcass traits among breeding programs in the japanese brown and the japanese black cattle. Journal of Animal Science 84: 317-323.

Schein, M. W., and M. H. Fohrman. 1955. Social dominance relationships in a herd of dairy cattle. The British Journal of Animal Behaviour 3: 45-55.

Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. Canadian Journal of Animal Science 84: 177-185.

Schick, R. R., G. J. Harty, T. L. Yaksh, and V. L. W. Go. 1990. Sites in the brain at which cholecystokinin octapeptide (cck-8) acts to suppress feeding in rats: A mapping study. Neuropharmacology 29: 109-118.

Schwartz, M. W., D. G. Baskin, T. R. Bukowski, J. L. Kuijper, D. Foster, G. Lasser, D. E. Prunkard, D. J. Porte, S. C. Woods, R. J. Seeley, and D. S. Weigle. 1996. Specificity of leptin action on elevated blood glucose levels and hypothalamic neuropeptide y gene expression in ob/ob mice. Diabetes 45: 531-535.

Schwartz, M. W., Woods, S. C., Porte, D. Jr, Seeley, R. J. & Baskin, D. G. . 2000. Central nervous system control of food intake. Nature 404: 661-671.

Schwartzkopf-Genswein, K. S., Beauchemin, K.A., Gibb, D.J., Crews, D.H., Jr., Hickman, D.D., et al. 2003. Effect of bunk management on feeding behavior, ruminal acidosis and performance of feedlot cattle: A review. Journal of Animal Science 81: E149-158.

Schwartzkopf-Genswein, K. S., S. Atwood, and T. A. McAllister. 2002. Relationships between bunk attendance, intake and performance of steers and heifers on varying feeding regimes. Applied Animal Behavioral Science 76: 179-188.

Shintani, M., Y. Ogawa, K. Ebihara, M. Aizawa-Abe, F. Miyanaga, K. Takaya, T. Hayashi, G. Inoue, K. Hosoda, M. Kojima, K. Kangawa, and K. Nakao. 2001. Ghrelin, an endogenous growth hormone secretagogue, is a novel orexigenic peptide that antagonizes leptin action through the activation of hypothalamic neuropeptide y/y1 receptor pathway. Diabetes 50: 227-232.

Short, R. E., and D. C. Adams. 1988. Nutritional and hormonal interrelationships in beef cattle reproduction. Canadian Journal of Animal Science 68: 29-39.

Stock, R. A., S. B. Laudert, W. W. Stroup, E. M. Larson, J. C. Parrott, and R. A. Britton. 1995. Effect of monensin and monensin and tylosin combination on feed intake variation of feedlot steers. Journal of Animal Science 73: 39-44.

Strain, G. M. 2004. Autonomic nervous system. In: H. H. Dukes and W. O. Reece (eds.) Dukes' physiology of domestic animals. Comstock Pub./Cornell University Press.

Stricklin, W. R., L. L. Wilson, and H. B. Graves. 1976. Feeding behavior of angus and charolais-angus cows during summer and winter. J. Anim. Sci. 43: 721-732.

Su, G., J. B. Kjaer, and P. Sorensen. 2006. Divergent selection on feather pecking behavior in laying hens has caused differences between lines in egg production, egg quality, and feed efficiency. Poultry Science 85: 191-197.

Sugino, T., Y. Hasegawa, Y. Kikkawa, J. Yamaura, M. Yamagishi, Y. Kurose, M. Kojima, K. Kangawa, and Y. Terashima. 2002. A transient ghrelin surge occurs just before feeding in a scheduled meal-fed sheep. Biochemical and Biophysical Research Communications 295: 255-260.

Tedeschi, L. O., D. G. Fox, M. J. Baker, and D. P. Kirschten. 2006. Identifying differences in feed efficiency among group-fed cattle. J Anim Sci 84: 767-776.

Tolkamp, B. J., D. J. Allcroft, E. J. Austin, B. L. Nielsen, and I. Kyriazakis. 1998. Satiety splits feeding behaviour into bouts. Journal of Theoretical Biology 194: 235-250.

Tolkamp, B. J., and I. Kyriazakis. 1999. A comparison of five methods that estimate meal criteria for cattle. Animal science (Penicuik, Scotland) 69: 501-514.

Trayhurn, P., and J. H. Beattie. 2001. Physiological role of adipose tissue: White adipose tissue as an endocrine and secretory organ. Proc Nutr Soc 60: 329-339.

Ueda, Y., A. Watanabe, M. Higuchi, H. Shingu, S. Kushibiki, and M. Shinoda. 2007. Effects of intramuscular fat deposition on the beef traits of japanese black steers (wagyu). Animal Science Journal 78: 189-194.

USDA. 2014. Informational memorandum: Pm-14-010, Kansas City, MO.

Val-Laillet, D., A. M. d. PassillÃ©, J. Rushen, and M. A. G. von Keyserlingk. 2008. The concept of social dominance and the social distribution of feeding-related displacements between cows. Applied Animal Behaviour Science 111: 158-172.

Valassi, E., M. Scacchi, and F. Cavagnini. 2008. Neuroendocrine control of food intake. Nutrition, Metabolism and Cardiovascular Diseases 18: 158-168.

Van der Walt, J. G. 1984. Herbivore nutrition in the sub-tropics and tropics. Science Press, South Africa.

Van Harmelen, V., A. Dicker, M. Ryden, H. Hauner, F. Lonnqvist, E. Naslund, and P. Arner. 2002. Increased lipolysis and decreased leptin production by human omental as compared with subcutaneous preadipocytes. Diabetes 51: 2029-2036.

Vernon, R. G., R. A. Clegg, and D. J. Flint. 1981. Metabolism of sheep adipose tissue during pregnancy and lactation. Adaptation and regulation. Biochem J 200: 307-314.

Vernon, R. G., R. G. P. Denis, and A. Sorensen. 2001. Signals of adiposity. Domestic Animal Endocrinology 21: 197-214.

Voisinet, B. D., T. Grandin, J.D. Tatum, S.F. O'Connor and J.J. Struthers. . 1997. Feedlot cattle with calm temperaments have higher average daily gains than cattle with excitable temperaments. . Journal of Animal Science 75: 892-896.

Wagnon, K. A. 1966 Social dominance in range cows and its effect on supplemental feeding. . Calif. Agric. Exp. Sta. Bull. # 819 1-32.

Warnick, V. D., C. W. Arave, and C. H. Mickelsen. 1977. Effects of group, individula, and isolated rearing of calves on weight gain and behavior. J. Dairy Sci. 60: 943-953.

Weary, D. M., J. M. Huzzey, and M. A. G. von Keyserlingk. 2009. Board-invited review: Using behavior to predict and identify ill health in animals. Journal of Animal Science 87: 770-777.

Wegner, J., P. Huff, C. P. Xie, F. Schneider, F. Teuscher, P. S. Mir, Z. Mir, E. C. Kazala, R. J. Weselake, and K. Ender. 2001. Relationship of plasma leptin concentration to intramuscular fat content in beef from crossbred wagyu cattle. Canadian Journal of Animal Science 81: 451-457.

Welch, C. M., J. K. Ahola, J. B. Hall, G. K. Murdoch, D. H. Crews, L. C. Davis, M. E. Doumit, W. J. Price, L. D. Keenan, and R. A. Hill. 2012. Relationships among performance, residual feed intake, and product quality of progeny from red angus sires divergent for maintenance energy epd. Journal of Animal Science 90: 5107-5117.

Wertz-Lutz, A. E., T. J. Knight, R. H. Pritchard, J. A. Daniel, J. A. Clapper, A. J. Smart, A. Trenkle, and D. C. Beitz. 2006. Bovine ghrelin fluctuates relative to nutritional status and influences feeding behavior. . Journal of Animal Science 84: 3285-3300.

Westcott, P. C. 2007. Ethanol expansion in the united states: How will the agricultural sector adjust? DIANE Publishing Company.

Wierenga, H. K. 1990. Social dominance in dairy cattle and the influences of housing and management. Applied Animal Behaviour Science 27: 201-229.

Zhang, H. H., S. Kumar, A. H. Barnett, and M. C. Eggo. 2001. Dexamethasone inhibits tumor necrosis factor-alpha-induced apoptosis and interleukin-1 beta release in human subcutaneous adipocytes and preadipocytes. J Clin Endocrinol Metab 86: 2817-2825.

Zurlo, F., K. Larson, C. Bogardus, and E. Ravussin. 1990. Skeletal muscle metabolism is a major determinant of resting energy expenditure. The Journal of Clinical Investigation 86: 1423-1427.

CHAPTER 2

Evaluation of Wagyu for Residual Feed Intake: Optimizing Feed Efficiency, Growth, and Marbling in Wagyu Cattle.

M. McGee[1], C.M. Welch[1], J.B. Hall[2], W. Small[3] and R.A. Hill[1]

[1]Department of Animal and Veterinary Science, University of Idaho, Moscow 83844;

[2]University of Idaho Nancy M. Cummings Research, Education, and Extension Center, Carmen, ID 83467;

[3]AB Genetics LLC, Boise, ID 83702

Professional Animal Scientist 2013 29:51-56

Abstract

Ninety-two yearling Wagyu bulls were evaluated for residual feed intake (**RFI**) and other performance variables during a 70-d testing period. Bulls were fed a diet in which ingredients were formulated to match the nutritional equivalent of the diet fed to finishing Wagyu cattle. Post RFI testing, bulls were classified into the following groups: efficient (RFI < 0.5 SD below the mean; n = 32), marginal (RFI ±0.5 SD of the mean; n = 34), and inefficient (RFI > 0.5 SD above the mean; n = 26). Residual feed intake was positively correlated with DMI ($r = 0.56$; $P < 0.01$) but was not correlated ($r < 0.10$) with ADG. Metabolic BW was not correlated ($r = 0.00$) with RFI. Intramuscular fat % (**IMF**) tended to be negatively correlated with RFI ($r = -0.17$, $P = 0.11$). Efficient, marginal and inefficient groups showed differences in gain:feed G:F ($P < 0.01$), and DMI ($P < 0.01$), but no differences were observed for metabolic BW or ADG ($P = 0.71$ and $P = 0.96$ respectively). Inefficient bulls had greater DMI ($P < 0.01$) than efficient bulls. Marginal bulls also had greater DMI ($P < 0.01$) than efficient bulls. All groups did not differ ($P > 0.05$) in ultrasound measures for rib fat, LM, area and IMF. No differences ($P > 0.05$) were observed between groups for the other

performance variables tested. Observations from the current study suggest that Wagyu sires that are superior for both feed efficiency and marbling can be identified with assistance from RFI analysis.

Introduction

Production systems in the beef cattle industry aim to produce high-quality beef. To this end, enhanced product quality attributes of tenderness, juiciness, and flavor are highly favored by exclusive restaurants, as well as the general consumers. Beef products from Japanese black cattle (Wagyu) are priced with a premium due to superior palatability, as well as exclusivity. Wagyu, as well as Wagyu-influenced cattle, have demonstrated superior marbling traits (Mir et al., 1999). Increased marbling has been associated with greater tenderness, and reduced cooking loss (Mitsumoto et al., 1992). Wagyu cattle are typically fed costly high-grain finishing diets which enhance their propensity to deposit intramuscular fat percentage (**IMF**) improving grade scores at harvest. Although marbling is increased, the literature reports that Wagyu cattle show inferior red meat yield and feedlot performance when compared to other breeds (Mir et al., 1999; Ueda et al., 2007). Due to this trade-off between quantity and quality, it is important to maximize profits by identifying feed efficient animals that also have high IMF and a desirable growth rate.

The incorporation of residual feed intake (**RFI**) evaluation along with IMF, growth, and feed intake measurements in identifying superior animals provides a possible approach to improve the profitability of Wagyu cattle. Residual feed intake is moderately heritable with values ranging from 0.16 to 0.43 (Herd et al., 2003). Residual feed intake has been researched extensively in British and continental breeds; however, only a few large scale evaluations of Wagyu or Wagyu-influenced cattle have been reported (Sasaki et al., 1982; Lejukole et al., 1993; Mukai et al., 1995; Oikawa et al., 2000; Shojo et al., 2005). The present study provides a quantitative phenotypic evaluation of yearling Wagyu bulls for RFI, ADG, DMI, growth, subcutaneous, and IMF deposition.

Materials and Methods

Procedures involving the use of animals in this study were approved by the University of Idaho Animal Care and Use Committee.

Animal Acquisition and Acclimation

Ninety-two yearling Wagyu bulls (starting BW 415 ± 55 kg; Age 474 ± 17 d) obtained from Snake River Farms (AgriBeef Co., 1555 Shoreline Drive, Boise, ID 83702) were transported to the University of Idaho Nancy M. Cummings Research Education and Extension Center (NMCREEC). Prior to delivery, animals were feed a diet similar to the one used during test period at a Snake River Farm facility. Post-arrival, all animals were allotted a 14 d adaptation period before to a standard 70 d post-weaning RFI test to normalize intake as well as acclimation to the GrowSafe system (GrowSafe Systems Ltd, Airdrie, Alberta, Canada). The Growsafe system at NMCREEC is composed of four (21.34 x 54.86m) bunks, with each pen containing 5 feeding nodes (Growsafe bunks). The pens are located outside without cover. Bulls were randomly allocated to 1 of 3 pens of the GrowSafe feed intake monitoring system. The 3 pens contained 30, 31, and 31 bulls at initiation of the adaptation period.

Feeding and Management Practices

Bulls were provided a diet (PerforMix Nutrition Systems, Nampa, Idaho 83687) formulated to match the nutritional equivalent of the diet fed to finishing Wagyu cattle (Tables 2.1 and 2.2). During the test period, the diet remained consistent with samples taken daily for DM as well as weekly composite samples for proximate analysis performed by a commercial laboratory (SDK Laboratories Hutchinson, KS 67504). Feed was mixed daily and provided in a single feeding to all animals to facilitate *ad libitum* feeding each morning between 08:00 and 10:00 h. At the beginning of the 70 d RFI test period, bulls were weighed on 2 consecutive days and again at the completion of the 70 d test period. Within the test period, bulls were weighed every 2 wks.

Ultrasound measurements

An independent technician performed ultrasound measurements for rib fat (**RF**) thickness, IMF, and LM recorded on d 0 and ~~d~~ 70 without hair removal between the 12th and 13th ribs. Ultrasounds images were captured by an Aloka 500ssd Scanner (Hitachi Aloka Medical, Ltd)

Statistical analysis

Analyses were conducted using SAS (Version 9.2, SAS Inst., Inc., Cary, NC). Residual feed intake was calculated as the difference between actual and predicted feed intake by regressing DMI on mid-test $BW^{0.75}$ and ADG (Koch et al., 1963) with the addition of RF thickness (Basarab et al., 2003) to the model. Thus, the final model for predicting RFI was:

$DMI = -0.2851 - 0.1134(ADG) + 0.1076(BW^{0.75}) – 0.5505(RF\ thickness).$

Correlations were calculated among growth efficiency, performance and ultrasound measurements via the CORR procedures of SAS (SAS Inst., Inc).

Post RFI test, bulls were classified into the following groups: efficient (RFI >0.5 SD below the mean; n = 32), marginal (RFI ±0.5 SD of the mean; n = 34), and inefficient (RFI >0.5 SD above the mean; n = 26). Least-square means were compared using the Studentized t-test.

Results and Discussion

Mean performance values for all bulls were: DMI, 10.35 kg/d, ADG, 1.39 kg/d; G:F 0.13kg/kg, $BW^{0.75}$, 102.96 kg, LM area, 86.46 cm^2 and IMF, 6.26% (Table 2.3).

Residual feed intake was not correlated with ADG ($r = 0.01$; $P = 0.91$; Figure 2.1 A).A positive correlation was observed between RFI and DMI ($r = 0.56$; $P < 0.0001$; Figure 2.1 B). RFI tended to be negatively correlated with IMF ($r = -0.17$, $P = 0.11$) in our test population (Table 2.4 and Figure 2.1 C). As expected, RFI was not correlated with RF thickness ($P = 0.80$; Figure 2.1 D), as RF thickness was included in the model to estimate RFI. Average daily gain and IMF were correlated ($r = -0.34$; $P < 0.01$; Figure 2.1 E). Longissimuss muscle area and IMF were negatively correlated ($r = -0.30$; $P = 0.004$; Figure 2.1 F). Metabolic body weight and RFI were not correlated (r

= -0.10; *P* = 0.33; Table 2.4). Residual feed intake was negatively correlated with G:F (r = -0.49; *P* <0.01; Table 2.4).

Performance traits were plotted to determine relationships within the study population (Figure 2.2). Traits chosen (RFI, ADG, and IMF) identify a population of efficient cattle that meet industry needs in terms of market demanded characteristics. To this end, a small group, encircled, represent animals that are highly desirable for all traits within the population of bulls used in this experiment (Figure 2.2).

Efficient, marginal, and inefficient RFI groups exhibited differences in G:F (*P* < 0.01) and DMI (*P* < 0.01), but no differences were observed for metabolic BW or ADG (*P* = 0.71 and P = 0.96 respectively; Table 2.5). Initial and final BW did not exhibit differences between RFI groups. The group classified as marginal had greater DMI (*P* < 0.01) than the efficient group. All classification categories of bulls showed similar (*P* > 0.05) ultrasound measures for initial and final analysis of RF thickness, LM area and IMF percentage. No differences were observed between the marginal group and the efficient or inefficient groups for other performance variables assessed.

In early experiments, a testing period of 112 d was cited as an industry standard for RFI determinations (Franklin, 1987). It was later estimated that a 70 d test period is suitable for accurate RFI measurements (Archer et al., 1997). As mentioned by Wang et al. (2006) the reduction of days on test would be cost efficient due to savings in management and feed costs.

Data from the current experiment show the correlation of RFI and ADG as approaching 0.00 which is consistent with previous experiments (Koch et al., 1963; Archer et al., 1997; Baker et al., 2006; Cruz et al., 2010). Thus, it can be inferred that RFI is independent of ADG, which potentially increases the value of RFI as part of a selection index.

Positive correlations of RFI and DMI have been previously reported in several British and continental breeds (Herd and Bishop, 2000; Arthur et al., 2001a; Arthur et al., 2001b; Herd et al., 2003; Schenkel et al., 2004). Additionally, experiments in cross-bred cattle similarly support this observation (Basarab et al., 2003; Nkrumah et al., 2004; 2007; Elzo et al., 2009). The current experiment also found a positive correlation (r = 0.56; *P* < 0.01) between RFI and DMI of Wagyu bulls.

The G:F ratio in the current experiment was negatively correlated (r = - 0.49; *P* < 0.01) with RFI as seen in similar studies for feed conversion ratio of British, continental, and crossbred cattle (Arthur et al., 2001a; 2001b; Basarab et al., 2003; Herd et al., 2003; Nkrumah et al., 2004; Schenkel et al., 2004; Nkrumah et al., 2007; Elzo et al., 2009). The current experiment also shows that this relationship is consistent in Wagyu cattle. Dry matter intake was greater in inefficient and marginal groups when compared to the efficient group in the current study. The efficient group of bulls showed superior G:F to the inefficient group (Table 2.5). Data ~~are~~ suggest that animals classified as efficient consume less feed, improving G:F, and produce similar BW gains to marginal and inefficient bulls. Baker et al. (2006) reported that low RFI steers (efficient) consumed less feed (DMI = 9.3kg/d) than high RFI steers (inefficient DMI = 10.3kg/d) with similar ADG in an experiment with purebred Angus steers, which is also consistent with data from other researchers (Basarab et al., 2003).

There was no correlation between RFI and LM area (r = -0.06, *P* = 0.54; Table 4). Importantly, these data provide a preliminary suggestion that the yield grade of Wagyu cattle is not antagonistic with RFI. Estimates of final RF thickness, LM area, and IMF were similar among efficiency groups, consistent with findings from previous studies of Cruz et al., (2010). It should be noted that in the present experiment, the model used to determine RFI included ultrasound RF thickness. This procedure accounts for variability in subcutaneous fat thickness between RFI groups. It is well accepted that about 5% of the total variation in RFI is attributable to differences in body composition (Richardson and Herd, 2004), with more efficient animals tending to be leaner. Richardson et al. (1998) also reported that in steers selected for RFI, there was no compromise in meeting carcass specifications for market demanded beef.

Robinson et al. (1999) and McDonagh et al. (2001) found a small positive correlation (r = 0.17) and no correlation, respectively, between RFI and IMF. Contrasting these experiments, Herd and Bishop (2000) reported negative correlations (r = - 0.22) between these 2 variables. Evidence of RFI and IMF correlations should be further investigated for use in Wagyu bull selection. The present experiment suggests a trend toward a favorable correlation between RFI and ultrasound IMF (r = -0.17, *P* = 0.11, Table 2.4). This observation is especially important in the context of the present study. It should be noted that RF thickness was included in the model to predict RFI. Data in previously mentioned studies are not adjusted for animal compositional variance. Thus, the variation observed in IMF the current experiment is independent of RF thickness and the favorable correlation between IMF and RFI is encouraging . Given the potential importance of this correlation as a possible favorable relationship, evaluation of additional Wagyu cattle will provide much needed clarification of the relationship between IMF and RFI. Experiments by Okanishi et al.(2008) noted the heritability of RFI in Wagyu cattle ranged from 0.10 to 0.33, higher than their observed estimates for feed conversion ratios. Estimated genetic correlations between IMF and RF thickness were low in an experiment conducted by Hoque et al. (2006) indicating the possibility of improving marbling while reducing subcutaneous fat in Wagyu cattle. Other studies have also reported a low negative correlation between IMF and FT ranging from -0.10 to -0.04 (Yang et al., 1985; Hoque et al., 2005) A study by Exton et at., (2004) reports examples of high yielding Angus bulls that had desirable estimated breeding values (EBV) for RFI and IMF. This observation has clear implications for selection of sires for generation of superior progeny for markets where improved feed efficiency as well as marbling are important. Exton et al. (2004) were able to identify bulls having both low RFI EBV values, and high IMF EBV values without accompanying changes in fat depth EBV in their experiment. These latter observations suggest that it should also be possible to identify Wagyu bulls that can sire progeny with lower RFI and yield carcasses with similar or even superior IMF.

The similarity of both initial and final ultrasound measures provide insight of generating marketable cattle without negating consumer priorities such as marbling. All groups had similar ultrasound performance, however, the efficient group had lessened DMI providing a profit benefit to producers. This provides insight that efficient Wagyu cattle (low RFI) can perform as well as inefficient (high RFI) animals in feedlot situations. Though general observations suggest that leaner animals are more efficient, in the current experiment, all animals performed with no significant differences in growth traits. To this end, the correlation found between RFI and IMF is slightly confounding. Between RFI groups within the current experiment, the efficient group was numerically (*P* = 0.15) higher (5.55 ± 1.08, IMF%) in IMF than marginal (5.19 ± 1.09, IMF%) and inefficient groupings (5.02 ± 0.94, IMF%). Though significant differences were not noted, further research with larger animal numbers may provide greater insight into this correlation. Initial RF thickness was also numerically (*P* = 0.80) higher in efficient animals. By the end of study, significances between final RF thickness was negated further (*P* = 0.69). Such data shows that all groupings were performing in a comparable manner. However, the data also suggests that efficient animals can provide a marketable product as well as their inefficient counterparts.

Feed efficiency is a plausible means to increase profitability in many beef cattle production systems. Due to rising feed costs, it is important to use animals that are highly efficient as well as producing the necessary carcass values for marketability. Research by Archer et al. (2004) estimates long-term improvement in profitability between 9% and 33% via use of efficient animals consuming less feed. Due to the small number of animals used in the present study, it is not possible to provide a meaningful genetic analysis. Wagyu cattle are well known for substantial marbling abilities and marketing for these cattle is based around this trait. However, the use of RFI as an added measure of feed efficiency could improve profitability of Wagyu beef production. A more complete genetic analysis incorporating additional animals will be required before selection strategies can be recommended. Experience indicates the dangers of single trait selection and it is strongly recommended that a multi-trait index approach is considered in order to optimize desired high IMF with balance for other performance and quality traits. Measures for market value (e.g. IMF, LM area, and RF thickness) should also be examined.

Implications

The present study shows that there is phenotypic variability of RFI within Wagyu bulls that may be useful for eventual consideration in a selection index. However, a full genetic analysis will be needed before this step can be recommended. There is a lack of research providing definitive answers towards the use of RFI as a possible component of a selection index for improved performance of Wagyu cattle. It is necessary to conduct further experiments that investigate detailed genotypic parameters of RFI in Wagyu cattle as well as extensive exploration of genetic correlations of RFI with IMF, and RFI with other performance measures.

Table 2.1. Dietary ingredients of test ration fed to Wagyu bulls

Ingredient	% as fed
Alfalfa Hay Early Bloom	21
Corn Grain Cracked	56
Distillers Grains	13
Rumax FL10*	10

Rumax FL10 Ingredients: corn soy blend, cane molasses, corn steep, ammonium polyphosphate, salt, limestone, Attaflow™, whey, water, fat, anhydrous ammonia, Deccox 6%™,zinc sulfate, manganese sulfate, copper sulfate, vitamin E premix 60%, selenium 4%, vitamin A 1000, cobalt sulfate EDDI (organic iodized salt), vitamin D3 500.

Table 2.2. Nutrient analysis of ration (DM basis)

Analysis	Unit of Measure	Value
DM	%	87.1
CP	%	15.2
NEm	Mcal/cwt	84.4
NEg	Mcal/cwt	57.4
Forage DM	%	22.0
ADF	%	11.1
NDF	%	19.9
Fat	%	4.3
Calcium	%	0.7
Phosphorus	%	0.5
Magnesium	%	0.2
Sulfur	%	0.2
Salt	%	0.7
Vit A	IU/kg	782.8
Vit D	IU/kg	78.3
Vit E	IU/kg	1.3
Zinc	Ppm	59.8
Copper	ppm	20.5
Selenium	ppm	0.4

Table 2.3. Mean performance traits and ultrasound measurements of Wagyu bulls

Traits	Mean	Stdev	Median	Minimum	Maximum
Initial BW, kg	413.83	56.04	408.01	307.99	639.57
Final BW, kg	483.54	63.54	472.64	364.69	736.63
DMI, kg/d	10.35	1.49	10.12	7.36	15.87
ADG, kg/d	1.39	0.30	1.35	0.79	2.30
RFI, kg/d	-	0.85	-0.02	-1.71	1.99
G:F, kg of gain/ kg of DM	0.13	0.02	0.13	0.08	0.19
Metabolic BW, kg of BW $^{0.75}$	102.96	10.02	101.37	83.45	141.40
Initial LM area cm^2	67.45	7.74	66.26	52.90	97.81
Final LM area cm^2	86.46	9.57	85.81	65.16	119.36
Initial RF Thickness cm	0.42	0.09	0.41	0.23	0.64
Final RF Thickness cm	0.56	0.16	0.53	0.33	1.09
Initial IMF, %	5.72	1.06	5.16	3.48	8.26
Final IMF, %	6.26	1.25	6.18	3.88	10.84

RFI[1] = residual feed intake
IMF[2] = percentage of intramuscular fat measurement via ultrasound

Table 2.4. Partial Correlations (*P*–values) of residual feed intake (RFI) with other performance measures in Wagyu bulls.

Trait	RFI
ADG, kg/d	0.01 (0.91)
DMI, kg/d	0.56 (< 0.01)
RFI[1], kg/d	-
G:F, kg of gain/ kg of DM	-0.49 (<0.01)
Metabolic BW, kg of BW $^{0.75}$	-0.10 (0.33)
RF Thickness, cm	-0.17 (0.11)
LM area, cm^2	-0.06 (0.54)
IMF[2], %	-0.17(0.11)

RFI[1] = residual feed intake
IMF[2] = percentage of intramuscular fat measurement via ultrasound

Table 2.5. Relationship of residual feed intake (RFI, kg of DM/d) of Wagyu bulls (n = 92) with performance measures (least squares means ± SE).[1]

	RFI Classification			
	Efficient	Marginal	Inefficient	*P*-value
No. of bulls	32	34	26	
Initial BW, kg	422 ± 47.3	404 ± 58.1	417 ± 63.1	0.41
Final BW, kg	490 ± 55.2	477 ± 66.4	484 ± 70.8	0.73
Metabolic BW, kg of BW $^{0.75}$	104 ± 1.78	102 ± 1.73	103 ± 1.98	0.71
DMI, kg/d	9.51 ± 0.23^{a}	10.3 ± 0.22^{ab}	11.4 ± 0.25^{b}	<0.01
ADG, kg/d	1.38 ± 0.05	1.40 ± 0.05	1.39 ± 0.06	0.96
RFI, kg/d	-0.90 ± 0.06	0.02 ± 0.06	1.07 ± 0.07	<0.01
G:F, kg of gain/ kg of DM	0.14 ± 0.02^{a}	0.14 ± 0.02^{ab}	0.12 ± 0.02^{b}	<0.01
Initial RF, cm	0.44 ± 0.09	0.39 ± 0.09	0.43 ± 0.09	0.80
Final RF, cm	0.58 ± 0.16	0.54 ± 0.15	0.57 ± 0.17	0.69
Initial LM area, cm^2	66.7 ± 7.49	67.3 ± 6.94	68.6 ± 8.22	0.61
Final LM area, cm^2	86.8 ± 9.35	86.4 ± 9.88	86.2 ± 9.80	0.97
Initial IMF%	5.55 ± 1.08	5.19 ± 1.09	5.02 ± 0.94	0.15
Final IMF%	6.47 ± 1.17	6.28 ± 1.45	5.98 ± 1.04	0.34

[a,b] Means within a row lacking a common superscript letter differ ($P < 0.05$).

[1] Bulls are classified into groups as: efficient (RFI < 0.5 SD below the mean; n = 32), marginal (RFI ± 0.5 SD mean; n = 34), and inefficient (RFI > 0.5 SD above the mean; n = 26)

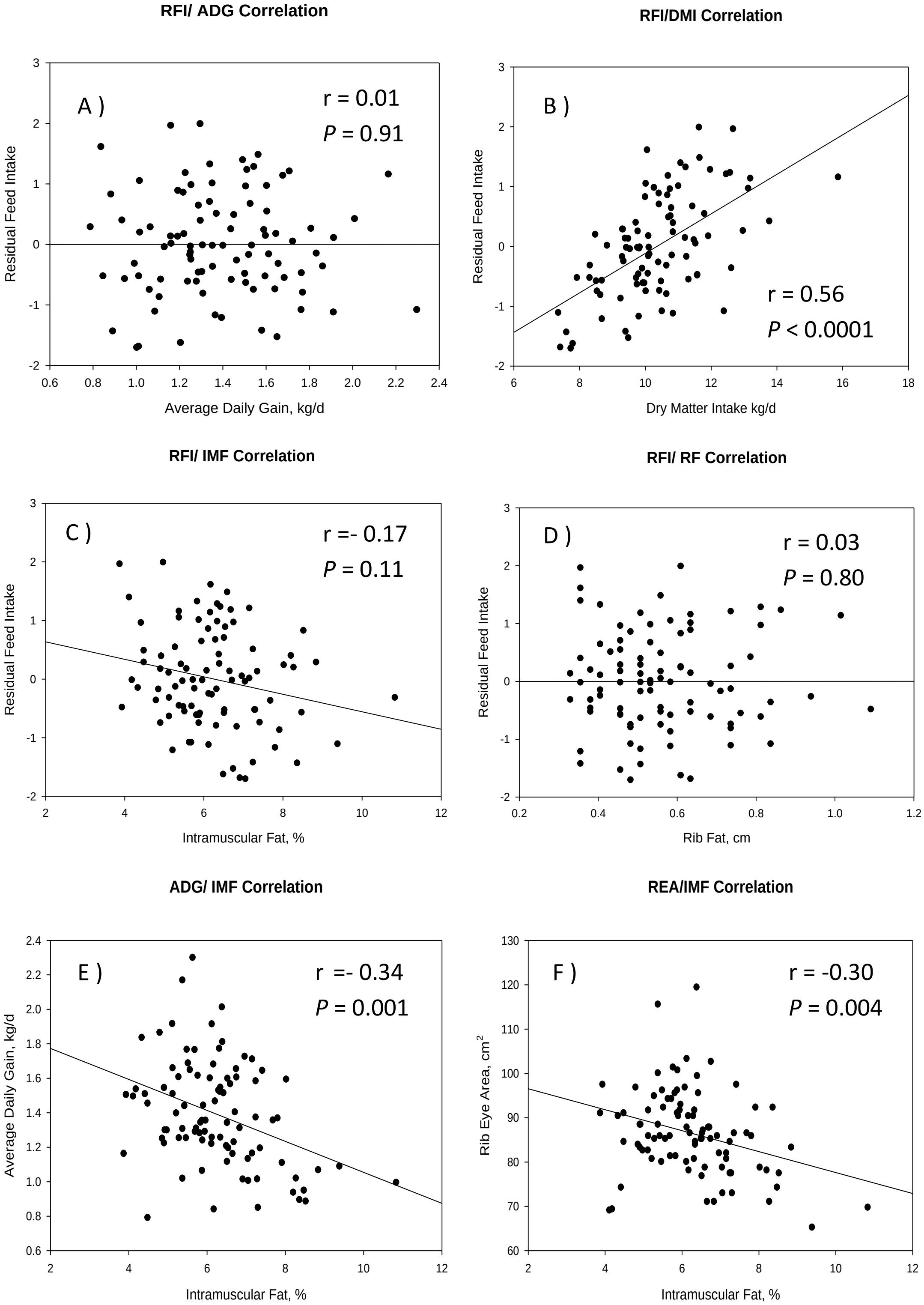

Figure 2.1. Correlations of Wagyu performance traits : A) Residual feed intake (RFI) with ADG, B) RFI with dry matter intake

(DMI), C) RFI with percent intramuscular fat via ultrasound (IMF), D) RFI with rib fat (RF) thickness, E) ADG with IMF, F) LM area with IMF.

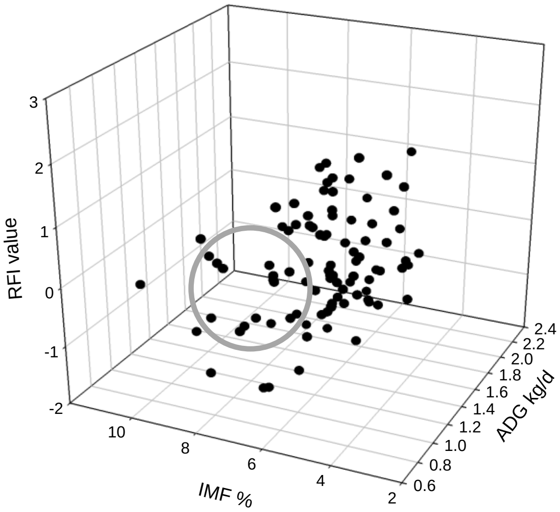

Figure 2.2. Relationships of desirable Wagyu performance traits

Literature cited

Archer, J. A., P. F. Arthur, R. M. Herd, P. F. Parnell, and W. S. Pitchford. 1997. Optimum postweaning test for measurement of growth rate, feed intake, and feed efficiency in british breed cattle. Journal of Animal Science 75: 2024-2032.

Archer, J. A., S. A. Barwick, and H. U. Graser. 2004. Economic evaluation of beef cattle breeding schemes incorporating performance testing of young bulls for feed intake. Australian Journal of Experimental Agriculture 44: 393-404.

Arthur, P. F., J. A. Archer, D. J. Johnston, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001a. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency, and other postweaning traits in angus cattle. Journal of Animal Science 79: 2805-2811.

Arthur, P. F., G. Renand, and D. Krauss. 2001b. Genetic parameters for growth and feed efficiency in weaner versus yearling charolais bulls. Australian Journal of Agricultural Research 52: 471-476.

Baker, S. D., J. I. Szasz, T. A. Klein, P. S. Kuber, C. W. Hunt, J. B. Glaze, Jr., D. Falk, R. Richard, J. C. Miller, R. A. Battaglia, and R. A. Hill. 2006. Residual feed intake of purebred angus steers: Effects on meat quality and palatability. J Anim Sci 84: 938-945.

Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Canadian Journal of Animal Science 83: 189-204.

Cruz, G. D., J. A. RodrÃguez-SÃ¡nchez, J. W. Oltjen, and R. D. Sainz. 2010. Performance, residual feed intake, digestibility, carcass traits, and profitability of angus-hereford steers housed in individual or group pens. Journal of Animal Science 88: 324 - 329.

Elzo, M. A., D. G. Riley, G. R. Hansen, D. D. Johnson, R. O. Myer, S. W. Coleman, C. C. Chase, J. G. Wasdin, and J. D. Driver. 2009. Effect of breed composition on phenotypic residual feed intake and growth in angus, brahman, and angus x brahman crossbred cattle. Journal of Animal Science 87: 3877-3886.

Exton, S. C., R. M. Herd, and P. F. Arthur. 2004. Identifying bulls superior for net feed intake, intramuscular fat and subcutaneous fat. Animal Production in Australia 25: 57-60.

Franklin, C. L. 1987. Factors affecting gain of beef bulls consigned to a central test station. . West Virginia University, Morgantown, W.Va.

Herd, R. M., J. A. Archer, and P. F. Arthur. 2003. Reducing the cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application. Journal of Animal Science 81(E Suppl. 1): E9-E17.

Herd, R. M., and S. C. Bishop. 2000. Genetic variation in residual feed intake and its association with other production traits in british hereford cattle. Livestock Production Science 63: 111-119.

Hoque, M. A., P. F. Arthur, K. Hiramoto, and T. Oikawa. 2006. Genetic relationship between different measures of feed efficiency and its component traits in japanese black (wagyu) bulls. Livestock Science 99: 111-118.

Hoque, M. A., K. Hiramoto, and T. Oikawa. 2005. Genetic relationship of feed efficiency traits of bulls with growth and carcass traits of their progeny for japanese black (wagyu) cattle. Animal Science Journal 76: 107-114.

Koch, R. M., D. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. Journal of Animal Science 22: 486-494.

Lejukole, H., R. Sakuma, K. Moriya, and Y. Sasaki. 1993. Restricted maximum likelihood estimation of heritabilities for growth and feed utilization traits in japanese black using performance-test records. Animal Science and Technology 64: 659-668.

McDonagh, M. B., R. M. Herd, E. C. Richardson, V. H. Oddy, J. A. Archer, and P. F. Arthur. 2001. Meat quality and the calpain system of feedlot steers following a single generation of divergent selection for residual feed intake. Australian Journal of Experimental Agriculture 41: 1013-1021.

Mir, P. S., D. R. C. Bailey, Z. Mir, T. Entz, S. D. M. Jones, W. M. R. Tson, R. J. Weselake, and F. J. Lozeman. 1999. Growth, carcass and meat quality characteristics of beef cattle with 0, 50 and 75 percent wagyu genetic influence. Canadian Journal of Animal Science 79: 129-137.

Mitsumoto, M., T. Mitsuhashi, and S. Ozawa. 1992. Influence of slaughter weight, sire, concentrate feeding and muscle on the physical and chemical characteristics in japanese black beef. Asian-Australasian Journal of Animal Sciences 5: 629.

Mukai, F., K. Oyama, and S. Kohno. 1995. Genetic relationships between performance test traits and field carcass traits in japanese black cattle. 44: 199-205.

Nkrumah, J. D., J. A. Basarab, M. A. Price, E. K. Okine, A. Ammoura, S. Guercio, C. Hansen, C. Li, B. Benkel, B. Murdoch, and S. S. Moore. 2004. Different measures of energetic efficiency and their phenotypic relationships with growth, feed intake, and ultrasound and carcass merit in hybrid cattle. J Anim Sci 82: 2451-2459.

Nkrumah, J. D., D. H. Crews, Jr., J. A. Basarab, M. A. Price, E. K. Okine, Z. Wang, C. Li, and S. S. Moore. 2007. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J Anim Sci 85: 2382-2390.

Oikawa, T., T. Sanehira, K. Sato, Y. Mizoguchi, H. Yamamoto, and M. Bada. 2000. Genetic parameters for growth and carcass traits of japanese black (wagyu) cattle. Animal Science 71: 59–64.

Okanishi, T., M. Shojo, T. Katsuta, K. Oyama, and F. Mukai. 2008. Genetic analysis of residual feed intakes and other performance test traits of japanese black cattle from revised protocol. Animal Science Journal 79: 291-296.

Richardson, E. C., R. M. Herd, J. A. Archer, R. T. Woodgate, and P. F. Arthur. 1998. Steers bred for improved net feed efficiency eat less for the same feedlot performance. Animal Production in Australia. Proceedings of the Australian Society of Animal Production 22: 213-216.

Robinson, D. L., V. H. Oddy, and C. Smith. 1999. Preliminary genetic parameters for feed intake and efficiency in feedlot cattle. In: Proceedings of the Thirteenth Conference Association for the Advancement of Animal Breeding and Genetics. p 492-495.

Sasaki, Y., H. Iwaisaki, T. Mansuno, and S. Asoh. 1982. Interaction of sire × length of testing period and estimation of genetic parameters for performance testing traits of japanese black bulls. Journal of Animal Science 55: 771-779.

Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed differences for feed efficiency, growth, and body composition traits of young beef bulls. Canadian Journal of Animal Science 84: 177-185.

Shojo, M., J. Yong, K. Anada, K. Oyama, and F. Mukai. 2005. Estimation of genetic parameters for growth and feed utilization traits in japanese black cattle. Animal Science Journal 76: 115-119.

Ueda, Y., A. Watanabe, M. Higuchi, H. Shingu, S. Kushibiki, and M. Shinoda. 2007. Effects of intramuscular fat deposition on the beef traits of japanese black steers (wagyu). Animal Science Journal 78: 189-194.

Wang, Z., J. D. Nkrumah, C. Li, J. A. Basarab, L. A. Goonewardene, E. K. Okine, D. H. Crews, Jr., and S. S. Moore. 2006. Test duration for growth, feed intake, and feed efficiency in beef cattle using the growsafe system. J Anim Sci 84: 2289-2298.

Yang, M., Y. Sasaki, and F. Mukai. 1985. Estimation of heritabilities for growth and carcass traits and their genetic and phenotypic correlations in japanese black cattle. Japanese Journal of Zootechnical Science 56: 193-198.

CHAPTER 3

Feeding behavior and efficiency in Wagyu cattle; Relationships of feeding behaviors with efficiency in RFI-divergent Japanese Black cattle[1]

M. McGee*, J.A. Ramirez‡, G.E. Carstens‡, W.J. Price†, J.B. Hall**, and R.A. Hill*[2]

*Department of Animal and Veterinary Science, University of Idaho, Moscow 83844;

**Department of Animal Science, Texas A&M University, College Station, TX, 77843

†Statistical Programs, University of Idaho, Moscow, Idaho 83844

**University of Idaho Nancy M. Cummings Research, Education, and Extension Center, Carmen, ID 83467

Journal of Animal Science (June 19th 2014 Jas.2013-7360)

Abstract

New approaches to limit expenses associated with input, without compromising profit are needed in the beef industry. Residual feed intake (RFI) is an efficiency trait that measures variation in feed intake beyond maintenance, growth, and body composition. The addition of feeding behavior analysis to standard RFI tests may provide an approach to more readily identify feed efficient cattle. The current study analyzes 7 feeding behaviors (BVFREQ: bunk visit frequency, BVDUR: bunk visit duration, FBFREQ: feed bout frequency, FBDUR: feed bout duration, MFREQ: meal frequency, MDUR: meal duration, and AMINT: average meal intake) and their relationships with RFI, ADG, and DMI in Japanese Black (Wagyu) cattle. Three cohorts of yearling Wagyu animals were studied using a standard 70d RFI test and data from divergent (±0.5 SD from population RFI mean) subsets of animals were analyzed for feeding behaviors (n= 58 bulls on high concentrate diet (C1), n= 36, bulls on a lower concentrate diet (C2), n = 34 heifers on a lower concentrate diet (C3)).

The following behaviors were correlated with ADG: BVFREQ (r = 0.32, $P = 0.01$; C1 bulls), BVDUR (r = 0.42, $P = 0.01$, C2 bulls), FBFREQ (r = 0.37, $P < 0.01$; C1 bulls), FBDUR (r = 0.46, $P < 0.01$, C1 bulls), and MFREQ (r = 0.42, $P < 0.01$, C2 bulls). Behaviors were trending or significantly correlated with DMI for all cases except for MFREQ for C3 and AMINT for C2. Residual feed intake was positively correlated with MDUR across all cohorts (r =0.31, $P = 0.02$; r = 0.38, $P = 0.02$; r = 0.54, $P \leq 0.01$, respectively). For C2 bulls and C3 heifers, RFI was positively correlated with behavior frequency categories (BVFREQ; r = 0.44, $P = 0.01$; r = 0.60, $P \leq 0.01$, respectively and FBFREQ r = 0.46, $P \leq 0.01$; r = 0.60, $P \leq 0.01$, respectively). Bunk visit frequency and FBFREQ were highly correlated with RFI status (high or low) in C2 bulls and C3 heifers. Behavior duration categories (BVDUR FBDUR and MDUR) were most correlated with efficiency status in C1 bulls. However, behavior frequency categories (BVFREQ and FBFREQ), as well as MDUR were most correlated with efficiency status in C2 bulls and C3 heifers. Inclusion of meal duration measurements when evaluating RFI provides an additional tool in understanding the drivers of variation in this important trait in Wagyu cattle. The present study provides new insights into feed intake patterns of a beef breed for which there are few reports of feeding behavior.

Introduction

A review of literature shows that feed cost is one of the largest variable expenses in livestock production (Archer et al., 1999; Miller et al., 2001; Basarab et al., 2007; Lancaster et al., 2008). Thus, there is a great need to develop approaches to limit expenses associated with input, without compromising profit margin. Output associated traits (i.e. F:G and ADG) fail to accurately reflect efficiency due to increased feed costs associated with higher rates of gain (Lancaster et al., 2009). This suggests focus should be placed on input traits that reduce feed costs without compromising other production traits or product quality (Baker et al., 2006). Residual feed intake (**RFI**) is an efficiency trait that measures variation in feed intake beyond that driven by maintenance, growth, and body composition. Advances utilizing radio-frequency identification (**RFID**) technology allows measurement of individual animal intake and in addition individual animal feeding behavior patterns can be quantified. Feeding behavior has been the focus of some research over the past several years (Weary et al., 2009). Previously, Richardson and Herd (2004) noted that feeding patterns account for only 2% of variation in RFI. However, a more recent report (Lancaster et al., 2009) notes that variation in feeding behavior can account for as much as 35% of differences in animal performance and ultrasound traits. Knowing this, the contributing role of variation in feeding behavior within feed efficiency is unclear. The current study aims to provide insight of these relationships in Japanese Black cattle (Wagyu).

Materials and methods

Procedures involving the use of animals in this study were approved by the University of Idaho Animal Care and Use Committee (2010-52) as required by federal law and University of Idaho policy.

Animals and Adaptation for RFI Analysis

Three cohorts of animals were examined during this experiment. All behavioral analyses were performed post RFI determination. Cohort 1 (C1; evaluated summer 2010) consisted of 92 yearling Wagyu bulls (initial BW: 415 ± 55 kg; age 474 ± 17 d). Cohort 2 (C2; evaluated summer 2012) consisted of 60 yearling Wagyu bulls (initial BW: 360.82 ± 40.97 kg; age: 423 ± 13 d). Cohort 3 (C3; evaluated summer 2012) consisted of 45 yearling Wagyu heifers (initial BW: 295.56 ± 26.79 kg; age: 433 ± 10 d).

All animals were sourced from Snake River Farms (AgriBeef Co., 1555 Shoreline Drive, Boise, ID 83702) and transported to the University of Idaho Nancy M. Cummings Research Education and Extension Center (NMCREEC). Prior to delivery, each cohort was provided a diet nutritionally similar to that offered to finishing phase animals at the Snake River Farm facility. Post-arrival, all animals were allotted a 14 d adaptation period prior to a standard 70 d post-weaning RFI test to normalize intake as well as acclimation to the GrowSafe system (GrowSafe Systems Ltd, Airdrie, Alberta, Canada,). The GrowSafe system at NMCREEC is composed of four (21.34 x 54.86m) pens, with each pen containing 5 feeding nodes. The pens are located outside without cover. Animals were randomly allocated within sex to 1 of 4 pens of the GrowSafe feed intake monitoring system.

Feeding and Management Practices

Diets were formulated by PerforMix Nutrition Systems (Nampa, Idaho 83687) such that C1 animals received a diet nutritionally equivalent to that fed to finishing Wagyu cattle, and C2 and C3 animals received a diet based on the C1 diet with increased roughage and decreased concentrate percentages (Table 1). During testing within cohort, the diet remained consistent and samples were collected routinely for daily DM and weekly composite samples. The latter were shipped to a commercial laboratory for proximate analysis (SDK Laboratories Hutchinson, KS 67504). Daily feed delivery was provided in a single feeding to C1; however due to the increased roughage percentage, feed was delivered twice daily for C2 and C3 animals. All feeding was managed to facilitate ad libitum access with bunks managed to contain no less than 10% of feed delivered. Feeding was scheduled between 08:00 and 10:00 h for all cohorts with subsequent feedings between 14:00 and 15:00 h for C2 and C3. All animals were weighed 2 consecutive days at initiation and completion of 70 d test periods. Within test period, animals were weighed every 2 wk. Ultrasound procedures were performed for live animal characteristics by an independent technician. Ultrasound measurements included rib fat (**RF**) thickness, intramuscular fat (**IMF**), and LM area. Measurements were performed on d 0 and 70 between the 12th and 13th ribs. All images were captured by an Aloka 500ssd Scanner (Hitachi Aloka Medical, Ltd.). Residual feed intake was calculated separately for each cohort. Post RFI test, all animals were classified into the following groups: efficient (RFI > 0.5 SD below the mean), marginal (RFI ± 0.5 SD of the mean), and inefficient (RFI > 0.5 SD above the mean).

Feeding Behavior Analysis

Behaviors analyzed were: bunk visit frequency (**BVFREQ**: transponder readings for a single animal entering a feed bunk) and bunk visit duration (**BVDUR**: time during transponder readings with animal at a bunk; ending when there were no readings for > 300 s). Feed bout behaviors were: feed bout frequency (**FBFREQ**: transponder readings for a single animal entering a feed bunk and consuming feed) and feed bout duration (**FBDUR**: time during transponder reading with animal at a bunk consuming feed; ending when there were no readings for > 300s). Meal data included 3 behavior measurements: meal frequency (**MFREQ**: cluster of feed bouts in which the non-feeding event was shorter than meal criterion), meal duration (**MDUR**: time during transponder readings with animal at a bunk consuming feed per meal), and average meal intake (**AMINT**: sum of feed event intakes during a meal). Cohort 1 RFI-divergent subsets consisted of 58 animals (efficient: n = 32; inefficient n = 26; 64% of total population); C2 RFI-divergent subsets consisted of 36 animals (efficient: n = 17; inefficient: n = 19; 60% of total population); C3 RFI-divergent subsets consisted of 34 animals (efficient: n =17; inefficient n = 17; 75.5% of total population). All behaviors were analyzed for correlations with RFI, DMI, and ADG within cohort.

Statistical Analysis

Residual feed intake was calculated as the difference between actual and predicted feed intake by regressing DMI on mid-test $BW^{0.75}$ and ADG (Koch et al., 1963) with the addition of RF thickness (Basarab et al., 2003) to the model predicting DMI. The addition of feeding behavior to the base model used to predict DMI was performed using PROC REG procedures including Mallow’s C***p***.

Spearman correlation analysis was used to assess the association among and between feeding behavior responses and RFI values within each cohort subset. Analysis of variance (ANOVA) was used to discern the effects of RFI classifications (efficient and inefficient) on feeding behaviors assuming a completely random design.

Period effects (time periods within test) were also examined within cohort using a repeated measures ANOVA (Supplementary data). Each 70 day RFI study was split into four time-periods to examine changes in behavior by time-period between and within animal classifications. Time periods were not evenly split due to small variations in trial duration of some cohorts; however, with the greatest variation between period lengths being 2 d (Supplementary Table S1), hence, the differences were deemed negligible. Each cohort was analyzed independently.

Analyses were conducted using SAS (Version 9.2, SAS Inst., Inc., Cary, NC). All mean differences were assessed using pair-wise comparisons of least squares means. Significance was noted at the $P = 0.05$ level.

Results

Mean performance and behavior parameters of efficient and inefficient groups for cohorts C1, C2, and C3. Mean values of initial and final BW, ADG, IMF, and RF thickness within cohort were similar between efficiency groups ($P < 0.05$ for all cohorts, Table 2). As expected, DMI differed between efficiency groups within cohort ($P < 0.01$ for all cohorts).

Bunk visit frequency was significantly different between efficiency groups for all cohorts ($P = 0.05$, C1, $P = 0.04$, C2 and $P < 0.01$, C3), with efficient animals visiting the bunk less frequently than their inefficient counterparts. Bunk visit duration was significantly different between efficiency groups for C1 and C2 ($P = 0.03$ and 0.01, respectively) suggesting inefficient animals spent longer times at the bunk than efficient animals. For C3 heifers, efficient and inefficient groups did not differ in BVDUR ($P = 0.16$). Feed bout frequency was different between efficiency groups across all cohorts ($P = 0.04$, C1 $P = 0.03$, C2, $P < 0.01$, C3) with inefficient groups visiting the bunk and consuming feed more often than efficient groups. Feed bout duration followed a similar trend to BVDUR, differing between efficiency groups for C1 and C2 only ($P = 0.02$ and $P = 0.01$). For C3 heifers FBDUR was similar ($P = 0.18$). Meal frequency differed between divergent groups of C1 bulls ($P = 0.05$), but was similar for C2 bulls and C3 heifers ($P = 0.28$ and $P = 0.27$, respectively).

Meal duration tended to differ between efficiency groups for C1 bulls (*P* = 0.08), and was significantly different between efficiency groups for C2 and C3 (*P* = 0.01 and *P* < 0.01, respectively). Average meal intake was similar between efficiency groups across all cohorts (*P* = 0.15, C1, *P* = 0.73, C2, and *P* = 0.40, C3).

Correlations of Feeding Frequency Behaviors with ADG, DMI and RFI

All three frequency behaviors, BVFREQ, FBFREQ and MFREQ were correlated with ADG for C1 bulls (r = 0.32, *P* = 0.01, r = 0.37, *P* < 0.01, r = 0.42, P <0.01, respectively Table 3).

Behaviors BVFREQ, FBFREQ and MFREQ were also correlated with DMI for C1 bulls (r = 0.29, *P* = 0.03, r = 0.32, *P* = 0.03, r = 0.41, *P* =< 0.01, respectively) and BVFREQ showed a tendency for C2 bulls and C3 heifers (r = 0.32, *P* = 0.06, and r = 0.33, *P* = 0.06, respectively) while there was also a similar trend for MFREQ for C2 bulls only (r = 0.29, *P* = 0.09).

Bunk visit frequency was correlated with RFI for C2 bulls and C3 heifers (r = 0.44, *P* = 0.01, and r = 0.60, *P* <0.01) and showed a tendency for C1 bulls (r = 0.23, and *P* = 0.08). The relationship between FBFREQ and RFI recapitulated that between BVFREQ and RFI (Table 3) being almost identical in each case. Of the frequency behaviors, MFREQ was least correlated with RFI, showing a tendency for C1 bulls only (r = 0.24, *P* = 0.07).

Correlations of Feeding Duration Behaviors with ADG, DMI and RFI

Bunk visit duration was correlated with ADG for C2 bulls only (r = 0.42, *P* = 0.01), and this pattern was reflected for FBDUR also being correlated for C2 bulls (r = 0.46, *P* < 0.01). In addition FBDUR showed a similar tendency for C1 bulls (r = 0.23, *P* = 0.09).

Behavior BVDUR was correlated with DMI for both bull cohorts (r = 0.32, and *P* = 0.01, C1 and r = 0.56, *P* < 0.01, C2) and showed a tendency for C3 heifers (r = 0.33, *P* = 0.06). Behavior FBDUR and DMI were correlated for all cohorts (r = 0.36, *P* < 0.01, C1 r = 0.57, *P* < 0.01, C2 and r

= 0.34, *P* = 0.05, C3). However, MDUR and DMI were correlated for C2 bulls and C3 heifers (r = 0.41, *P* = 0.01, and r = 0.34, *P* = 0.05, respectively) and showed a tendency for C1 bulls (r = 0.22 *P* = 0.09).

Duration behaviors BVDUR and FBDUR were correlated with RFI for C1 bulls (r = 0.37, *P* <0.01, and r = 0.38, *P* < 0.01) and similarly showed a tendency for C2 bulls (r = 0.31, *P* = 0.06, and r = 0.31, *P* = 0.07, respectively). Of the three feeding duration behaviors, MDUR was most consistently correlated with RFI being significant for all cohorts (r = 0.31, *P* = 0.02, C1, r = 0.38, *P* = 0.02, C2 and r = 0.54, *P* < 0.01, C3).

Correlations of Behavior AMINT with ADG, DMI and RFI.

Average meal intake and DMI were correlated for C1 bulls and C3 heifers (r = 0.27, *P* = 0.04; and r = 0.41, *P* = 0.02, respectively). Average meal intake tended to be correlated with RFI for C1 bulls only (r = 0.25, *P* = 0.06).

Period Analysis of Feeding Behaviors.

Analyses of variation in behaviors by period within the standard 70 day RFI test are presented here and in the Supplementary Tables (S1, S2 and S3)

Cohort 1: Period effects were examined for differences between RFI classifications of C1 bulls and feeding behaviors over time (Supplementary Table S1). Bunk visit frequency during periods 1 and 2 of the 4-period trial were different (*P* = 0.03, 0.02 respectively) between C1 RFI-efficient and inefficient bulls and there was a similar trend during period 3 (*P* = 0.07). However by end of trial, period 4, there was no difference in BVFREQ between the 2 efficiency classifications (*P* = 0.15). Bunk visit duration during periods 1 and 2 of the 4-period trial were also different ($P \leq 0$ .01 for periods 1 and 2) between cohort 1 efficient and inefficient bulls. During the latter half of the study there were no differences of BVDUR between the 2 RFI groups (period 3, *P* = 0.13 and period 4, *P* = 0.25).

Feed bout analysis showed similar relationships to those shown for bunk visit, likely due to the close relationship between these 2 measures. Cohort 1 Wagyu bull RFI groups differed for FBFREQ for periods 1-3 (*P* = 0.04, 0.01, and 0.05 respectively). However, for period 4, FBFREQ was similar between groups (*P* = 0.14). Durations of feed bouts (FBDUR) were different between cohort1 RFI groups in the first 2 periods of the trial (*P* = 0.01 for both periods). For both periods 3 and 4 there were no differences between RFI groups (*P* = 0.11 and 0.24, respectively).

Meal data analysis across periods showed few differences between the C1 RFI groups. Average meal frequency was greater for RFI-inefficient groups within the first 3 periods of the study (*P* = 0.05, 0.01, 0.04, respectively). By period 4, RFI groups had similar meal frequencies (*P* = 0.18). Average meal duration for cohort 1 Wagyu bulls did not differ between RFI groups during any period of the study. During period 2 there was a trend (*P* = 0.08) to differ, however, for periods 1, 3, and 4 AMDUR was similar between efficiency classifications (*P* = 0.13, 0.16, and 0.16, respectively). Within behavior trait AMINT, there was tendency for C1 RFI-efficient animals to consume less during a meal within period 1 of the study (*P* = 0.06). For all other periods (periods 2-4) AMINT were similar between RFI groups (*P* = 0.22, 0.31 and 0.18, respectively).

Cohort 2: Period effects between divergent groups of C2 Wagyu bulls and feeding behaviors over time are presented in Supplementary Table S2. Efficiency groups differed in BVFREQ during periods 1, 2, and 4 (*P* = 0.04, 0.02, and 0.05 respectively). However, groups were similar for period 3 (*P* = 0.12). Bunk visit duration was different between cohort 2 RFI-efficiency groups in periods 1, 3, and 4 (*P* = 0.01, 0.04, and 0.01). During period 2, BVDUR showed a similar trend between groups (*P* = 0.10).

Feed bunk data for frequency and duration also show some differences between cohort 2 RFI-efficiency groups. Efficiency groups differed in FBFREQ during periods 1, 2, and 4 (*P* = 0.04, 0.01, and 0.03). Within period 3, there was a similar trend (P = 0.08). Feed bunk duration was different between RFI-efficiency groups in periods 1, 3, and 4 (*P* = 0.01, 0.03, 0.01). During period 2, FBDUR showed a similar trend between groups (*P* = 0.10).

Meal data analysis showed few differences between cohort 2 efficiency groups. There were no differences between groups for MFREQ throughout the entire trial. For the behavior trait MDUR, period 1 was the only period during which efficiency groups differed ($P \leq 0.01$). There was a similar tendency for differences between groups in periods 2 and 3 ($P = 0.07$ and 0.09, respectively). There was no difference in MDUR between cohort 2 RFI-efficiency groups during period 4. Also, there were no differences between C2 efficiency groups for AMINT in any of the 4 periods.

Cohort 3: Bunk visit frequency was different between C3 efficiency groups throughout all 4 periods ($P \leq 0.01$ for all periods). Bunk visit duration tended to differ between cohort 3 RFI-efficiency groups during the first half of the trial (period 1: $P = 0.07$; period 2: $P = 0.06$); however there were no differences between cohort 3 efficiency groups in BVDUR during periods 3 or 4 ($P= 0.43$, and 0.44 respectively).

For C3 Wagyu heifers, (reflecting the relationships shown in the C1 bulls) feed bout analysis showed similar relationships to those shown for bunk visit, likely due to the close relationship between these 2 measures. Cohort 3 Wagyu heifer RFI groups differed for FBFREQ during all 4 periods ($P \leq 0.001$ for all 4 periods). Feed bout duration tended to differ during periods 1 and 2 ($P = 0.08$ and 0.06, respectively) but did not differ during periods 3 or 4 ($P = 0.51$ and $P = 0.48$ respectively). Analysis of meal data showed few differences between cohort 3 Wagyu heifer RFI-efficiency groups. Meal frequency was similar between groups throughout all 4 periods. However, there were differences between groups in MDUR ($P \leq 0.1$, for all 4 periods). There were no differences between C3 RFI-efficiency groups for AMINT for any period.

Including behaviors in the model to predict DMI in calculating Residual Feed Intake (RFI).

Analysis of modifying the base model used to predict DMI for the calculation of RFI by including individual feeding behaviors is presented in Table 4, with best fit models presented in Table 5. Within cohort, only behaviors that were significantly correlated with RFI were included in the model to predict DMI. For C1 bulls, behaviors BVDUR, FBDUR, and MDUR were significantly correlated with RFI. The addition of BVDUR decreased variation (MSE; mean square error) by

7.53%. By adding FBDUR and MDUR individually, the MSE was decreased by 8.77 and 4.84% respectively. For this cohort, modifying the base model for the prediction of DMI by adding BVDUR, FBDUR, and MDUR accounted for 17.8% of variation in MSE (Table 5).

Cohort 2 bull behaviors BVFREQ, FBFREQ, and MDUR were significantly correlated with RFI. Adding BVFREQ, FBFREQ, and MDUR to the base model decreased MSE by 2.44, 17.1, and 11.6%, respectively. For this cohort, modifying the base model for the prediction of DMI by adding BVFREQ, FBFREQ, and MDUR accounted for 13.6% of variation in MSE (Table 5).

For C3 heifers, behaviors BVFREQ, FBFREQ, and MDUR were also significantly correlated with RFI. Adding BVFREQ, FBFREQ, and MDUR to the base model individually, decreased MSE by 0.43, 32.1, and 5.06%, respectively. For this cohort, modifying the base model for the prediction of DMI by including BVFREQ, FBFREQ, and MDUR accounted for 39.1% of variation in MSE (Table 5).

Discussion

The current study provides some insight of correlations between feeding behavior and feed efficiency in a niche breed of cattle (Wagyu). Wagyu cattle have a lower appetite compared to traditional finishing cattle. Whereas traditional beef cattle have been bred to attain greater red meat yield and marbling via increased appetite, little selection of Wagyu cattle has been focused upon appetite or gain as noted by lower intakes in previous studies (McGee et al., 2013). The focus of Wagyu carcass composition is intramuscular fat, which is deposited last in the sequence of adipose accumulation. This focus has resulted in outcomes such as longer days on feed in which animals are traditionally fed a lower concentrate diet. Such issues must be considered when analyzing Wagyu feeding behavior. Comparisons of behavior values reported in the literature must include consideration of different methodologies used to collect data (RFID vs. video recording) as well as differences in animal age, sex, diet, and other variables found across such studies. Mendes et al (2010) provides a table describing variance of analytical methods and values across several studies showing discrepancies within several feeding behaviors. This work also provides insight into different population statistics that create a disconnect in otherwise comparable data sets. To this end, caution must be used when generalizing relationships between feeding behavior traits in other studies.

In the present report, consistent differences in feeding behaviors amongst efficiency groups were observed across all 3 cohorts. It is important to note that a higher concentrate diet was offered to C1 than for C2, and C3. This difference in diet composition may play a role in variation of DMI, ADG and also feeding behaviors.

Feeding frequency behaviors showed some consistent relationships with performance measurements across all cohorts. The positive correlations of BVFREQ, FBFREQ and MFREQ with ADG for C1 indicate that feeding frequency behaviors are more closely related to ADG across efficiency groups offered a high concentrate diet, while DMI is more strongly related to these behaviors across high and moderate concentrate diets. There was no correlation between feeding frequency behavior for growing Angus and Hereford bulls offered a roughage diet and either ADG or DMI indicating that diet type may influence these relationships with feeding behaviors (Kayser and Hill, 2013). This contrasts with the relationship found in finishing phase crossbred steers (Durunna et al., 2011b), who found a negative correlation of FBFREQ with ADG (r = -0.07) possibly indicating a breed difference or stage of maturity difference compared to the present study. Consistent with our observations we propose that a high concentrate diet may allow animals to reach satiation faster, with decreased time of rumen (and gut) fill due to more rapid nutrient breakdown. In the case of higher roughage diets, rumen fill may cause decreased initiative to consume feed, manifested as lower feeding frequency behaviors.

The positive correlation of BVFREQ with RFI in C2 bulls and C3 heifers indicates that animals having higher RFI values visit the bunk more often (but may or may not consume feed). Thus, RFI-inefficient Wagyu animals may be more active than RFI-efficient animals, consistent with the observations of Richardson and Herd (2004). A similar trend in BVFREQ observed in C1

Wagyu bulls may suggest that animals offered lower or high concentrate diets behave similarly with respect to BVFREQ. Differences between efficiency groups for BVFREQ across the 3 cohorts ranged from 12 to 31 %, with C3 heifers having the most extreme differences.

Feed bout frequency also differed amongst efficiency groups in all cohorts, indicating that low RFI Wagyu cattle (bulls and heifers) visit the bunk and consume feed less frequently than inefficient counterparts. These observations agree with those of Kelly et al (2010), who found positive correlations of RFI and daily feeding events (r = 0.45). Robinson and Oddy (2004), also noted positive genetic and phenotypic correlations between feeding events (FBFREQ) and RFI. In contrast, Nkrumah et al (2007) found no relationship between feeding frequency and feed conversion ratio in crossbred cattle.

Mean values for MFREQ in the current study are similar to those found by Lancaster et al (2009) of 6.9-8.7 events/d. Lancaster et al (2009) showed no relationship between MFREQ and ADG in purebred Angus bulls. However, Kelley et al (2010) found a trend towards correlations of feeding events and ADG in finishing heifers.

Meal frequency was strongly correlated with DMI in C2 bulls, with a tendency in C1 bulls. The lack of relationship for C3 heifers may indicate a sex effect. For C3, MFREQ averaged 12 events per day, with C2 bulls on the same diet averaging 14 events per day. Analysis of DMI indicates that heifers did consume approximately 1kg less DM than bulls on the same diet. This interpretation is consistent with a study by Friggens et al (1998), who showed when dairy cows were offered a high concentrate versus a low concentrate diets, MFREQ was lower. However, further analysis of the present study indicates a 60 kg starting and 90 kg finishing BW difference in C2 bulls and C3 heifers on the same diet recapitulating the correlation between MFREQ and ADG.

Meal Frequency does not explain variation in RFI of Wagyu cattle. In the present report, of the 3 cohorts studied, MFREQ was only significantly different in C1 (offered a high concentrate diet) efficient versus inefficient Wagyu bulls. As noted above, the variable response across cohorts is possibly due to diet differences. Cohorts 2 and 3 were offered a lower concentrate diet and thus had numerically higher MFREQ values than C1 bulls.

Feeding duration behaviors also showed some consistent relationships with performance measurements across all cohorts. The significant correlations of BVDUR and FBDUR with ADG for C2 and a trend for FBDUR for C1 is in agreement with Kayser and Hill (2013) who found similar trends in growing Angus and Hereford bulls.

The consistent correlation of FBDUR with DMI across all cohorts indicates that animals spent longer times at the bunk and were in fact consuming more feed, rather than only visiting the bunk. These results are consistent with findings of Nkrumah et al (2007), Robinson and Oddy (2004), and Kayser and Hill (2013) and contrast with those of Kelly et al (2010).

Bingham et al., (2009) analyzed head down durations in Brangus heifers using periodic video recording analysis. Their findings indicated that inefficient animals had 22.9% lower head down duration (similar to FBDUR) than efficient heifers. The present study shows no difference between efficiency heifer groups in FBDUR. However, results for C1 and C2 Wagyu bulls suggest that FBDUR of efficient groups is 10 to 13 % lower than for inefficient groups. These results are in agreement with Nkrumah et al., (2007), who reported a large difference in FBDUR between low and high RFI steers (40%). Bingham et al (2009) suggested that differences between their findings and those of Nkrumah et al., may be due to use of Calan Gate systems compared to results from RFID based intake systems.

It is also possible that dominance may play a role in determining variation in BVDUR. Huzzey et al (2006) report a high displacement of subordinate animals from feed bunks in competitive environments. Research in dairy cows by Bouissou et al (1970) found that a hierarchy is established rapidly, and with approximately 50% of the dominant- submissive relationships determined during the first hour in unacquainted animals. Although this was early research, the role of social dominance does indeed play a role in feeding behavior as evidenced by more current studies (Gonyou and Stricklin, 1981; Grant and Albright, 1995; Olofsson, 1999; Grant, 2000; Grant and Albright, 2001). Thus, it is important to consider social hierarchy as a parameter influencing feeding behavior in group housed bulls and heifers. Also, expression of estrus and other reproductive status may play a role in fluctuating intakes (Huzzey et al., 2007). Further studies with larger populations of animals are needed to draw more definitive conclusions on this aspect of Wagyu animal feeding behavior. However, the present study provides insight that efficient Wagyu bulls fed a high concentrate diet visit the bunk for shorter periods than their inefficient counterparts.

In the present study, the differences between efficiency groups in MDUR for C2 (bulls) and C3 (heifers), with a similar trend for C1 bull efficiency groups are consistent with results reported by Durunna et al (2011a) with feeding duration for RFI-efficient animals decreasing from 104 min/d to 63 min/d during growth and finishing phases, respectively. Feeding durations over the two feeding periods for inefficient animals were reported as 118 min/d and 78 min/d, respectively. The positive correlation of MDUR with RFI observed in the current study is also similar to results reported by others indicating that RFI-efficient animals spend less time consuming meals, including Nkrumah et al., (2007) for cross-bred steers, Lancaster et al., (2009) for Angus bulls and Schwartzkopf-Genswein et al., (2011) for cross-bred Charolais steers. In the present study, AMINT was similar between RFI-efficiency groups across all cohorts.

Meal duration was not related to ADG in any cohort of Wagyu animals. The correlations of MDUR and DMI in C2 and C3 indicate that diet composition (higher roughage) is an important factor in the relationship between MDUR and DMI. Animals on a higher concentrate diet (C1) consumed approximately 14% less DM than those on higher concentrate diets (C2 and C3). Also, C2 and C3 animals spent longer times feeding on average than C1 bulls (11% and 34% respectively). It may be that in measuring the shorter MDUR of animals on a high concentrate diet, sensitivity to detect differences associated with DMI are more difficult to detect.

Meal duration was correlated with RFI across all cohorts signifying that longer meal times are associated with less efficient (higher RFI) animals. Kelly et al (2010) found no correlation between feeding duration and feed efficiency traits. However, Mendes et al (2010) found correlations between efficiency traits and length of meal (r = 0.36). These disparities indicate that further studies of the relationship between MDUR and RFI are needed. In the present study MDUR means numerically increased across cohorts as the diet included more roughage (C2 and C3). Thus, it is likely that higher roughage inclusion extends meal durations thereby creating a greater difference between efficiency classifications. Cohort 2 and 3 animals differed in MDUR with C3 animals having 24% and 27% higher values for inefficient and efficient animals, respectively. This phenomenon may be a sex effect, as C2 and C3 animals were from the same season, and calf crop. It is possible that a lack of feed competition plays a role in the increased MDUR. As reported by DeVries and von Keyserlingk (2009), dairy heifers fed in a competitive environment had shorter feeding times and greater day to day variation in feeding times. In the present study, the heifer group was small (n = 34) with relatively few animals per feeding node, and may have been less likely to engage in hierarchy related feeding challenges often associated with bulls. Thus, C3 heifers may have encountered fewer dominance challenges during feeding, leading to increased MDUR and slower eating rate. This is important to note, as AMINT of C2 and C3 animals were similar indicating similar intakes with longer times spent feeding for C3 heifers versus C2 bulls.

Average meal intake was not correlated with ADG in any Wagyu cohort. Roughage based diet fed animals (C2 and C3) ate less per meal (0.90 kg) than C1 bulls offered the concentrate based diet (1.51 kg), however, there were no differences between efficiency groups in AMINT. In contrast, Kayser and Hill (2013) found correlations between meal size and performance measurements in growing Angus and Hereford bulls (ADG, r = 0.16 and r = 0.17, DMI, r = 0.57 and r = 0.54 and RFI, r = 0.52 and r = 0.53, respectively). Mendes et al (2010) also found correlations of RFI with meal size (r = 0.44). This may suggest a breed effect and further studies are required to clarify this point.

For the present study, analysis of time periods (4 periods) throughout the feed intake evaluation trials yields interesting results. In reviewing the literature, we found no reports of feeding behavior traits over contiguous time periods. This approach appears to be novel and provides some useful insights into Wagyu cattle feeding behavior over time. Analysis of such studies may provide evidence of optimal time periods in which animals can be classified by efficiency status. Thus, it may be possible to simplify behavioral analysis into shorter time trials, instead of requiring data generated from a typical 70 d RFI evaluation.

Differences in means were observed from all cohorts for BVFREQ with results suggesting efficient animals visit the bunk less than inefficient animals over several calculated periods of test. Analysis of C3 heifer data show differences among all 4 periods of test signifying a direct relationship between BVFREQ and RFI. Cohorts 1 and 2 (bulls) show strong differences in the first two periods of test but thereafter there are no consistent patterns linking BVFREQ and RFI, suggesting that RFI divergent bulls (C1 and C2) differ greatly in BVFREQ during the first half of test, while heifers (C3) differ throughout the 70 d test.

Analysis of BVDUR showed differences between efficiency groups in C1 and C2 bulls, with trends noted in the first half of trial for C3 heifers. Thus, as for BVFREQ periods 1 and 2 may provide the best indicator of efficiency status via BVDUR. Further studies are required to validate this speculation.

Feed bout frequency showed strong indications of efficiency status differentiation among all cohorts. Wagyu bulls (C 1 and C2) showed efficient animals visiting the bunk to feed less often than their inefficient counterparts during the first 2 periods of the trial. As for BVFREQ and BVDUR the relationships between FBFREQ and RFI are less consistent in the latter periods.

Results from behavior trait FBDUR were inconsistent for the identification of efficiency status when examined using period effects. Meal frequency only provided indications of efficiency status in C1 bulls. This may be attributable to diet effects alone, as neither C2 bulls nor C3 heifers showed any differentiation in MFREQ between RFI groups.

Behavior MDUR provided an indication of efficiency classification in C3 heifers. Efficient heifers had shorter meal durations than counterparts throughout the entire period. On the same diet, C2 bulls showed significant differences, or trends between RFI groups throughout test. However, for C1 bulls, MDUR was not different between RFI groups. Thus, animals fed a high concentrate diet are less likely to show differences in MDUR when classified by efficiency status. There were few differences in AMINT across RFI groups for any cohort, suggesting that AMINT is not a good indicator of efficiency classification for Wagyu animals.

Time period analysis yielded several trends between cohorts. Most importantly, there are no behaviors in which animals did not differ in the initial period, but did so in the latter. This suggests that animals in the current Wagyu cohorts differ greatly at trial initiation, and become more similar (for some traits) towards trial completion. Furthermore, efficiency groups of C1 bulls only differed in the first half the testing period for all correlated behaviors, with these bull efficiency groups being most similar at trial completion (period 4). Cohort 2 bull efficiency groups seemed to be similar in period 2 for duration traits, and period 3 frequency traits (correlated traits). The cause of this phenomenon is not presently understood. Results from the current study suggest that approximately 42 days of behavioral analysis is needed to predict feeding behaviors of Wagyu bulls on a high concentrate diet, while the feeding behavior of the bull group on a lower concentrate diet was highly variable throughout time-points. The present study supports consistent feeding behavior of heifers fed a lower concentrate diet throughout the study. There is a need for further investigations of feeding behavior over time-points to more clearly elucidate relationships with RFI in Wagyu cattle.

The addition of feeding behavior traits to the model used to predict DMI in RFI analysis showed that the “best-fit” model used for C1 bulls accounted for a substantial reduction in MSE (18%). Including duration traits (BVDUR, FBDUR, and MDUR), that is, those behaviors that were significantly correlated with RFI (Table 3) is an approach also reported by Lancaster et al (2009). In further support of this notion, Kelley et al (2010) added daily feeding events to the RFI model (to predict DMI), noting that 20% of variation in DMI could be explained from its inclusion. Thus, variations in feeding-associated activity (i.e. FBFREQ and FBDUR) may account for substantial variation in feed efficiency. Kayser and Hill (2013) found that addition of duration behaviors to the base model significantly improved MSE% but feeding frequency did not, consistent with the analysis in the present study. However, the model used for C2 bulls and C3 heifers in which BVFREQ, FBFREQ, and MDUR were correlated with RFI, reduced variation in MSE% by 14% in the case of C2 bulls and by a substantially greater margin, 39% for C3 heifers. It has also been suggested by other authors that feeding frequency behaviors explain changes in MSE (Nkrumah et al., 2007; Durunna et al., 2011b). Also, MDUR was significantly correlated with RFI for all three cohorts. This indicates that MDUR is an important marker for variation in RFI of Wagyu animals. There is a considerable amount of energy expenditure associated with activity-related feeding. Luiting et al (1991) found that these expenditures can account for as much as 54% of total energy expenditure in laying hens divergently selected for RFI. Susenbeth et al (1998) showed total energy expenditure in cattle was 19% greater during standing vs. lying. Thus, it can be speculated that increases in energy expenditure during feeding, as well as other ongoing physiological processes from nutrient influx can account for a large variation in efficiency. Thus, MDUR provides a useful target as a possible predictor of RFI. This is an area of research that requires further validation.

Implications

The current study provides insight into differences in feeding behavior of Wagyu cattle. With rising feed costs, and unstable market sectors, the use of feed efficient animals will soon become more of a necessity than a preference. The use of feeding behavior is not a standalone selection criterion; however, it does provide some understanding of the variance in feed efficiency. Newer technologies (RFID based feed intake systems) allow researchers to more easily determine individual animal feed intake, and in addition provides a means to conduct feed intake behavioral research. This study has also elucidated some aspects of diet interaction in feeding behaviors of Wagyu cattle, by examining the effects of dietary differences on feeding behaviors and intake patterns. Although further research with substantial animal numbers is needed, the current study aims to assist in spearheading the use of feeding behavior analysis in conjunction with feed efficiency to improve the profitability of beef cattle production.

Table 3.1. Dietary ingredients (% DM basis) and energy values (Mcal/kg; %DM basis) of diets fed to Wagyu cohorts 1, 2, and 3.

Item	**Cohort 1**	**Cohorts 2 & 3**
Alfalfa Hay Early Bloom	18.3	43.6
Corn Grain Cracked	48.8	26.1
Distillers Grains Soluble	11.3	8.7
Molasses (VTM)*	8.7	8.7
DM	87.1	85.2
Crude Protein	15.2	16.9
Crude Fiber	22.0	23.1
NEm	0.38	0.32
NEg	0.26	0.17
Fat (EE)	4.30	2.60

Vitamin Premix Ingredients: corn soy blend, cane molasses, corn steep, ammonium polyphosphate, salt, limestone, Attaflow™, whey, water, fat, anhydrous ammonia, Deccox 6%™,zinc sulfate, manganese sulfate, copper sulfate, vitamin E premix 60%, selenium 4%, vitamin A 1000, cobalt sulfate EDDI (organic iodized salt), vitamin D3 500.

Table 3.2. Comparison of means ± SE between RFI-efficient and RFI-inefficient groups for feeding behavior parameters and performance traits in Wagyu cohorts (C1, C2 and C3).

Behavior	**Cohort**[1]	**Efficient**	**Inefficient**	***P***
Initial BW *kg*	**1**	422 ± 9.7	417 ± 10.8	0.77
	2	362 ± 10.3	366 ± 9.8	0.79
	3	300 ± 6.8	297 ± 6.8	0.72
Final BW *kg*	**1**	489 ± 11.1	484 ± 12.3	0.76
	2	449 ± 11.6	458 ± 11.0	0.55
	3	366 ± 7.8	365 ± 7.8	0.89
ADG *kg/d*	**1**	1.38 ± 0.05	1.39 ± 0.06	0.89
	2	1.26 ± 0.05	1.28 ± 0.05	0.74
	3	1.94 ± 0.07	1.91 ± 0.07	0.8
DMI, *kg/d*	**1**	9.51 ± 0.23	11.44 ± 0.26	< 0.01
	2	8.67 ± 0.19	10.4 ± 0.22	< 0.01
	3	7.98 ± 0.19	9.07 ± 0.19	< 0.01
IMF, %	**1**	6.47 ± 0.20	5.98 ± 0.22	0.11
	2	3.85 ± 0.25	4.39 ± 0.23	0.13
	3	6.43 ± 0.28	5.49 ± 0.28	0.10
Rib Fat Thickness, mm	**1**	0.58 ± 0.03	0.57 ± 0.03	0.86
	2	0.18 ± 0.01	0.18 ± 0.01	0.56
	3	0.20 ± 0.01	0.20 ± 0.01	0.82
RFI *kg/d*	**1**	-0.90 ± 0.07	1.08 ± 0.08	< 0.01
	2	-0.90 ± 0.09	0.74 ± 0.09	< 0.01
	3	-0.56 ± 0.07	0.61 ± 0.07	< 0.01
Bunk Visit Frequency, *events/d*	**1**	35.9 ± 1.53	40.6 ± 1.70	0.05
	2	46.3 ± 3.09	55.4 ± 2.92	0.04
	3	49.4 ± 2.92	67.0 ± 2.92	< 0.01
Bunk Visit Duration, *min/d*	**1**	69.6 ± 2.22	77.1 ± 2.47	0.03
	2	93.5 ± 3.81	107 ± 3.61	0.01
	3	127 ± 5.67	139 ± 5.68	0.16
Feed Bout Frequency, *events/d*	**1**	31.7 ± 1.36	35.9 ± 1.51	0.04
	2	43.3 ± 2.79	52.0 ± 2.64	0.03
	3	44.8 ± 2.57	60.3 ± 2.57	< 0.01

Feed Bout Duration, *min/d*	**1**	67.5 ± 2.12	74.9 ± 2.36	0.02
	2	91.8 ± 3.76	105 ± 3.56	0.01
	3	123 ± 5.42	134 ± 5.42	0.18
Meal Frequency, *events/d*	**1**	7.67 ± 0.38	8.84 ± 0.42	0.05
	2	13.3 ± 1.03	14.8 ± 0.97	0.28
	3	11.7 ± 0.61	12.7 ± 0.61	0.27
Meal Duration, *min/d*	**1**	119 ± 3.92	130 ± 4.35	0.08
	2	132 ± 4.58	149 ± 4.33	0.01
	3	173 ± 6.09	205 ± 6.09	< 0.01
Average Meal Intake, k*g/event*	**1**	1.45 ± 0.06	1.58 ± 0.06	0.15
	2	0.89 ± 0.06	0.92 ± 0.06	0.73
	3	0.87 ± 0.05	0.93 ± 0.05	0.40

[1] Cohorts of Wagyu Animals; Cohort 1 Wagyu Bulls, efficient n= 32, inefficient n = 26; Cohort 2: Wagyu Bulls, efficient n = 18, inefficient n = 18; Cohort 3: Wagyu Heifers, efficient n = 17, inefficient n = 19.

Table 3.3. Spearman correlations of feeding behavior with ADG, DMI and residual feed intake (RFI) for Wagyu cohorts (C1, C2 and C3).

		ADG	**DMI**	**RFI**
Behavior	**Cohort**	**r (*P*)**	**r (*P*)**	**r (*P*)**
Bunk Visit Frequency, *events/d*	**1**	0.32 (0.01)	0.29 (0.03)	0.23 (0.08)
	2	0.00 (0.97)	0.32 (0.06)	0.44 (0.01)
	3	-0.21 (0.23)	0.33 (0.06)	0.60 (<0.01)
Bunk Visit Duration, *min/d*	**1**	0.20 (0.13)	0.32 (0.01)	0.37 (<0.01)
	2	0.42 (0.01)	0.56 (<0.01)	0.31 (0.06)
	3	0.23 (0.20)	0.33 (0.06)	0.27 (0.12)
Feed Bout Frequency, *events/d*	**1**	0.37 (<0.01)	0.32 (0.01)	0.24 (0.07)
	2	0.03 (0.86)	0.35 (0.04)	0.46 (<0.01)
	3	-0.18 (0.30)	0.50 (<0.01)	0.60 (<0.01)
Feed Bout Duration, *min/d*	**1**	0.23 (0.09)	0.36 (<0.01)	0.38 (<0.01)
	2	0.46 (<0.01)	0.57 (<0.01)	0.31 (0.07)
	3	0.24 (0.16)	0.34 (0.05)	0.27 (0.13)
Meal Frequency, *events/d*	**1**	0.42 (<0.01)	0.41 (<0.01)	0.24 (0.07)
	2	0.25 (0.15)	0.29 (0.09)	0.24 (0.16)
	3	0.10 (0.57)	0.05 (0.79)	0.18 (0.30)
Meal Duration, *min/d*	**1**	0.12 (0.35)	0.22 (0.09)	0.31 (0.02)
	2	0.23 (0.18)	0.41 (0.01)	0.38 (0.02)
	3	-0.22 (0.21)	0.34 (0.05)	0.54 (<0.01)
Average Meal Intake, k*g/event*	**1**	0.05 (0.69)	0.27 (0.04)	0.25 (0.06)
	2	-0.07 (0.67)	0.02 (0.91)	-0.04 (0.83)
	3	0.11 (0.55)	0.41 (0.02)	0.21 (0.24)

---

[1] Cohorts of Wagyu Animals; Cohort 1 Wagyu Bulls, efficient n= 32, inefficient n = 26; Cohort 2: Wagyu Bulls, efficient n = 18, inefficient n = 18, Cohort 3: Wagyu Heifers, efficient n = 17, inefficient n = 19.

Table 3.4. Percent reduction in the mean squared error (MSE %) of the model predicting DMI due to the inclusion of the individual variables of feeding behavior in Wagyu cohorts 1, 2, and 3.

Variables in Model	Cohort	R^2	MSE	ΔMSE%
Base[1]	1	0.67	0.75	-
	2	0.55	0.53	-
	3	0.56	0.35	-
BVFREQ[2]	1	0.68	0.74	2.32
	2	0.57	0.52	2.44
	3	0.57	0.35	0.43
BVDUR[3]	1	0.70	0.70	7.53
	2	0.56	0.54	-1.50
	3	0.61	0.32	9.65
FBFREQ[4]	1	0.68	0.73	2.78
	2	0.64	0.44	17.1
	3	0.71	0.24	32.1
FBDUR[5]	1	0.70	0.69	8.77
	2	0.61	0.47	11.7
	3	0.59	0.33	5.42
MFREQ[6]	1	0.69	0.71	5.26
	2	0.65	0.43	19.1
	3	0.71	0.24	32.9
MDUR[7]	1	0.69	0.72	4.84
	2	0.61	0.47	11.6
	3	0.59	0.34	5.06
AMINT[8]	1	0.69	0.72	4.19
	2	0.57	0.52	2.68
	3	0.57	0.35	0.59

[1] Base model for prediction of DMI; mid-test body weight, average daily gain, and rib fat thickness

[2] Bunk visit frequency, events/day,

[3] Bunk visit duration, min/event;

[4] Feed bout frequency, events/d;

[5] Feed bout duration, min/ event;

[6] Meal frequency, events/ d
[7] Meal duration, min/ event;
[8] Average meal intake, kg/ event

Table 3.5. Best fit model for elimination of variation in base model for predicting DMI in Wagyu cohorts 1, 2, and 3.

Cohort	**Variables in Model**[¥]	**R^2**	**MSE**	**ΔMSE%**
1	BVDUR FBDUR MDUR	0.74	0.62	17.8
2	BVFREQ FBFREQ MDUR	0.64	0.46	13.6
3	BVFREQ FBFREQ MDUR	0.75	0.22	39.1

[¥] Variables added to base model predicting DMI consisting of mid-test body weight, average daily gain, and rib fat thickness.

BVFREQ: Bunk visit frequency, events/day
FBFREQ: Feed bout frequency, events/day
BVDUR: Bunk visit duration, min/event
FBDUR: Feed bout duration, min/event
MDUR: Meal duration, min/event

Literature cited

Archer, J. A., E. C. Richardson, R. M. Herd, and P. F. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. Australian Journal of Agricultural Research 50: 147-161.

Baker, S. D., J. I. Szasz, T. A. Klein, P. S. Kuber, C. W. Hunt, J. B. Glaze, Jr., D. Falk, R. Richard, J. C. Miller, R. A. Battaglia, and R. A. Hill. 2006. Residual feed intake of purebred Angus steers: effects on meat quality and palatability. J Anim Sci 84: 938-945.

Basarab, J., D. McCartney, E. K. Okine, and V. S. Baron. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87: 489-502.

Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Canadian Journal of Animal Science 83: 189-204.

Bingham, G. M., T. H. Friend, P. A. Lancaster, and G. E. Carstens. 2009. Relationship between feeding behavior and residual feed intake in growing Brangus heifers. Journal of Animal Science 87: 2685-2689.

Bouissou, M.-F., C. Lavenet, and P. Orgeur. 1970. Rã”le du contact physique dans la manifestation des relations hiã‰rarchiques chez les bovins. Consã‰quences pratiques. Ann. Zootech. 19: 279-285.

DeVries, T. J., and M. A. G. von Keyserlingk. 2009. Competition for feed affects the feeding behavior of growing dairy heifers. Journal of dairy science 92: 3922-3929.

Durunna, O. N., F. D. N. Mujibi, L. Goonewardene, E. K. Okine, J. A. Basarab, Z. Wang, and S. S. Moore. 2011a. Feed efficiency differences and reranking in beef steers fed grower and finisher diets. Journal of Animal Science 89: 158-167.

Durunna, O. N., Z. Wang, J. A. Basarab, E. K. Okine, and S. S. Moore. 2011b. Phenotypic and genetic relationships among feeding behavior traits, feed intake, and residual feed intake in steers fed grower and finisher diets. Journal of Animal Science 89: 3401-3409.

Gonyou, H. W., and W. R. Stricklin. 1981. Eating behavior of beef cattle groups fed from a single stall or trough. Applied Animal Ethology 7: 123-133.

Grant, R. J., and J. L. Albright. 1995. Feeding behavior and management factors during the transition period in dairy cattle. Journal of Animal Science 73: 2791-2803.

Grant, R. J., and J. L. Albright. 2001. Effect of Animal Grouping on Feeding Behavior and Intake of Dairy Cattle. Journal of dairy science 84: E156-E163.

Grant, R. J., and J. L. Albright 2000. Feeding behaviour. In: J. P. F. D-Mello (ed.) Farm Animal Metabolism and Nutrition. p 365-382. CABI Publishing, Wallingford, Oxon, UK.

Huzzey, J. M., T. J. DeVries, P. Valois, and M. A. G. von Keyserlingk. 2006. Stocking Density and Feed Barrier Design Affect the Feeding and Social Behavior of Dairy Cattle. Journal of dairy science 89: 126-133.

Huzzey, J. M., D. M. Veira, D. M. Weary, and M. A. G. von Keyserlingk. 2007. Prepartum Behavior and Dry Matter Intake Identify Dairy Cows at Risk for Metritis. Journal of dairy science 90: 3220-3233.

Kayser, W., and R. A. Hill. 2013. Relationship between feed intake, feeding behaviors, performance and ultrasound carcass measurements in growing purebred Angus and Hereford bulls. Journal of Animal Science.

Kelly, A. K., M. McGee, D. H. Crews, Jr., A. G. Fahey, A. R. Wylie, and D. A. Kenny. 2010. Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables, and body composition traits in growing beef heifers. Journal of Animal Science 88: 109-123.

Koch, R. M., D. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. Journal of Animal Science 22: 486-494.

Lancaster, P. A., G. E. Carstens, F. R. Ribeiro, M. E. Davis, J. G. Lyons, and T. H. Welsh, Jr. 2008. Effects of divergent selection for serum insulin-like growth factor-I concentration on performance, feed efficiency, and ultrasound measures of carcass composition traits in Angus bulls and heifers. J Anim Sci 86: 2862-2871.

Lancaster, P. A., G. E. Carstens, F. R. B. Ribeiro, L. O. Tedeschi, and D. H. Crews. 2009. Characterization of feed efficiency traits and relationships with feeding behavior and ultrasound carcass traits in growing bulls. Journal of Animal Science 87: 1528-1539.

Luiting, P. 1991. The value of feed consumption data for breeding in laying hens, Wageningen Agricultural University, The Netherlands.

McGee, M., C. M. Welch, J. B. Hall, W. Small, and R. A. Hill. 2013. Evaluation of Wagyu for residual feed intake: Optimizing feed efficiency, growth, and marbling in Wagyu cattle. The Professional Animal Scientist 29: 51-56.

Mendes, E. D. M. 2010. Characterization of feeding behavior traits and associations with performance and feed efficiency in finishing beef cattle, Texas A&M University, College Station.

Miller, A. J., D. B. Faulkner, R. K. Knipe, D. R. Strohbehn, D. F. Parrett, and L. L. Berger. 2001. Critical Control Points for Profitability in the Cow-Calf Enterprise. The Professional Animal Scientist 17: 295-302.

Nkrumah, J. D., D. H. Crews, Jr., J. A. Basarab, M. A. Price, E. K. Okine, Z. Wang, C. Li, and S. S. Moore. 2007. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J Anim Sci 85: 2382-2390.

Olofsson, J. 1999. Competition for Total Mixed Diets Fed for Ad Libitum Intake Using One or Four Cows per Feeding Station. Journal of dairy science 82: 69-79.

Richardson, E. C., and R. M. Herd. 2004. Biological basis for variation in residual feed intake in beef cattle. 2. Synthesis of results following divergent selection. Australian Journal of Experimental Agriculture 44: 431-440.

Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. Livestock Production Science 90: 255-270.

Schwartzkopf-Genswein, K. S., D. D. Hickman, M. A. Shah, C. R. Krehbiel, B. M. Genswein, R. Silasi, D. G. Gibb, D. H. Crews, and T. A. McAllister. 2011. Relationship between feeding behavior and performance of feedlot steers fed barley-based diets. J Anim Sci 89: 1180-1192.

Susenbeth, A., R. Mayer, B. Kiehler, and O. Neumann. 1998. Energy requirements for eating in cattle. . J. Anim. Sci. 76: 2701–2705.

Weary, D. M., J. M. Huzzey, and M. A. G. von Keyserlingk. 2009. BOARD-INVITED REVIEW: Using behavior to predict and identify ill health in animals. Journal of Animal Science 87: 770-777.

CHAPTER 4

Feeding behavior and efficiency measures in Red Angus cattle; Relationships of feeding behaviors with average daily gain, dry matter intake and residual feed intake in Red Angus-sired cattle

M. McGee*, C.M. Welch*, J.A. Ramirez**, G.E. Carstens**, W.J. Price†, J.B. Hall‡, and R.A. Hill*[2]

*Department of Animal and Veterinary Science, University of Idaho, Moscow 83844;

**Department of Animal Science, Texas A&M University, College Station, TX, 77843

†Statistical Programs, University of Idaho, Moscow, Idaho 83844

‡University of Idaho Nancy M. Cummings Research, Education, and Extension Center,
Carmen, ID 83467

Journal of Animal Science (in review)

Abstract

Feeding behavior has the potential to enhance prediction of feed intake and to improve understanding of the relationships between behavior, DMI, ADG and residual feed intake (RFI) in beef cattle. Two cohorts, born in 2009 and 2010, the progeny of Red Angus bulls (n = 58 heifers, n = 53 steers), were evaluated during the growing phase, and the latter group of steers was also evaluated during the finishing phase. All behavior analyses were based on 7 feeding behavior traits (bunk visit frequency, bunk visit duration, feed bout frequency, feed bout duration, meal frequency, meal duration, and average meal intake) and their relationships with ADG, DMI, and RFI. During the growing phase, feeding duration traits were most indicative of DMI with positive correlations between bunk visit duration (BVDUR) and DMI for cohort 1 steers (C1SG, n = 28, r = 0.52, P = 0.00) and cohort 2 steers (C2SG, n = 25, r = 0.44, P = 0.01) and heifers (C2HG, n = 29, r = 0.28 P = 0.05). There were similar trends toward correlation of BVDUR and RFI for both steer groups and

C1HG (n = 29, r = 0.27, *P* = 0.06; r = 0.30, *P* = 0.07, r = 0.26, *P* = 0.08, respectively). Feed bout frequency was correlated with ADG in C1HG and in finishing phase steers (C2SF), r = - 0.31, *P* = 0.04 and r = 0.43, *P* = 0.01, respectively). Feed bout duration (FBDUR) was correlated with ADG in heifer groups (r = 0.29 and 0.28, *P* = 0.05 for both groups) and DMI for all growing phase animals (r = 0.29 to 0.55, $P \leq 0.05$ for all groups). Evaluation of growing vs. finishing phase steer groups suggests that all behaviors, RFI, and DMI, but not ADG, are correlated through the growing and finishing phases ($P \leq 0.01$ for all variables excluding ADG), implying that feeding behaviors determined during the growing phase are strong predictors of DMI in either life-stage . Sire maintenance energy EPD (ME_M EPD) effects (measured as high or low groups) on progeny feeding behaviors revealed a difference in meal duration with a tendency to differ in average meal intake (*P* = 0.01 and 0.07, respectively). Feeding behavior duration traits may be useful predictors of DMI in Red Angus cattle.

Keywords: Red Angus, Feeding Behavior, RFI, Efficiency

Introduction

With the recent increase in feed costs (since 2006), there ~~is~~ has been a greater need to identify methods to reduce input costs in the beef industry. An improvement in feed efficiency can reduce input costs, as well as maximizing profits (Archer et al., 1999; Miller et al., 2001; Basarab et al., 2007; 2008). Previous research denotes individual animal variation of feed intake above and below that anticipated using size and growth rate indicators (Herd et al., 2003a, b). Residual feed intake (RFI) provides a tool that takes advantage of natural variability in feed efficiency that is independent of traits that are important in the breeding herd (Tedeschi et al., 2006). It identifies efficient animals (Koch et al., 1963) by measuring the difference between expected and actual animal feed intake through regression of growth over a specified time period. This methodology has been proven successful; however underlying biological mechanisms surrounding these variations are still unclear. Herd et al. (2004) found that feeding behavior contributed to 2% of the variation in RFI. Other research, however, has suggested that an animal's feeding behavior can account for a higher percentage (35%) of this deviation (Lancaster et al., 2009). In swine studies, Haer et al. (1993) noted that feeding behavior accounted for 44% of variation in RFI. Radio frequency identification (RFID) equipped animal feed intake systems allow researchers to examine large populations of animals with individual parameters, including patterns of feed intake and associated behaviors. The current study aims to provide insights into the prediction of DMI and variations of efficiency status using feeding behavior parameters.

Materials and methods

Procedures involving the use of animals in this study were approved by the University of Idaho Animal Care and Use Committee (2011-3).

Animals and Adaptation for RFI Analysis

The current study is associated with a larger evaluation of the progeny of Red Angus sires. For a more detailed description of sires and progeny post-weaning RFI evaluation, and finishing phase feed efficiency evaluation, please refer to Welch et al. (2012). In brief, a total of 12 Red Angus sires divergent for maintenance energy (**$\mathbf{ME_M}$**) EPD were chosen based on the Red Angus Association of America-generated ME_M EPD. Crossbred cows were estrus synchronized and bred by AI over 3 yr, with each sire being represented across 2 to 3 cohorts and 11 out of 12 sires producing 15 or more progeny. The current study evaluates progeny from the latter 2 years of this study, henceforth designated by sex, cohort and either growing or finishing phase evaluation as follows: cohort 1 heifers, growing phase, (**C1HG**, n = 29), cohort 1 steers growing phase, (**C1SG**, n = 28), cohort 2 heifers, growing phase, (**C2HG**, n = 29), cohort 2 steers, growing phase (**C2SG,** n = 25) and the latter group of steers also evaluated during the finishing phase (**C2SF**, n = 25).

Red Angus steers (n = 53) and heifers (n = 58) were evaluated using electronic individual feed intake recording equipment (GrowSafe Systems Ltd, Airdrie, Alberta, Canada) at the University of Idaho Nancy M. Cummings Research, Education, and Extension Center (NMCREEC). Animals were adapted to the GrowSafe system using stability of intake as the primary indicator of test initiation. Acclimation was generally for 2 wk prior to the test periods. Animals were weighed in mornings (prior to feeding) for 2 consecutive days at trail initiation and termination and also weighed every 2 wk (prior to feeding) for ADG and RFI determinations. The GrowSafe system at NMCREEC is composed of four (21.34 x 54.86 m) pens each containing 5 feeding nodes. The pens are located outside without cover. Animals were randomly allocated (within sex) to 1 of 4 pens of the GrowSafe feed intake monitoring system. Ultrasound procedures were performed for live animal carcass characteristics by an independent technician. Ultrasound measurements included rib fat (RF) thickness, IMF, and LM area. Measurements were performed on d 0 and 70 between the 12th and 13th ribs. All images were captured by an Aloka 500ssd Scanner (Hitachi Aloka Medical, Ltd.)

The C2SG steer group growing diet was modified (Table 1) to a finishing phase diet through 4 steps after a post-weaning (growing phase) RFI evaluation. During this final finishing period, this group of steers, designated C2SF, was evaluated for individual DMI, ADG, finishing phase feed efficiency and feeding behaviors. Test protocols used for post-weaning RFI evaluations were also implemented for finishing phase feed efficiency evaluation. Steers were finished to a target BW of 591kg (group average) before harvest, resulting in a recorded intake period of approximately 110 d (including all modifications of the finishing rations).

Post RFI evaluation, RFI-divergent groups (defined as efficient: RFI > 0.5 SD below the mean, and inefficient RFI > 0.5 SD above the mean) were examined for feeding behaviors based on data collected from the GrowSafe output. Behaviors analyzed were classified as bunk visit data, feed bout data, and meal data. Bunk visit parameters were bunk visit frequency (BVFREQ: transponder readings for a single animal entering feed bunk) and bunk visit duration (BVDUR: time during transponder readings with animal at bunk; ending when there are no readings for > 300s). Feed bout behaviors are feed bout frequency (FBFREQ: transponder readings for single animal entering feed bunk and consuming feed) and feed bout duration (FBDUR: time during transponder reading with animal at bunk consuming feed; ending when the time between the last two readings was > 300s or when a new transponder was detected. Meal data has three behavior parameters; meal frequency (MFREQ: cluster of feed bouts in which the non-feeding event was shorter than meal criterion), meal duration (MDUR: time during transponder readings with animal at bunk consuming feed per meal), and average meal intake (AMINT: sum of feed event intakes during a meal). The meal criterion used in the present study was 300 s as described by Schwartzkopf-Genswein et al (2004). Groups of animals (C1SG, C1HG, C2HG C2SG, and C2SF), were examined by efficiency classification (efficient: C1SG n = 14; C1HG n = 14; C2HG n = 15; C2SG, n = 12 and C2SF, n =13; inefficient: C1SG n = 14; C1HG n = 15; C2HG n = 14; C2SG n = 12 and C2SF, n = 13.

Statistical analysis

Residual Feed intake analyses were conducted using SAS (Version 9.2, SAS Inst., Inc., Cary, NC). Residual feed intake was calculated as the difference between actual and predicted feed intake by regressing DMI on mid-test $BW^{0.75}$ and ADG (Koch et al., 1963) with the addition of RF thickness (Basarab et al., 2003) to the model. Correlation coefficients for RFI prediction for each group were as follows: C1HG, 0.76, C1SG, 0.89, C2HG, 0.68, C2SG, 0.39 and C2SF, 0.42. Post RFI test, animals were classified into the following groups: efficient (RFI > 0.5 SD below the mean), marginal (RFI ± 0.5 SD of the mean), and inefficient (RFI > 0.5 SD above the mean).

Feeding behavior parameters were examined for each RFI test phase by Spearman’s rank correlation with ADG, DMI, and RFI values. Each behavior was averaged over days within each of the four test periods. With these averages, a mixed model repeated measures completely random design was used to assess feeding behaviors considering RFI group as a fixed effect and the four test periods as a repeated measure, with animals considered as random effects. An autoregressive lag 1 correlation structure was assumed for the repeated effect of test period. The PROC MIXED procedures of SAS were used to examine these effects. The effect of sire ME_M EPD on progeny feeding behaviors was measured by defining high or low sire ME_M EPD. For further details of sire classification please see Welch et al. (2012). Pair-wise comparisons of least squares group means was carried out for all responses. An α of 0.05 was set to designate statistically significant differences.

Results

Performance and behavior parameters of efficient and inefficient divergent RFI cohort groups

Mean body weight (initial and final), ADG, and RF thickness were similar among efficiency groups within Red Angus cohorts (Table 2; $P > 0.10$ for all traits). As expected, DMI and RFI differed between efficiency classifications within cohorts ($P < 0.01$ for all cohorts). Behavior traits BVFREQ, BVDUR, FBFREQ, FBDUR, MFREQ, MDUR, and AMINT were similar among efficiency classifications within Red Angus cohorts ($P > 0.10$ for all).

Associations of feeding behaviors with ADG, DMI, and RFI

Spearman rank correlations between behaviors, and ADG, DMI and RFI are presented in Table 3. Behavior BVFREQ was significantly correlated with ADG only in C2SF (r = 0.43, $P = 0.01$). Conversely, there was a tendency towards negative correlation between BVFREQ and ADG in C1HG (r = -0.29, $P = 0.06$). There were no significant correlations between BVFREQ and DMI or RFI across any cohorts of Red Angus cattle.

Bunk visit duration indicated some associations with ADG in growing Red Angus heifers (C1HG and C2HG, r = -0.29 $P = 0.06$ and r = -0.13, $P = 0.07$, respectively). Bunk visit duration was significantly correlated with DMI in C1SG, C2HG, and C2SG (r = 0.52, $P < 0.0001$; r = 0.28, $P = 0.05$; and r = 0.44, $P = 0.01$ respectively), with a similar trend in C1HG (r = 0.28, $P = 0.06$), with no relationship between BVDUR and DMI in C2SF. Moderate correlation of BVDUR with RFI was detected in C1HG, C1SG and C2SG (r = 0.26, $P = 0.08$, r = 0.27, $P = 0.06$, and r = 0.30, $P = 0.07$, respectively). No significant correlations were found between BVDUR and RFI in C2HG or C2SF.

Feed bout frequency and ADG were negatively correlated in C1HG, yet positively correlated in C2SF (r = -0.31, *P* = 0.04 and r = 0.43, *P* = 0.01). Behavior FBFREQ and DMI were not correlated for any cohort (*P* > 0.10 for all). Similarly, FBFREQ and RFI were unrelated for all cohorts.

Feed bout duration and ADG were positively correlated in C1HG and C2HG, with a similar trend in C1SG (r = 0.29, *P* = 0.05; r = 0.28, *P* = 0.28, r = 0.26, *P* = 0.08 respectively). Feed bout duration was significantly correlated with DMI for all growing phase groups (C1HG, C1SG, C2HG, and C2SG; *P* ≤ 0.05 for all) but was not correlated in finishing phase steers. Behavior FBDUR and RFI trended towards a positive correlation in C1HG and C1SG (*P* = 0.08 and 0.09, heifers and steers, respectively).

Meal frequency and ADG were unrelated across all cohorts (*P* > 0.10), as was MFREQ and DMI. There was a trend towards positive correlation between MFREQ and RFI (*P* = 0.09), in the C1SG group only. Meal duration was not correlated with ADG, DMI, or RFI for any cohort. Behavior AMINT trended towards positive correlations with both ADG and DMI in C1HG (both, *P* = 0.06).

Relationships of performance and feeding behaviors between growing and finishing phase Red Angus steers

In comparing growing and finishing phase Red Angus steer groups, ADG was not correlated (*P* = 0.56; Table 4), while DMI was strongly correlated (r = 0.56, and *P* < 0.01). Similar to DMI, RFI was also strongly correlated between the growing and finishing phases (r = 0.50, *P* = 0.01). All seven behaviors were also strongly correlated between growing and finishing phases (*P* < 0.01 for all behaviors).

Effects of sire ME_M EPD on performance and feeding behaviors of Red Angus progeny

Table 5 shows the effects of sire ME_M EPD group (low ME_M EPD vs high ME_M EPD) on progeny feeding behaviors. Meal duration of the high ME_M EPD sired group was greater than for their low ME_M EPD progeny counterparts ($P = 0.01$) There was a trend towards the high ME_M EPD sired group consuming more feed during each meal event (AMINT, $P = 0.07$). There were no other differences in behaviors between high and low sire ME_M EPD progeny ($P > 0.10$).

Discussion

Characterizing cattle populations using feeding behaviors could prove beneficial in predicting DMI and towards identifying underlying variations in feed efficiency. The current study has identified some of these quantifiable behavioral indicators.

In the present study feeding duration behaviors (BVDUR and FBDUR) were most correlated with performance measures (ADG and DMI) in Red Angus cattle. Interestingly, these traits were only correlated in growing phase animals, suggesting either a diet effect (high concentrate vs. lower concentrate) or a stage of maturity effect. Feed bout duration and ADG was significantly correlated in heifers with a trend towards positive correlation in C1SG. This suggests that ADG increases as the time spent consuming feed (in bouts) increases. These results are in agreement with Kelly et al (2010) noting a trend ($P < 0.10$) amongst a mixed population of steers and heifers. Our findings indicate Red Angus heifer ADG is characterized most by FBDUR, with some correlation shown for BVDUR.

Previous researchers have also found positive correlations of FBFREQ and ADG in steer populations (Montanholi et al., 2010). In the present study, however, FBFREQ and BVFREQ were negatively correlated with ADG in heifers.

Feed bout duration was correlated with DMI in all growing phase Red Angus groups. This may imply that FBDUR is dependent on diet components, as C2SF did not show this relationship.

Current results indicate individual feed bouts are more indicative of DMI than meal duration. In previous studies (Kayser and Hill, 2013), we have also observed strong correlations between feeding duration behaviors (head down duration and head down duration per meal) in growing Angus and Hereford bulls (correlation coefficients in the range, r, 0.34 – 0.52, all $P < 0.0001$). However, results of the present study differ from those reported by Montanholi et al (2010) who found significant correlations ($P < 0.01$) of time per meal and DMI.

Associations of meal traits and efficiency have been reported in literature (Schwartzkopf-Genswein, 2002; Nkrumah et al., 2007; Paddock, 2008; Bingham et al., 2009; Lancaster et al., 2009; Kayser and Hill, 2013). The current study did not show significant correlations between meal traits and ADG or DMI or RFI. This suggests that Red Angus animals have similar meal-related behaviors, limiting the ability of meal traits to predict efficiency classification. Values for MDUR during both growing (206 to 236 min/d) and the finishing phase (148 to 158 min/d) were substantially higher than those reported by Lancaster et al. (2009) around 100 min/d who reported behaviors and performance of young Angus bulls on a forage-based diet. The diet composition, animal body weight, individual animal appetite, total population of animals per pen, and number of bunks available are variables that determine the time required for feed consumption (de Haer et al., 1993; Bingham et al., 2009). Thus, multiple factors impact the scale and variability of this behavior and limit its predictive ability.

Red Angus groups examined in the current study did not show correlations between feeding frequency behavior traits and RFI noted in previous studies. Significant correlations of RFI and BVFREQ in beef cattle of 0.18, and 0.50 have been reported (Robinson and Oddy, 2004; Basarab et al., 2007). Similarly, Nkrumah et al (2007) found both phenotypic and genetic correlations of FBFREQ and RFI in Angus and Charolais sired cattle offered a high concentrate diet.

In the present study, both BVDUR and FBDUR showed trends towards correlation with RFI in C1HG. Similar to C1HG, BVDUR and RFI tended toward correlation for C1SG and C2SG growing steers. These trends may suggest that animals with higher RFI values (lower efficiency) visit the bunk and consume feed over a longer period. These relationships are not completely repeated in FBDUR. This implies time spent at the bunk without feed intake may have shifted the correlation. These trends are comparable to those observed in our previous studies of growing Angus and Hereford bulls for which head down duration and head down duration per meal were highly correlated with RFI (correlation coefficients in the range, r, 0.40 to 0.59, all $P < 0.0001$). Similarly, Schwartzkopf-Genswein et al. (2011) reported a study of steers through backgrounding and finishing phases with animals classified by G:F rather than RFI. These authors report that both BVFREQ and BVDUR showed trends in which inefficient animals tended to consume feed during longer duration bouts and more frequently, with groups differing significantly for BVFREQ during the finishing phase. Consistent with these observations, Golden et al. (2008) reported daily eating bouts that significantly differed between RFI efficiency groups in the first of two experiments and trended similarly in the second experiment.

In the present study, strong correlations between growing and finishing phase steer behaviors, DMI, and RFI provide evidence of the value of feeding behaviors in predicting DMI across the two phases. Feeding behaviors measured during the post-weaning phase are also predictive of those during later stages of the life cycle. Relationships of growing and finishing phase efficiency have been noted in the literature (Archer et al., 1998). However it is suggested that several underlying mechanisms are implied in driving the efficiency status of animals, such as variations in intake and digestion of feed, basal metabolism, activity and thermoregulation (Herd and Arthur, 2009). Previous studies have noted effects of diet type and feeding period in beef steers, causing a re-ranking in feed efficiency (Durunna et al., 2011). Changes in efficiency and intake caused by diet (high vs low concentrate) may be due to shifts in rumen pH and microbial population (Calsamiglia et al., 2008). Goonewardene et al. (2004) found rank associations of RFI measured in animals over three test periods, suggesting that RFI is highly correlated throughout the production life of animals. A study by Black et al. (2013) examined relationships of RFI and performance of beef heifers during growth and as 3 year old lactating cows. Results from their study also suggest that animals classified as efficient during growth phase performed similarly as mature cows. The encouraging data reported within our study suggesting the power of feeding behaviors in predicting DMI across life-stages require extensive further studies to determine whether there are breed-specific (or study-specific) elements of these relationships or whether they can be generalized.

Sire ME_M EPD effect on progeny behaviors provides insight that feeding behavior may have a genetic component. The maintenance energy requirement of an animal is an indicator of energy expenditure associated with sustaining body tissues (Ferrell and Jenkins, 1985). By reducing maintenance energy, it may be possible to reduce nutrient intake associated with maintenance, and shift this towards gain. Correlations of MDUR and the trend of AMINT suggest that meal data may be most indicative of sire ME_M EPD effect as compared to other feeding behaviors observed in this study. These results are important as it has been implied that improved RFI may be associated with decreased maintenance energy requirements via more effective feed conversion (Richardson and Herd, 2004). The present study implies that sires with lower ME_M produce progeny with lower MDUR, and possibly lower AMINT. As ME_M EPD is also positively associated with growth and size traits, it will be important to determine whether these factors are also related to MDUR and AMINT. These results suggest lower feed consumption of low ME_M EPD sire progeny. Thus, these results imply the need for further analysis. Results from Welch et al (2012) showed no relationship between of sire ME_M EPD and progeny phenotypic RFI. The relationship of ME_M and feeding behavior has not been examined to the authors’ knowledge.

The use of feeding behaviors to predict DMI and efficiency in Red Angus cattle may have potential to predict all-of-life DMI, especially with respect to BVDUR and FBDUR behaviors. Such analysis may also provide additional insight into variation of phenotypic RFI. Correlations of behaviors across growing and finishing phase Red Angus steers suggest that behaviors are conserved and thus may be useful for animal assessment outside of traditional (post weaning) test periods. Should these behaviors be shown to be predictive in a more general context, it is possible that the need to estimate individual animal intake in determining feed efficiency could be overcome. The equipment needed to measure individual BVDUR and FBDUR is less complex and less expensive than equipment needed to accurately measure individual animal DMI. However, the gold standard in measuring DMI will likely remain with actual measurements of DMI mass required well into the future.

Table 4.1. Ingredient (% DM basis), chemical composition, and energy values of diets fed to Red Angus cohorts.

Item	**Grower Diet[1]**	**Finishing Diet[2]**
Alfalfa Hay mid bloom	60.0	31.0
Corn grain cracked	30.0	46.0
Molasses (VTM)	10.0	13.0
Distillers grain soluble	-	10.0
Dry Matter, *%*	80.9	81.1
Crude Protein, *%*	16.4	15.2
Fiber Crude, *%*	20.7	12.3
Fat (EE), *%*	2.3	3.9
NEm, *Mcal/ kg*	1.6	1.9
NEg, Mcal/ kg	0.9	1.1
Ash, *%*	8.1	6.8

[1] *C1SG- Cohort 1 steers, growing phase, n = 28; C1HG- Cohort 1 heifers, growing phase, n = 29; C2HG- Cohort 2 heifers, growing phase, n = 29; C2SG – Cohort 2 steers growing phase, n = 25;*

[2] *C2SF- Cohort 2 steers finishing phase, n = 25.*

[3] *Vitamin Premix Ingredients: corn soy blend, cane molasses, corn steep, ammonium polyphosphate, salt, limestone, Attaflow™, whey, water, fat, anhydrous ammonia, Deccox 6%™,zinc sulfate, manganese sulfate, copper sulfate, vitamin E premix 60%, selenium 4%, vitamin A 1000, cobalt sulfate EDDI (organic iodized salt), vitamin D3 500.*

Table 4.2. Comparison of means ± SE between RFI-efficient and RFI-inefficient Red Angus steers and heifers for performance measures and feeding behaviors.

Measurement	Cohort*	Efficient	Inefficient	*P*
Initial BW, *Kg*	**C1HG**	305 ± 10.3	306 ± 9.90	0.96
	C1SG	320 ± 10.4	322 ± 10.4	0.92
	C2HG	307 ± 8.23	307 ± 8.56	0.96
	C2SG	332 ± 8.08	323 ± 8.44	0.44
	C2SF	503 ± 10.3	513 ± 9.85	0.47
Final BW, *Kg*	**C1HG**	427 ± 13.2	428 ± 12.7	0.97
	C1SG	448 ± 12.6	454 ± 12.6	0.75
	C2HG	411 ± 11.5	419 ± 11.9	0.67
	C2SG	450 ± 10.6	454 ± 11.1	0.83
	C2SF	593 ± 11.8	608 ± 11.3	0.37
ADG, *Kg/ d*	**C1HG**	1.47 ± 0.05	1.45 ± 0.05	0.78
	C1SG	1.62 ± 0.05	1.63 ± 0.05	0.92
	C2HG	1.27 ± 0.05	1.31 ± 0.50	0.67
	C2SG	1.48 ± 0.11	1.52 ± 0.12	0.80
	C2SF	1.28 ± 0.06	1.36 ± 0.50	0.35
DMI, *kg/ d*	**C1HG**	10.7 ± 0.34	11.9 ± 0.33	<0.01
	C1SG	10.6 ± 0.29	12.2 ± 0.28	<0.01
	C2HG	10.1 ± 0.26	11.7 ± 0.27	<0.01
	C2SG	10.3 ± 0.24	12.3 ± 0.25	<0.01
	C2SF	12.6 ± 0.31	15.0 ± 0.30	<0.01
Rib Fat Thickness, *cm*	**C1HG**	1.22 ± 0.08	1.22 ± 0.07	0.99
	C1SG	1.14 ± 0.08	1.16 ± 0.08	0.81
	C2HG	1.02 ± 0.06	0.99 ± 0.06	0.68
	C2SG	1.05 ± 0.06	1.07 ± 0.07	0.82
	C2SF	1.41 ± 0.10	1.41 ± 0.09	0.99
RFI, *kg/ d*	**C1HG**	-0.71 ± 0.10	0.68 ± 0.09	<0.01
	C1SG	-0.77 ± 0.10	0.70 ± 0.10	<0.01
	C2HG	-0.75 ± 0.09	0.76 ± 0.09	<0.01
	C2SG	-0.93 ± 0.11	1.03 ± 0.12	<0.01
	C2SF	-1.07 ± 0.13	0.96 ± 0.12	<0.01

Bunk Visit Frequency, *events/d*	**C1HG**	74.3 ± 4.96	83.3 ± 4.79	0.20
	C1SG	68.3 ± 3.47	74.3 ± 3.47	0.23
	C2HG	77.4 ± 3.76	79.9 ± 3.89	0.64
	C2SG	43.4 ± 2.93	50.6 ± 3.06	0.10
	C2SF	40.5 ± 1.78	42.5 ± 1.71	0.41
Bunk Visit Duration, *min/d*	**C1HG**	138 ± 5.07	148 ± 4.90	0.14
	C1SG	118 ± 4.69	129 ± 4.69	0.12
	C2HG	150 ± 4.74	156 ± 4.91	0.40
	C2SG	138 ± 5.80	153 ± 6.06	0.09
	C2SF	97.9 ± 3.52	104 ± 3.38	0.24
Feed Bout Frequency, *events/d*	**C1HG**	63.5 ± 4.06	68.9 ± 2.99	0.35
	C1SG	57.3 ± 2.99	61.8 ± 2.99	0.29
	C2HG	65.8 ± 3.47	66.3 ± 3.60	0.92
	C2SG	36.4 ± 2.54	42.3 ± 2.65	0.12
	C2SF	35.8 ± 1.62	38.4 ± 1.56	0.26
Feed Bout Duration, *min/d*	**C1HG**	134 ± 4.92	144 ± 4.75	0.14
	C1SG	115 ± 4.62	125 ± 4.62	0.13
	C2HG	145 ± 4.63	151 ± 4.80	0.42
	C2SG	135 ± 5.69	149 ± 5.95	0.12
	C2SF	96.0 ± 3.41	102 ± 3.28	0.20
Meal Frequency, *events/d*	**C1HG**	11.6 ± 1.57	12.8 ± 1.51	0.20
	C1SG	10.1 ± 1.40	12.7 ± 1.40	0.20
	C2HG	12.8 ± 1.33	13.3 ± 1.37	0.79
	C2SG	9.31 ± 1.72	10.6 ± 1.79	0.60
	C2SF	8.60 ± 1.08	10.0 ± 1.04	0.38
Meal Duration, *min/d*	**C1HG**	227 ± 12.7	222 ± 12.3	0.79
	C1SG	206 ± 14.0	209 ± 14.0	0.86
	C2HG	228 ± 11.3	236 ± 11.7	0.63
	C2SG	219 ± 22.3	235 ± 23.3	0.62
	C2SF	158 ± 14.8	148 ± 14.2	0.60
Average Meal Intake, k*g/event*	**C1HG**	1.40 ± 0.19	1.35 ± 0.19	0.85
	C1SG	1.54 ± 0.18	1.39 ± 0.18	0.54
	C2HG	1.24 ± 0.13	1.30 ± 0.13	0.75
	C2SG	1.77 ± 0.31	2.04 ± 0.32	0.55
	C2SF	2.32 ± 0.39	2.40 ± 0.37	0.89

** C1SG- Cohort 1 steers, growing phase n = 28; C1HG- Cohort 1 heifers growing phase, n = 29; C2HG- Cohort 2 heifers, growing phase, n = 29; C2SG – Cohort 2 steers growing phase, n = 25; C2SF- Cohort 2 steers finishing phase, n = 25.*

Table 4.3. Spearman’s rank correlations of feeding behaviors with ADG, DMI, and RFI of Red Angus steers and heifers.

		ADG	**DMI**	**RFI**
	Cohort	**r (*P*)**	**r (*P*)**	**r (*P*)**
Bunk Visit Frequency, *events/d*	**C1HG**	-0.29 (0.06)	-0.15 (0.32)	0.15 (0.38)
	C1SG	-0.22 (0.14)	-0.17 (0.27)	0.14 (0.34)
	C2HG	-0.13 (0.35)	-0.22 (0.13)	0.01 (0.92)
	C2SG	0.19 (0.27)	0.17 (0.30)	0.20 (0.24)
	C2SF	0.43 (0.01)	0.22 (0.19)	0.16 (0.34)
Bunk Visit Duration, *min/d*	**C1HG**	0.29 (0.06)	0.28 (0.06)	0.26 (0.08)
	C1SG	0.22 (0.14)	0.52 (0.00)	0.27 (0.06)
	C2HG	0.26 (0.07)	0.28 (0.05)	0.13 (0.37)
	C2SG	0.19 (0.25)	0.44 (0.01)	0.30 (0.07)
	C2SF	0.06 (0.74)	0.16 (0.35)	0.21 (0.21)
Feed Bout Frequency, *events/d*	**C1HG**	-0.31 (0.04)	-0.19 (0.21)	0.09 (0.57)
	C1SG	-0.18 (0.23)	-0.15 (0.30)	0.15 (0.32)
	C2HG	-0.12 (0.40)	-0.19 (0.18)	-0.01 (0.95)
	C2SG	0.18 (0.30)	0.15 (0.38)	0.20 (0.23)
	C2SF	0.43 (0.01)	0.27 (0.11)	0.22 (0.19)
Feed Bout Duration, *min/d*	**C1HG**	0.29 (0.05)	0.29 (0.05)	0.26 (0.08)
	C1SG	0.26 (0.08)	0.55 (<0.01)	0.25 (0.09)
	C2HG	0.28 (0.05)	0.31 (0.03)	0.11 (0.45)
	C2SG	0.21 (0.21)	0.44 (0.01)	0.10 (0.54)
	C2SF	0.06 (0.74)	0.16 (0.33)	0.22 (0.19)
Meal Frequency, *events/d*	**C1HG**	-0.10 (0.52)	-0.18 (0.25)	0.10 (0.51)
	C1SG	0.03 (0.85)	0.15 (0.32)	0.25 (0.09)
	C2HG	0.07 (0.64)	0.06 (0.66)	0.02 (0.89)
	C2SG	0.05 (0.76)	-0.03 (0.87)	0.03 (0.87)
	C2SF	0.00 (1.00)	0.23 (0.16)	0.08 (0.64)
Meal Duration, *min/d*	**C1HG**	-0.06 (0.69)	-0.06 (0.69)	0.02 (0.88)
	C1SG	-0.11 (0.45)	0.01 (0.96)	0.08 (0.61)
	C2HG	0.06 (0.69)	0.00 (0.97)	-0.03 (0.85)
	C2SG	-0.01 (0.95)	0.15 (0.37)	0.10 (0.54)
	C2SF	0.12 (0.50)	-0.16 (0.34)	-0.04 (0.82)

Average Meal Intake, k*g/event*	**C1HG**	0.28 (0.06)	0.28 (0.06)	-0.01 (0.93)
	C1SG	0.12 (0.43)	0.06 (0.71)	-0.19 (0.20)
	C2HG	0.09 (0.54)	0.15 (0.29)	-0.01 (0.92)
	C2SG	0.07 (0.69)	0.19 (0.26)	0.07 (0.69)
	C2SF	0.14 (0.39)	0.00 (0.99)	0.08 (0.62)

* *C1SG Cohort 1 steers, growing phase, n = 28; C1HG- Cohort 1 heifers, growing phase n = 29; C2HG- Cohort 2 heifers growing phase, n = 29; C2SG – Cohort 2 steers growing phase, n = 25; C2SF- Cohort 2 steers finishing phase, n = 25.*

Table 4.4. Spearman rank correlations for performance and feeding behaviors between growing and finishing phases in Red Angus steers (C2SG and C2SF)[1].

Trait	**r (*P*)**
ADG*	0.10 (0.56)
DMI*	0.56 (<0.01)
RFI*	0.50 (0.01)
Bunk Visit Frequency, *events/d*	0.56 (<0.01)
Bunk Visit Duration, *min/d*	0.47 (<0.01)
Feed Bout Frequency, *events/d*	0.57 (<0.01)
Feed Bout Duration, *min/d*	0.47 (<0.01)
Meal Frequency, *events/d*	0.55 (<0.01)
Meal Duration, *min/d*	0.56 (<0.01)
Average Meal Intake, k*g/event*	0.52 (<0.01)

*Correlations for ADG, DMI, and RFI obtained from Welch et al 2012.

[1] *C2SG – Cohort 2 steers growing phase, n = 38; C2SF- Cohort 2 steers finishing phase, n = 38.*

Table 4.5. Effect of Red Angus sire ME_M EPD group on progeny feeding behaviors.*

Behavior	**High Sire ME_M EPD Group**	**Low Sire ME_M EPD Group**	***P***
Bunk Visit Frequency, *events/d*	70.1 ± 1.87	68.6 ± 2.27	0.60
Bunk Visit Duration, *min/d*	143 ± 2.25	145 ± 2.73	0.58
Feed Bout Frequency, *events/d*	59.2 ± 1.59	56.9 ± 1.93	0.37
Feed Bout Duration, *min/d*	139 ± 2.19	141 ± 2.65	0.51
Meal Frequency, *events/d*	11.7 ± 0.53	11.8 ± 0.64	0.89
Meal Duration, *min/d*	228 ± 4.76	209 ± 5.77	0.01
Average Meal Intake, k*g/event*	1.55 ± 0.07	1.35 ± 0.09	0.07

*Mean ± SE; n = 178 total progeny; n = 106 high ME_M EPD sire group, n = 72 low ME_M EPD sire group.

Literature cited

Archer, J. A., W. S. Pitchford, T. E. Hughes, and P. F. Parnell. 1998. Genetic and phenotypic relationships between food intake, growth, efficiency and body composition of mice post weaning and at maturity. Animal Science 67: 171-182.

Archer, J. A., E. C. Richardson, R. M. Herd, and P. F. Arthur. 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. Australian Journal of Agricultural Research 50: 147-161.

Basarab, J., D. McCartney, E. K. Okine, and V. S. Baron. 2007. Relationships between progeny residual feed intake and dam productivity traits. Can. J. Anim. Sci. 87: 489-502.

Basarab, J. A., M. A. Price, J. L. Aalhus, E. K. Okine, W. M. Snelling, and K. L. Lyle. 2003. Residual feed intake and body composition in young growing cattle. Canadian Journal of Animal Science 83: 189-204.

Bingham, G. M., T. H. Friend, P. A. Lancaster, and G. E. Carstens. 2009. Relationship between feeding behavior and residual feed intake in growing Brangus heifers. Journal of Animal Science 87: 2685-2689.

Black, T. E., K. M. Bischoff, V. R. G. Mercadante, G. H. L. Marquezini, N. DiLorenzo, C. C. Chase, S. W. Coleman, T. D. Maddock, and G. C. Lamb. 2013. Relationships among performance, residual feed intake, and temperament assessed in growing beef heifers and subsequently as 3-year-old, lactating beef cows. Journal of Animal Science 91: 2254-2263.

Calsamiglia, S., P. W. Cardozo, A. Ferret, and A. Bach. 2008. Changes in rumen microbial fermentation are due to a combined effect of type of diet and pH. Journal of Animal Science 86: 702-711.

de Haer, L. C. M., P. Luiting, and H. L. M. Aarts. 1993. Relations among individual (residual) feed intake, growth performance and feed intake pattern of growing pigs in group housing. Livestock Production Science 36: 233-253.

DeVries, T. J., M. A. G. von Keyserlingk, and D. M. Weary. 2004. Effect of Feeding Space on the Inter-Cow Distance, Aggression, and Feeding Behavior of Free-Stall Housed Lactating Dairy Cows. Journal of Dairy science 87: 1432-1438.

Durunna, O. N., F. D. N. Mujibi, L. Goonewardene, E. K. Okine, J. A. Basarab, Z. Wang, and S. S. Moore. 2011. Feed efficiency differences and reranking in beef steers fed grower and finisher diets. Journal of Animal Science 89: 158-167.

Ferrell, C. L., and T. G. Jenkins. 1985. Cow type and the nutritional environment: Nutritional aspects. Journal of Animal Science 61: 725-741.

Golden, J. W., M. S. Kerley, and W. H. Kolath. 2008. The relationship of feeding behavior to residual feed intake in crossbred Angus steers fed traditional and no-roughage diets. J Anim Sci 86: 180-186.

Goonewardene, L. A., E. Okine, Z. Wang, D. Spaner, P. S. Mir, Z. Mir, and T. Marx. 2004. Residual metabolizable energy intake and its association with diet and test duration. Canadian Journal of Animal Science 84: 291-295.

Herd, R. M., J. A. Archer, and P. F. Arthur. 2003a. Reducing the cost of beef production through genetic improvement in residual feed intake: Opportunity and challenges to application. Journal of Animal Science 81(E Suppl. 1): E9-E17.

Herd, R. M., J. A. Archer, and P. F. Arthur. 2003b. Selection for low postweaning residual feed intake improves feed efficiency of steers in the feedlot 50 years of DNA: Proceedings of the Fifteenth Conference, Association for the Advancement of Animal Breeding and Genetics, Melbourne, Australia, 7-11 July 2003.

Herd, R. M., and P. F. Arthur. 2009. Physiological basis for residual feed intake. J. Anim Sci. 87: E64-71.

Herd, R. M., V. H. Oddy, and E. C. Richardson. 2004. Biological basis for variation in residual feed intake in beef cattle. 1. Review of potential mechanisms. Australian Journal of Experimental Agriculture 44: 423-430.

Kayser, W., and R. A. Hill. 2013. Relationship between feed intake, feeding behaviors, performance, and ultrasound carcass measurements in growing purebred Angus and Hereford bulls. J Anim Sci 91: 5492-5499.

Kelly, A. K., M. McGee, D. H. Crews, Jr., A. G. Fahey, A. R. Wylie, and D. A. Kenny. 2010. Effect of divergence in residual feed intake on feeding behavior, blood metabolic variables, and body composition traits in growing beef heifers. Journal of Animal Science 88: 109-123.

Koch, R. M., D. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. Journal of Animal Science 22: 486-494.

Lancaster, P. A., G. E. Carstens, F. R. Ribeiro, M. E. Davis, J. G. Lyons, and T. H. Welsh, Jr. 2008. Effects of divergent selection for serum insulin-like growth factor-I concentration on performance, feed efficiency, and ultrasound measures of carcass composition traits in Angus bulls and heifers. J Anim Sci 86: 2862-2871.

Lancaster, P. A., G. E. Carstens, F. R. B. Ribeiro, L. O. Tedeschi, and D. H. Crews. 2009. Characterization of feed efficiency traits and relationships with feeding behavior and ultrasound carcass traits in growing bulls. Journal of Animal Science 87: 1528-1539.

Miller, A. J., D. B. Faulkner, R. K. Knipe, D. R. Strohbehn, D. F. Parrett, and L. L. Berger. 2001. Critical Control Points for Profitability in the Cow-Calf Enterprise. The Professional Animal Scientist 17: 295-302.

Montanholi, Y. R., K. C. Swanson, R. Palme, F. S. Schenkel, B. W. McBride, D. Lu, and S. P. Miller. 2010. Assessing feed efficiency in beef steers through feeding behavior, infrared thermography and glucocorticoids. Animal 4: 692-701.

Nkrumah, J. D., D. H. Crews, Jr., J. A. Basarab, M. A. Price, E. K. Okine, Z. Wang, C. Li, and S. S. Moore. 2007. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. J Anim Sci 85: 2382-2390.

Paddock, Z. D., Carstens, G. E., Lancaster, P. A., McDonald, L. R. & Williams, S. 2008. Evaluation of feed efficiency and feeding behavior traits in Angus and Red Angus growing bulls. Journal of Animal Science 86: E-Suppl. 2 Abstract.

Richardson, E. C., and R. M. Herd. 2004. Biological basis for variation in residual feed intake in beef cattle. 2. Synthesis of results following divergent selection. Australian Journal of Experimental Agriculture 44: 431-440.

Robinson, D. L., and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, muscle area and feeding behaviour of feedlot finished beef cattle. Livestock Production Science 90: 255-270.

Schwartzkopf-Genswein, K. S., S. Atwood, and T. A. McAllister. 2002. Relationships between bunk attendance, intake and performance of steers and heifers on varying feeding regimes. Applied Animal Behavioral Science 76: 179-188.

Schwartzkopf-Genswein, K. S., D. D. Hickman, M. A. Shah, C. R. Krehbiel, B. M. A. Genswein, R. Silasi, D. G. Gibb, D. H. Crews, and T. A. McAllister. 2011. Relationship between feeding behavior and performance of feedlot steers fed barley-based diets. Journal of Animal Science 89: 1180-1192.

Tedeschi, L. O., D. G. Fox, M. J. Baker, and D. P. Kirschten. 2006. Identifying differences in feed efficiency among group-fed cattle. J Anim Sci 84: 767-776.

Weary, D. M., J. M. Huzzey, and M. A. G. von Keyserlingk. 2009. BOARD-INVITED REVIEW: Using behavior to predict and identify ill health in animals. Journal of Animal Science 87: 770-777.

Welch, C. M., J. K. Ahola, J. B. Hall, G. K. Murdoch, D. H. Crews, Jr., L. C. Davis, M. E. Doumit, W. J. Price, L. D. Keenan, and R. A. Hill. 2012. Relationships among performance, residual feed intake, and product quality of progeny from Red Angus sires divergent for maintenance energy EPD. J Anim Sci 90: 5107-5117.

CHAPTER 5

Summary and Conclusions

This research aims to elucidate both benefits and downfalls of using feed efficiency measures in beef cattle. Measurements consist of well-known methods (RFI) as well as the use of feeding behavior traits (bunk visit frequency, bunk visit duration, feed bout frequency, feed bout duration, meal frequency, meal duration, and average meal intake) to obtain relationships with efficiency. Findings from these studies yield interesting results that may aid in future research in the areas of animal efficiency, and behavior.

Evaluation of Wagyu for residual feed intake: optimizing feed efficiency, growth and marbling in Wagyu cattle.

Results from this study provide interesting insight of the use of RFI in niche breed (Wagyu) cattle. Data suggest that by using efficient animals, it is possible to achieve highly marketable cattle that meet consumer demands for marbling and quality. More so, this study indicates a positive trend towards a favorable correlation between RFI and IMF. To this end, it is possible that Wagyu bulls deemed efficient through RFI testing may provide excellent marbling contrary to the noted trend of efficient animals producing leaner carcasses a potential issue for studies in which fat depth was not included in the model to estimate DMI in the calculation of RFI. These results may encourage producers of Wagyu cattle to select for efficiency, thereby lowering input costs without sacrificing carcass quality. This can provide economic benefits for both producers as well as consumers by reducing the costs associated with producing these niche market cattle. However, it is important to note that selection for a single trait can cause unwanted effects on other parameters of the growth and physiology of animals. With this known, it is important to use careful selection when adjusting any production system. More research is needed in this area, with larger populations of animals to help adjust for variability within studies. Overall, this study suggests feed efficiency as a plausible means to increase profitability and lower input costs associated with producing Wagyu beef.

Relationships of feeding behavior with residual feed intake (RFI) in RFI-divergent Japanese black cattle

This study focused on aspects of feeding behavior in correlation with animal efficiency and DMI in Wagyu cattle. Results indicate that variation within both bunk visit and feed bout behaviors between efficient and inefficient Wagyu animals. Findings suggest that feeding frequency traits (bunk visit frequency, feed bout frequency, and meal frequency) are correlated with ADG and DMI in Wagyu bulls consuming a high concentrate diet. Contrasting this, feeding duration traits were more notable in defining efficiency in Wagyu cattle feed a lower concentrate diet. This suggests that diet composition plays a role in these behaviors, therein contributing to the ability of determine efficiency status via feeding behavior. Within bull cohorts, bunk visit duration, feed bout duration, and meal duration were all positively correlated with RFI. These data suggest inefficient animals spend more time at the bunk either "visiting" or consuming feed. In Wagyu heifers, for the behaviors bunk visit duration, feed bout duration, and meal frequency, there was no correlation with RFI as seen in Wagyu bulls. Results indicate a gender interaction within feeding behavior. However, with bunk visit and feed bout frequency showing a similar pattern in heifers and bulls, it is possible that frequency traits are the most plausible means of identifying efficiency via feeding behavior of Wagyu animals. Including feeding behaviors in the base model to predict DMI, in the calculation of RFI,generated a significant reduction in MSE. However, the behaviors used across cohorts differed. With this known, there cannot be a single model used to predict DMI for RFI analysis without constructing a "best-fit" comparison for each cohort. The inclusion of feeding behavior for DMI prediction has potential to account for some variation within the model, however, caution is needed when considering this approach. Within this study, time intervals were introduced to examine chronological changes throughout trial between efficient and inefficient animals. Results from these analyses provide insight that in efficiency status variation via behavioral analysis are most notable in the first half of feeding trails. This is, to the knowledge of the authors, the first time a time period analysis of feeding behavior within trial has been performed. These results provide insight that feeding behavior may be most indicative of efficiency status within the first ~35-40 days of testing, limiting the need to examine animals for extended trial periods. Further research is needed to positively identify these results as the three populations used in the study are small .

Relationship of feeding behavior with ADG,DMI, and residual feed intake (RFI) in Red Angus-sired cattle

This study examined the progeny of Red Angus bulls cattle for feeding behavior during RFI testing. This chapter serves as a follow-up to the previous (Chapter III) using a more typical commercial breed of cattle. Results show feeding duration behaviors as the most prominent in defining efficiency status during growing phase RFI tests in Red Angus cattle. Both bunk visit and feed bout duration in heifer and steer cohorts have potential as predictors of DMI andfeed efficiency. The lack of repeatability in meal duration suggests that feeding bouts may be more indicative of feed efficiency than complete meals. Frequency behaviors were not indicative of variation in DMI or feed efficiency in Red Angus cattle. These behaviors were not found to be of value in predicting DMI or feed efficiency in Wagyu bulls either. To this end, frequency behaviors appear to be poor indicators of DMI or feed efficiency in cattle in the present study. Feeding behaviors were examined for steers across both growing and finishing phases . These analyses provide insight towards all-of life DMI prediction using bunk visit duration and feed bout duration behaviors. Examining sire maintenance energy EPD effect on progeny showed differences in meal duration between groups, with a trend in average meal intake. This suggests a potential sire component that can be observed by feeding behavior. More research in this area may provide relationships of sire metabolism on offspring feeding behavior. Collectively, data from this study provide insightful relationships of feeding behavior and sire effect on cattle efficiency. Periodic analysis of feeding behavior traits over the finishing phase Red Angus cattle only showed small variations in efficiency. Isolated events of correlations occurred during single periods within the study, however, further research is needed to validate these claims.

Implications and future directions

These studies suggest that improving cattle feed efficiency is a viable means to reduce input costs and in doing so, marketable cattle are not sacrificed. The use of feeding behavior, though novel, may provide some insight into underlying mechanisms of feed efficiency in cattle. The current body of work aims to clarify some of these ambiguities by aiding in future research as well as informing producers. Feeding behavior has the potential to indicate efficient animals, and as noted by the current studies over a shorter time period than the standard RFI testing period. However, there are differences noted in this research, as well as others, between breeds and gender of cattle. These are important factors to consider when examining behavioral indicators towards predicting feed efficiency. Many other dynamics play a role in animal efficiency and feeding behavior is only a small portion of a larger picture. Though feeding behavior is often deemed a small percentage of variation in animal efficiency, as researchers it is important to set upon an area and completely define its influence. This research is a small component that is hoped to aid in further clarification of efficiency and feeding behavior. In the future, research needs to examine the deeper mechanisms of feeding behavior. This may entail the use of biological markers, physiological markers (i.e. circulating hormones and proteins) and other tools that allow researchers to gather quantifiable measurements. Also, there should be a standardization of practices with protocols for each system used for monitoring feeding behavior. With the influx of new technology in animal science, methods currently used may be seen as incompatible with future devices. To this end, it is important that all measures have positively identifiable results that are repeatable across platforms with little alteration in design. Diet composition also plays a large role in feeding behavior. It is important to index these diets based on their components to clearly identify their effect on intake and therein behavior. The future of feeding behavior analysis is less limited by technology, but is often surpassed due to its limited influence in efficiency as noted by other researchers. However, with rising feed ingredient costs and increased population size, it will soon become apparent that all parameters that influence animal efficiency will need to be scrutinized to maximize the profitability of the beef industry.

Appendix A

Animal Care and Use Committee Approval from the University of Idaho

Date: Tuesday, June 01, 2010
To: Rod Hill
From: University of Idaho Institutional Animal Care and Use Committee
Re: Protocol 2010-52 Residual Feed Intake Quality Beef Production in Idaho

Your animal care and use protocol for the project shown above was reviewed and approved by the Institutional Animal Care and Use Committee on Tuesday, June 01, 2010.

This protocol was originally submitted for review on: Tuesday, May 04, 2010
The original approval date for this protocol is: Tuesday, June 01, 2010
This approval will remain in affect until: Saturday, June 01, 2013
The protocol may be continued by annual updates until: Saturday, June 01, 2013

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

Brad Williams, DVM
Campus Veterinarian
University of Idaho
208-885-8958

Date: Thursday, April 07, 2011
To: Rod Hill
From: University of Idaho Institutional Animal Care and Use Committee
Re: Protocol 2011-35 Efficient Production of Quality Beef in Idaho

Your animal care and use protocol for the project shown above was reviewed and approved by the Institutional Animal Care and Use Committee on Thursday, April 07, 2011.

This protocol was originally submitted for review on: Wednesday, April 06, 2011.
The original approval date for this protocol is: Thursday, April 07, 2011
This approval will remain in affect until: Friday, October 19, 2012.
The protocol may be continued by annual updates until: Monday, April 07, 2014.

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

Brad Williams, DVM
Campus Veterinarian
University of Idaho
208-885-8958

Appendix B

Copyright permission from *The Journal of Animal Nutrition*

AMERICAN SOCIETY FOR NUTRITION LICENSE TERMS AND CONDITIONS

May 27, 2014

This is a License Agreement between University of Idaho ("You") and American Society for Nutrition ("American Society for Nutrition") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by American Society for Nutrition, and the payment terms and conditions. All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

License Number	3396901405366
License date	May 27, 2014
Volume number	124
Issue number	8 Suppl
Licensed content publisher	American Society for Nutrition
Licensed content publication	The Journal of Nutrition
Licensed content title	Cholecystokinin and Control of Food Intake
Licensed content author	Roger D. Reidelberger
Licensed content date	Aug 1, 1994
Type of Use	Thesis/Dissertation
Requestor type	Student
Portion	Figures/table/illustration
Number of Figures/table/illustration	1
List of figures/table/ illustration	Figure 1
Order reference number	None
Title of your dissertation / thesis	Residual feed intake in beef cattle: In relation to breed, selection, and behavior
Expected completion date	June 2014
Estimated size(pages)	300
Total	0.00 USD

Appendix C

Copyright Permission from *Journal of Animal Science*

Copyright Clearance Center
5/27/2014

Customer Information
Confirmation Number: 11210868
Order Date: 05/27/2014
Customer: Marcus McGee
Account Number: 3000794703
Organization: University of Idaho
Email: mcge9693@vandals.uidaho.edu
Phone: +1 (601)2125102

Order Details
JOURNAL OF ANIMAL SCIENCE: LEADING SOURCE OF NEW KNOWLEDGE AND PERSPECTIVES IN ANIMAL SCIENCE

Order detail ID: 64973583
ISSN: 0021-8812
Publication Type: Monographic Series
Publisher: AMERICAN SOCIETY OF ANIMAL SCIENCE [ETC.]
Author/Editor: AMERIC AN SOCIETY OF ANIMAL SCIENCE; AMERICAN SOCIETY OF ANIMAL PRODUCTION; AMERICAN DAIRY SCIENCE ASSOCIATION
Permission Status: Granted
Permission type: Republish or display content
Type of use: Republish in a thesis/dissertation
Order License Id: 3396860033908

Requesting Information
Requestor type: Academic institution
Format: Print, Electronic
Portion: chart/graph/table/figure
Number of charts/graphs/tables/ figures: 1
Title or numeric reference of the portion(s): Chapter 1
Title of the article or chapter the portion is from: Overview of central targets for appetite regulation
Editor of portion(s): N/A
Author of portion(s): R.L. Matteri
Volume of serial or monograph: 79
Page range of portion: E148-E158
Publication date of portion: 2001
Rights for Main product: Duration of use Life of current edition
Creation of copies for the disabled: no
With minor editing privileges: no
For distribution to Worldwide in the following language(s): Original language of publication
With incidental promotional use: no
Lifetime unit quantity of new product: 0 to 499
Made available in the following markets: Higher Education
The requesting person/organization: Marcus McGee
Author/Editor Marcus McGee
The standard identifier: Ph.D. Dissertation
Title: Residual feed intake in beef cattle: In relation to breed, selection, and behavior

Publisher: University of Idaho
Expected publication date Jun 2014
Estimated size (pages) 300

Appendix D

Copyright Permission from Wiley-Blackwell Publishing

JOHN WILEY AND SONS LICENSE TERMS AND CONDITIONS

May 27, 2014

This is a License Agreement between University of Idaho ("You") and John Wiley and Sons ("John Wiley and Sons") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by John Wiley and Sons, and the payment terms and conditions. All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

License Number	3396890060706
License date	May 27, 2014
Licensed content publisher	John Wiley and Sons
Licensed content publication	Wiley Books
Licensed content title	Feed Efficiency in the Beef Industry
Book title	Feed Efficiency in the Beef Industry
Licensed copyright line	Copyright © 2012, John Wiley and Sons
Licensed content author	Rodney A. Hill (Editor)
Licensed content date	Sep 1, 2012
Type of use	Dissertation/Thesis
Requestor type	University/Academic
Format	Print and electronic
Portion	Figure/table
Number of figures/tables	1
Original Wiley figure/table number(s)	Figure 12.3
Will you be translating?	No
Title of your thesis / dissertation	Residual feed intake in beef cattle: In relation to breed, selection, and behavior
Expected completion date	Jun 2014
Expected size (number of pages)	300
Total	0.00 USD

Appendix E

Copyright permission from *Professional Animal Scientist*

Sent: Sat 5/31/2014 2:25 PM

From: Susan Pollock
To: Marcus McGee
CC: Wayne Kellogg
Subject: RE: Reprinting Permission

Dear Marcus McGee,

The Professional Animal Scientist grants you non-exclusive permission to reprint the following article in your dissertation, provided that it is not displayed or sold separately from the dissertation nor sold commercially.

Evaluation of Wagyu for residual feed intake: Optimizing feed efficiency, growth, and marbling in Wagyu cattle

M. McGee, C. M. Welch, J. B. Hall, PAS, W. Small and R. A. Hill, Professional Animal Scientist. February 2013 vol. 29 no. 1 51-56.

Best regards,

Susan Pollock
Managing Editor
ARPAS