

Characterization of Water Intake in Beef Cattle: Test Length Guidelines, Water Intake
Prediction, and Genetic Parameters

by

Cashley Marie Ahlberg

A.G.S. Northeastern Junior College, 2010
B.S., University of Nebraska-Lincoln, 2012
M.S., University of Nebraska-Lincoln, 2014

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Animal Science
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2018

Abstract

In the future, water may not be as readily available due to an increase in competition from a growing human population, wildlife, and other agricultural sectors. To better understand water demands in the beef industry, water intake has to be accurately measured. It is also critical to understand if water intake is a heritable trait and to determine its relationship to other production traits. This dissertation examines the number of days to accurately measure water intake in beef cattle, how to predict water intake in beef cattle using individual intakes, and estimates genetic parameters for water intake, dry matter intake (DMI), average daily gain (ADG), water efficiency measures, feed efficiency measures, and carcass traits. Study 1 investigates the test duration required to accurately measure water intake. Water intakes were collected over 70 d and shortened test periods (7 day intervals) were correlated with the full 70 day test to determine the minimum number of days required to accurately measure water intake. Water intake can be collected over a 35 to 42-day test period, with a minimal decrease in accuracy. Study 2 developed a water intake prediction equation that included different weather variables and average daily temperature (TAVG), average relative humidity (HAVG), solar radiation (SRAD), and wind speed (WSPD). Water intakes and feed intakes on individual animals were collected over a 70-day period along with (TAVG), (HAVG), (SRAD), (WSPD) for each day. Five different prediction equations were developed: summer, winter, slick bunk feed management, *ad libitum* feed management, and overall. All models included variables of DMI, metabolic mid test weight, TAVG, HAVG, SRAD, and WSPD, with R-squared values ranging from 0.34 to 0.41. Study 3 investigated the relationships between water intake and DMI, ADG, and water and feed efficiency traits. Variance components and

genetic correlations were estimated using single-step genomic best linear unbiased prediction (GBLUP), incorporating genotypes on approximately 150,000 single nucleotide polymorphisms. Water intake was moderately heritable (0.39) and had moderate genetic correlations with DMI and residual feed intake, high genetic correlations with residual water intake, water to gain ratio, and feed to gain ratio, and had a low genetic correlation with ADG. Study 4 investigated the relationship between water intake and carcass traits. Single-Step GBLUP was used to estimate variance components and genetic correlations between water intake and carcass traits. Similar to study 3, water intake was moderately heritable (0.42). Water intake was moderately correlated with hot carcass weight (0.38), back fat (0.36), yield grade (0.29), and final body weight (0.29), but had a low genetic correlation with longissimus muscle area (0.08) and marbling (0.17). More research must be done to determine the relationships between water intake and other economically important traits in beef cattle and to better understand how environment and genetic background affect water intake. Improvements in water efficiency could decrease the amount of water cattle consume and assist producers in managing on-farm water resources during times of water scarcity.

Characterization of Water Intake in Beef Cattle: Test Length guidelines, Water Intake
Prediction, and Genetic Parameters

by

Cashley Marie Ahlberg

A.G.S. Northeastern Junior College, 2010
B.S., University of Nebraska-Lincoln, 2012
M.S., University of Nebraska-Lincoln, 2014

A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Animal Science
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2018

Approved by:

Major Professor
Dr. Megan Rolf

Copyright

© Cashley Ahlberg 2018.

Abstract

In the future, water may not be as readily available due to an increase in competition from a growing human population, wildlife, and other agricultural sectors. To better understand water demands in the beef industry, water intake has to be accurately measured. It is also critical to understand if water intake is a heritable trait and to determine its relationship to other production traits. This dissertation examines the number of days to accurately measure water intake in beef cattle, how to predict water intake in beef cattle using individual intakes, and estimates genetic parameters for water intake, dry matter intake (DMI), average daily gain (ADG), water efficiency measures, feed efficiency measures, and carcass traits. Study 1 investigates the test duration required to accurately measure water intake. Water intakes were collected over 70 d and shortened test periods (7 day intervals) were correlated with the full 70 day test to determine the minimum number of days required to accurately measure water intake. Water intake can be collected over a 35 to 42-day test period, with a minimal decrease in accuracy. Study 2 developed a water intake prediction equation that included different weather variables and average daily temperature (TAVG), average relative humidity (HVAG), solar radiation (SRAD), and wind speed (WSPD). Water intakes and feed intakes on individual animals were collected over a 70-day period along with (TAVG), (HVAG), (SRAD), (WSPD) for each day. Five different prediction equations were developed: summer, winter, slick bunk feed management, *ad libitum* feed management, and overall. All models included variables of DMI, metabolic mid test weight, TAVG, HAVG, SRAD, and WSPD, with R-squared values ranging from 0.34 to 0.41. Study 3 investigated the relationships between water intake and DMI, ADG, and water and feed efficiency traits. Variance components and

genetic correlations were estimated using single-step genomic best linear unbiased prediction (GBLUP), incorporating genotypes on approximately 150,000 single nucleotide polymorphisms. Water intake was moderately heritable (0.39) and had moderate genetic correlations with DMI and residual feed intake, high genetic correlations with residual water intake, water to gain ratio, and feed to gain ratio, and had a low genetic correlation with ADG. Study 4 investigated the relationship between water intake and carcass traits. Single-Step GBLUP was used to estimate variance components and genetic correlations between water intake and carcass traits. Similar to study 3, water intake was moderately heritable (0.42). Water intake was moderately correlated with hot carcass weight (0.38), back fat (0.36), yield grade (0.29), and final body weight (0.29), but had a low genetic correlation with longissimus muscle area (0.08) and marbling (0.17). More research must be done to determine the relationships between water intake and other economically important traits in beef cattle and to better understand how environment and genetic background affect water intake. Improvements in water efficiency could decrease the amount of water cattle consume and assist producers in managing on-farm water resources during times of water scarcity.

Table of Contents

List of Figures	xi
List of Tables	xiii
Acknowledgements	xv
Chapter 1 - Literature Review.....	1
Introduction.....	1
Water Intake.....	2
Predicting Water Intake	6
<i>Beef Cattle:</i>	6
<i>Dairy:</i>	9
Test Duration	11
<i>Daily gain:</i>	11
<i>Dry matter intake:</i>	12
Genetic Parameter Estimates	13
<i>Heritability estimates:</i>	13
<i>Genetic correlations:</i>	15
<i>Phenotypic correlations:</i>	18
Conclusion	20
References.....	22
Chapter 2 - Test Duration of Water Intake, Average Daily Gain, and Dry Matter Intake in Beef Cattle	40
ABSTRACT.....	41
INTRODUCTION	42
MATERIALS AND METHODS.....	43
<i>Study Design</i>	43
<i>Phenotypic Data</i>	45
RESULTS AND DISCUSSION.....	47
<i>ADG Test Duration</i>	47
<i>DMI Test Duration</i>	50
<i>WI Test Duration</i>	53

CONCLUSION.....	55
REFERENCES	57
Chapter 3 - Environmental Effects on Water Intake and Water Intake Prediction in	
Growing Beef Cattle	74
ABSTRACT.....	75
INTRODUCTION	76
MATERIALS AND METHODS.....	77
<i>Phenotypic data</i>	77
<i>Environmental Data</i>	79
<i>Statistical Analysis</i>	80
<i>Effect of Environmental Conditions on Water Intake</i>	80
<i>Cross Validation</i>	83
RESULTS AND DISCUSSION	84
<i>Environmental Variables</i>	84
<i>Effect of Environmental Variables on Water Intake</i>	86
<i>Solar Radiation</i>	88
<i>Average Daily Temperature</i>	90
<i>Average Daily Relative Humidity</i>	92
<i>Average Daily Wind Speed</i>	93
<i>Water Intake Prediction</i>	95
<i>Cross validation</i>	95
<i>Overall Prediction</i>	96
<i>Seasonal Models</i>	101
<i>Ad libitum vs slick bunk management</i>	104
CONCLUSION.....	107
REFERENCES	109
Chapter 4 - Characterization of Water Intake and Water Efficiency in Beef Cattle.....	120
ABSTRACT.....	121
INTRODUCTION	122
MATERIALS AND METHODS.....	123
<i>Study Design</i>	123

<i>Phenotypic Data</i>	125
<i>Breed composition</i>	127
RESULTS AND DISCUSSION.....	131
<i>Water Intake Levels</i>	131
<i>Dry matter intake levels</i>	134
<i>Phenotypic correlations</i>	137
<i>Genetic parameters</i>	141
CONCLUSION.....	147
References.....	149
Chapter 5 - Phenotypic and Genetic Relationship between Water Intake and Carcass	
Traits in Beef Cattle.....	167
ABSTRACT.....	168
INTRODUCTION	169
MATERIALS AND METHODS.....	170
<i>Study Design</i>	170
<i>Carcass data</i>	172
<i>Statistical analysis</i>	173
RESULTS AND DISCUSSION.....	176
<i>Water intake levels</i>	176
<i>Phenotypic correlations</i>	181
<i>Genetic Parameters</i>	184
CONCLUSION.....	192
REFERENCES	194

List of Figures

Figure 2.1 Panel A - Mean average daily gain (ADG) for all animals throughout the 70 d test, Panel – B Mean average daily water intake (WI) and average daily dry matter intake (DMI) throughout the 70 d test	70
Figure 2.2 Panel A - Pearson correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Forward), Panel B - Pearson correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Reverse), Panel C - Spearman correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Forward), Panel D - Spearman correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Reverse).....	71
Figure 2.3 Panel A - Pearson correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Forward), Panel B - Pearson correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Reverse), Panel C - Spearman correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Forward), Panel D - Spearman correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Reverse).....	72
Figure 2.4 Panel A - Pearson correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Forward), Panel B - Pearson correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Reverse), Panel C - Spearman correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Forward), Panel D - Spearman correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Reverse)	73
Figure 3.1 Percent increase or decrease in water intake as a percent of body weight (WI%) within each group resulting from step-wise addition of weather variables to the model.....	118
Figure 4.1 Mean breed composition estimated for each group and across all groups for 16 different breeds	163

Figure 4.2 Mean breed composition when individual breeds were combined into their biological grouping within each group and across groups..... 164

Figure 4.3 Plots depicting relationships between water intake and various feed and water efficiency traits. Panel A: Dry matter intake (DMI) and water intake (WI), Panel B- Residual feed intake (RFI) and water intake (WI), Panel C- Feed to gain (F/G) and water intake (WI), Panel D- Water to gain (W/G) and water intake (WI), Panel E- Residual water intake (RWI) and water intake (WI), Panel F- Average daily gain (ADG) and water intake (WI) 165

Figure 4.4 Plots depicting relationships between various feed and water efficiency traits. Panel A - individual water to gain (W/G) plot against individual residual water intake (RWI), Panel B - individual residual feed intake (RFI) plot against individual feed to gain ratio (F/G), Panel C - individual residual feed intake (RFI) plot against individual residual water intake (RWI), Panel D - individual feed to gain ratio (F/G) plot against individual water to gain ratio (W/G) 166

List of Tables

Table 1.1 Heritability estimates (SE) for average daily gain (ADG), feed intake (FI), residual feed intake (RFI), and feed conversion ratio (FCR) in growing animals published within the scientific literature.....	38
Table 1.2 Estimates of heritability for carcass traits reported in the scientific literature categorized by end point	39
Table 2.1 Summary statistics for average daily gain, (ADG), dry matter intake (DMI), and water intake (WI) over the 70 d test period.....	61
Table 2.2 Means (standard deviations) for a 70-d average daily gain (ADG, kg) test. Shorter test durations are subsets of the full 70-d test of the specified duration. Forward analyses begin at d 0 and reverse analyses begin at d 70.	62
Table 2.3 Pearson and Spearman correlations for each shortened test duration and the full 70 d test period for ADG (kg).....	63
Table 2.4 Means (standard deviations) for a 70-d dry matter intake (DMI, kg) test. Shorter test durations are subsets of the full 70 d test of the specified duration. Forward analyses begin at d 0 and reverse analyses begin at d 70.	64
Table 2.5 Pearson and Spearman correlations for each shortened test duration and the full 70 d test period for DMI (kg).....	65
Table 2.6 Means (standard deviations) for a 70-d water intake (WI, kg) test. Shorter test durations are subsets of the full 70 d tests of the specified duration. Forward analyses begin at d 0 and reverse analyses begin at d 70.....	67
Table 2.7 Pearson and Spearman correlations for each shortened test duration and the full 70 d test period for water intake (WI, kg).....	68
Table 3.1 Means, standard deviations, minimums (Min) and maximums (Max) for environmental variables observed during the feeding period for each group.....	114
Table 3.2 LSMEANS for effect of environmental variables on mean water intake as a percent of mid-test body weight for cattle fed in different groups, seasons, and under different bunk management protocols. The baseline model with no environmental variables included was augmented with each additional weather variable in the table until all four variables were fit in the model.....	115

Table 3.3 Univariate regression analysis of each variable used for predicting water consumption (kg/d) of crossbred steers.	116
Table 4.1 Summary statistics for water intake (WI), Dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain ratio (W/G) and feed to gain ratio (F/G) for each group.....	157
Table 4.3 LSMEANS for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain (W/G), and feed to gain (F/G) for each group at low, medium, and high DMI levels ^a	159
Table 4.3 Genetic correlations ^a for water intake, (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain (W/G) and feed to gain (F/G).....	162
Table 5.1 Harvest location, number of head (n), and days on finishing ration (DOF) for each group.	203
Table 5.2 Summary statistics for hot carcass weight (HCW), rib eye area (REA), back fat (BFAT), marbling (MARB), yield grade (YG), and final body weight (FBW) for each group.	204
Table 5.3 LSMEANS for hot carcass weight (HCW), rib eye area (REA), back fat (BFAT), marbling (MARB), yield grade (YG), and final body weight (FBW) for each group	205
Table 5.4 LSMEANS for hot carcass weight (HCW), rib eye area (REA), back fat (BFAT), marbling (MARB), yield grade (YG), and final body weight (FBW) for each group at low, medium, and high water intake levels	206
Table 5.5 Pearson (above the diagonal) and Spearman (below the diagonal) phenotypic correlations between water intake (WI) and carcass traits ^a . P-values indicate whether the correlation was significantly different from zero	208
Table 5.6 Heritability estimates ^a (on the diagonal) and genetic correlations ^a (above the diagonal) for water intake and carcass traits ^b	209

Acknowledgements

I truly appreciate the funding from the supported by Agriculture and Food Research Initiative Competitive Grant No. 2014-67004-21624 from the U. S. Department of Agriculture National Institute of Food and Agriculture. Also, a special thank you to all of the professors, graduate students, and undergraduate student at Oklahoma State University for all the help collecting data and running the project.

Thank you to my advisor, Dr. Megan Rolf for granting me the opportunity to work on this project. Also, thank you to all the opportunities you presented me with to present my data, attend short courses and mentor fellow geneticist. Thank you for all the help dealing with all the challenges presented in this study.

Thank you Dr. Robert Weaber and Dr. Jennifer Bormann for all the support and guidance that you have provided throughout this project. Thank you to Dr. Larry Kuehn for serving as my outside committee member, your support and guidance has been greatly appreciated. Thank you for also allowing me to use breed allele frequencies to accomplish my genetic analysis.

Thank you to my parents for all your patience and support throughout this whole process. They have laid a great foundation and have given me the opportunity to full fill my dreams. I am truly appreciated of all the sacrifices that they have made for my sake.

Finally, thank you to my fiancé, Bill, for you time and support you have given throughout my PhD degree process. Thank you for being there when times were tough and encouraging me to continue and succeed.

Chapter 1 - Literature Review

Introduction

Over the past 10 years, the United States has had 5 to 80% of its land mass affected by drought (NOAA, 2018). The drought observed in the United States throughout 2012 was one of the worst since the 1950's. In 2012, 80% of agricultural land was affected by drought (USDA, 2012). In the 21st century, food and water security will be a priority for mankind (Nardone et al., 2010). The world is experiencing a change in global climate which will affect local climate as well as impact local and global agriculture (Thornton et al., 2007). Indirect effects of global warming that may impair animal production include soil infertility, water scarcity, decreasing grain yield and quality, and diffusion of pathogens (Nardone et al., 2010). Crop and livestock yields can be directly affected by change in climate factors such as temperature, precipitation, and the frequency and severity of extreme weather events like droughts, floods, and wind storms (Adams et al., 1998). Global warming is predicted to cause a 25% loss in animal production within developing countries, and may be more severe in Africa and some zones in Asia (Seguin, 2008).

Water scarcity is a global issue causing problems with food production, human health, and economic development which effects 1-2 billion people worldwide (Millennium Ecosystem Assessment, 2005). It is predicted that in 2025, 64% of the world population will live in a water-deprived basin, compared to 38% in 2009 (Rosegrant et al., 2002). With climate change, water may become the weak point in all livestock systems. Not only is water becoming more salinized, but water may also contain chemical contamination from either organic or inorganic material, as well as have high concentrations of heavy metal and biological contaminants (Nardone et al. 2010). Animals

that are in hot environments are expected to drink 2-3 times more than animals in cooler climates (Nardone et al. 2010), so these animals run a higher risk of exposure to contaminated water and water-borne diseases. The effects of global warming on water availability could force the livestock sector to establish a new priority in production of animal products that require less water (Nardone et al. 2010).

Water Intake

Growing concern over the availability of drinking water necessitates a greater understanding of the amount of water that is used by livestock. Freshwater is approximately 2.5% of all water resources, and of this water, almost 70% is unusable because it is tied up in glaciers and permanent ice (Thornton et al., 2009). Agriculture uses almost 70% of the world's freshwater resources (Thornton et al., 2009). Approximately 760 billion liters of water are consumed by beef cattle annually (Beckett and Oltjen, 1993). Daily water requirements in beef cattle are influenced by environmental factors, diet, breed, and body weight, and the interaction of these factors make it challenging to determine the daily water requirement for beef cattle (Arias and Mader, 2011). Winchester and Morris (1956) conducted the earliest research on water intake (WI) in cattle, which had been used as the basis for the daily water requirements for cattle published by the National Research Council (NRC, 2000). Winchester and Morris (1956) looked at ratio of dry matter intake (DMI) and WI at varying temperatures to predict WI in individual animals. However, the data in this study was collected on a small number of animals at each temperature and was collected over a short number of days. Brew et al. (2011) collected WI on individual animals housed in a pen setting using a GrowSafe™ system. Brew et al. (2011) reported a mean WI of 29.98 kg for growing steers, heifers, and young bull calves. Even though Brew

et al. (2011) performed their study in Florida, it was conducted from September to December when temperatures are lower, thus cattle are more likely experiencing thermal neutral conditions.

Parker et al. (2000) collected WI during the fall using a flow meter at the incoming water supply for each pen. Data were collected on 50,000 head of feedlot steers located in the high plains of Texas. In this study, WI was reported to be an average of 35.6 liter per day. Meyer et al. (2006) measured WI by taking the difference of the initial and final weight of the water bin for 62 German Holstein bulls and the average WI was 17.8 liters per day. Sexson et al. (2012) collected water intakes from April to October over a four-year period using water meters attached to each individual pen waterer. In this study, the average daily water consumption was 37.14 liters for feedlot steers housed in Colorado.

Winchester and Morris (1956) determined the amount of water consumption required in dairy animals and determined that the amount of water consumed by dairy animals is different between lactating and dry cows. Winchester and Morris (1956) also reported WI for dairy animals based on the amount of feed they consumed at different temperature levels (1.40 liter per kg of feed, 1.51 liter per kg of feed, 1.74 liter per kg of feed, 2.04 liter per kg of feed, 2.35 liter per kg of feed, and 3.33 liter per kg of feed, for 4.4°C, 10.0°C, 15.6°C, 21.1°C, 26.7°C, and 32.2°C, respectively, similar to their procedures in beef cattle. Meyer et al. (2004) collected water intake on 60 Holstein cows that were housed in a thermally non-isolated loose housing system. Thirty cows had access to 2 water vats that held 30 kg of water, and intakes were measured by taking the difference of the beginning and ending weight of the vats (Meyer et al., 2004). In this study, average daily WI for milking dairy cows was reported to be 81.5 kg, and values for individual animals

ranged from 14.2 to 171.4 kg. Melin et al. (2005) reported WI in lactating dairy cows averaged 84 liters per day. In their study, 30 fresh cows were utilized and 67,525 WI visits were recorded. Cardot et al. (2008) collected intake on 41 lactating dairy cows over a 70 d period during the spring, fall, and winter. Average daily WI was 82 liters per day. Higher water intakes in dairy cows (~80 liters) as compared to beef steers (~32 liters) is likely due to the fact that the dairy cows were utilizing more water to produce milk, due to its high water content (Winchester and Morris, 1956)

It has been shown that *Bos taurus* cattle have higher water consumption than *Bos indicus* breeds, especially as temperature increases (Winchester and Morris, 1956). Brew et al. (2011) also looked at differences in WI between various breeds of cattle. The Charolais x Angus cross steers consumed more water (42.8 kg; $P < 0.05$) than Angus x Brangus (30.8 kg), Brangus (30.8 kg), Charolais x Brangus (29.7 kg), Brangus x Romosinuano (24.1 kg), and Charolais x Romosinuano (20.7 kg; Brew et al., 2011). All the breed crosses that were examined, other than the Angus x Charolais and the Charolais x Romosinuano crosses, had some percentage of *Bos indicus* germplasm, which had shown by Winchester and Morris (1956) to consume less water. However, even though the Romosinuano breed is classified as a *Bos taurus* breed, they are known for their tropical adaptability (Riley et al., 2014). Some tropically adapted cattle, such as Romosinuano, do not have zebu influence, which suggests that other *Bos taurus* breeds could be selected to become more adaptable or drink less water while still maintaining positive performance characteristics.

Seasonal effects on WI were examined by Hoffman and Self (1972), and they found that cattle fed in the summer consume an average of 31.2 liters, and cattle fed during the

winter consumed an average of only 19.0 liters. Arias and Mader (2011) also reported that cattle finished during the summer season drink 87.3% more water than cattle finished during the winter season (32.4 liters vs 17.3 liters). Hicks et al. (1988) reported an average daily WI of 35.9 liters per day during the summer months when housed in confinement. During the summer season, cattle need to reduce heat load, which results in increased daily WI (Beede and Collier, 1986). The primary way cattle reduce heat load is through evaporative cooling (Morrison, 1983), which increases demand for water to maintain body homeostasis.

Cattle that have access to shade during the summer consume less water (30.1 vs 32.6 liters; $P < 0.01$) than cattle that do not have access to shade (Hoffman and Self, 1972). However, this trend was not been observed for cattle fed during the winter, where there is no difference in water consumption for animals that have access to shade (Hoffman and Self, 1972). The shade provided to the cattle in Hoffman and Self (1972) was an overhead structure that allowed for airflow. Shade structures that are closed on multiple sides would restrict airflow through the structure and would likely negatively impact heat stress and WI because airflow can help to cool animals (Mader et al. 2006). Effects of water temperature on WI were examined by Ittner et al. (1951). This study included two groups of Herefords consisting of 3 steers and 1 heifer per group. Water intake was collected from June to September using calibrated water meters on the pen waterers (Ittner et al., 1951). In this study, cattle that drank water that was cooled (58.14 liters) to 18°C had decreased water consumption (4.73 liters less per day) compared to cattle that had uncooled water which had an average temperature of 31.2°C (58.14 liters vs 62.87 liters). By providing shade over water sources the water temperature would be cooler than unshaded waters.

Predicting Water Intake

Beef Cattle:

Because WI phenotypes are not easy to collect, equations to predict WI have been developed. The first equation for WI prediction was developed in 1956 by Winchester and Morris (1956) and was based on DMI within a variety of temperature ranges. Winchester and Morris (1956) created a table with ranges of temperature, body weight, and DMI associated with expected daily water consumption for individuals reported in gallons. Over thirty years later, Hicks et al. (1988) developed a prediction equation describing the average daily WI for the week for feedlot steers that included daily maximum temperature, DMI, precipitation, and percentage of dietary salt. Daily maximum temperature and DMI were positively correlated with WI and daily precipitation and percentage of dietary salt are negatively correlated with WI (Hicks et al., 1988).

Twenty-three years later, Arias and Mader (2011) developed three prediction equations for WI based on pen WI data: summer, winter and general prediction equations that estimated the average daily WI of growing steers and heifers. They utilized seven different experiments conducted in Nebraska, consisting of 1,278 Angus and Angus cross steers and heifers that had pen WI phenotypes, to develop their WI prediction equation. For the summer and general model, Arias and Mader (2011) discovered that DMI, solar radiation, and minimum temperature were the best predictors of WI. However, for the winter model, DMI, solar radiation, maximum temperature, wind speed, relative humidity, and precipitation were the best predictors of WI. The summer and winter models explained 23% of the variation in WI, but the overall model explained 64% of the variation (Arias and Mader 2011). In the summer model, solar radiation explained the largest portion of the

variation ($R^2 = 0.14$), followed by minimum temperature ($R^2 = 0.05$) and DMI ($R^2 = 0.04$). However, in the overall model, minimum temperature explained the largest proportion of variation ($R^2 = 0.56$) followed by solar radiation ($R^2 = 0.07$) and DMI ($R^2 = 0.02$; Arias and Mader, 2011).

Shortly thereafter, Sexson et al. (2012) developed an equation to predict the average daily WI of growing steers utilizing pen water intakes ($n = 8,209$) that were collected over 4 years. Sexson et al. (2012) used more weather variables in their prediction equation, and the resulting equation explained more variation ($R^2 = 0.32$) than the summer and winter models developed by Arias and Mader (2011). The Sexson et al. (2012) prediction equation contained low and high temperature, low, average, and high relative humidity, low, average, and high sea level pressure, wind speed, body weight, metabolic body weight, previous day high temperature. Body weight and metabolic body weight were fit as linear variables and average humidity, high temperature, relative humidity, previous day high and low temperature were fit as quadratic variables. High and low temperature for the current day were fit as quadratics, and previous day high temperature explained the most variation (Sexson et al., 2012).

Dry matter intake and body weight are two variables that influence daily WI. During the winter, cattle tend to have higher DMI and decreased daily WI (Arias and Mader, 2011). However, the opposite tends to happen during the summer, where cattle tend to have decreased dry matter intake and increased in daily WI (Arias and Mader, 2011). Hicks et al. (1988) and NRC (2000) noted a positive relationship between dry matter intake and daily WI. The relationship between WI and DMI in beef cattle is not fully understood, and the impact that environmental variables have on this relationship may differ between

animals. Body weight ($R^2 = 0.012$) and metabolic body weight ($R^2 = 0.091$) are also important predictors of WI (Sexson et al., 2012). For cattle that have a body weight less than 500 kg, water consumption increases from 22 to 38 liters per animal per day as body weight increases. Cattle that weigh more than 500 kg have decreases in WI as body weight increases (Sexson et al., 2012). The decline in WI associated with animals larger than 500 kg could be a function of the change in composition of gain: as the proportion of fat increases, the proportion of protein and water gain decreases (NRC, 2000).

Sexson et al., (2012) found that water consumption increased by approximately 13 liters per animal per day when daily maximum temperature increased from 25°C to 45°C. Cattle that experience temperatures below 15°C exhibit large decreases in water consumption (Sexson et al., 2012). Arias and Mader (2011) found that for every 1-degree decrease in minimum temperature, WI decreases 0.5 kg per head per day.

Relative humidity also has an effect on the amount of water consumed by cattle. Small increases in WI are observed when humidity is less than 50%. However, when relative humidity is over 50%, water consumption in cattle decreases by 1 liter per head per day for every 10% increase in relative humidity (Sexson et al., 2012). When temperatures are below 24°C, humidity has limited impact on water consumption. However, at higher temperatures, water consumption is lower when humidity is high (Ragsdale et al., 1953). During the summer months, Arias and Mader (2011) saw no effect of relative humidity on WI. During the winter, a decrease in WI was observed concomitant with increased relative humidity (Arias and Mader, 2011).

Sexson et al. (2012) demonstrated that wind speed was a predictor of WI. Loneragan et al. (2001) also observed a positive correlation between wind speed and WI,

but wind speed explained only 0.5% of the variation observed in WI. Sexson et al. (2012) noted a positive affect between WI and average barometric pressure, but a negative affect between high and low barometric pressure and WI. Water vapor pressure gradient is modified by barometric pressure, which could lead to the loss of water during respiration (IOM, 2005).

Other than Winchester and Morris (1956), WI prediction equations found in the literature have been developed using pen intake data extrapolated to individual animals. However, in Winchester and Morris (1956) individual water intakes were measured on approximately 50 animals, which is a fairly small sample size. By definition, pen averages cannot account for or quantify individual-animal variation in any phenotype. Pen water intake are easier to predict due to normality properties that are assumed due to the central limit theorem. It is crucial to be able to quantify the variability in individual WI to be able to make selection decisions to improve water efficiency or to decrease the amount of water required for beef production without compromising performance, health, or welfare.

Dairy:

Cardot et al. (2008) created a prediction equation for lactating dairy cows that explained 44.6% of the variation in WI. In this study, the traits that were found to have the highest correlations with WI were DMI, daily milk yield (MY), lactation number, maximum temperature (TMAX), dry matter content of the ration (DMC), and rain fall (RF). Dry matter intake explained the most variation (28.7%) followed by milk yield (8.8%). Appuhamy et al. (2016) developed seven different models, four for lactating dairy cows and three for dry cows. The first two lactating dairy models were developed without mineral and temperature variables included in the model. Model one included DMI, dry

matter percent (DM%), ash percent (ASH%), and percent protein (CP%; Appuhamy et al., 2016). The second model included MY, DMI%, ASH%, and body weight (BW). The first model explained 51% of the heterogeneity, and model 2 explained only 46% of the heterogeneity (Appuhamy et al., 2016). Dry matter intake, DM%, and ASH% had a positive relationship with WI, which was independent of milk and body yield (Appuhamy et al., 2016). Models three and four were based on lactating dairy cows and included mineral and temperature variables. The third model included the following variables: DMI, DM%, joint concentration of Na and K in the diet (NaK), average temperature (TEMP), and CP% (Appuhamy et al. 2016). The fourth model included variables of MY, NaK, DM%, TEMP, and DMI (Appuhamy et al, 2016). The third model explained 76% of the heterogeneity, and the fourth model explained 63% of the heterogeneity. The joint concentration of Na and K and TEMP had a positive relationship with WI (Appuhamy et al., 2016). The increase in water consumption due to temperature is believed to be triggered by the increased need to support evaporative and respiratory heat losses (Appuhamy et al. 2016). Models 5, 6 and 7 were based on dry cow models. The fifth model included the following variables: DMI, DM% and TEMP. The sixth model included variables of DMI, DM%, TEMP and $TEMPC^2$ ($TEMP-16.4$)² and the seven model include variables of BW, DM%, TEMP and $TEMPC^2$ (Appuhamy et al., 2016). Dry matter intake, DMI%, and TEMP were positively associated with WI for models five and six. From the seventh model, it was determined that DMI was important to predict WI in dry cows (Appuhamy et al., 2016).

Test Duration

Accurate measurement of WI phenotypes is necessary to develop selection tools and make genetic progress in beef cattle. The Beef Improvement Federation (BIF) has already established guidelines for collection of data on many different traits (BIF, 2016). Traits like average daily gain (ADG), body weight, and feed intake on individual animals require multiple measurements over a period of time, and the time required for each is variable (Wang et al, 2006). Due to similarities in methodology of collection, WI would be expected to also require multiple measurements for accurate phenotype collection.

Daily gain:

Recommendations for a 112-day testing period for rate of gain in beef cattle were made by Franklin et al., (1987), Kemp, (1990) and Brown et al., (1991). Swiger and Hazel (1961) and Lui and Makarechian (1993a,b) demonstrated that the test length for ADG could be shortened to 84-days, and more recently, Archer et al. (1997) and Wang et al., (2006) have made recommendations for an even shorter test period of 70 and 63 days, respectively. One reason for reduced test length in recent studies is increased frequency of body weight measures. The more frequently body weights are measured, the more gain information is available, thus allowing a shorter test duration (Archer et al., 1999; Graham et al., 1999). Archer and Bergh (2000), Kearney et al., (2004), and Culbertson et al., (2015) showed that test length could be shorted to 56-days if body weights were collected daily. However, BIF guidelines (BIF, 2016) require that feed intake data must be removed on days where weights are collected, due to the lack of access to feed for a portion of the day. Thus, weighing cattle every day would not be practical unless accurate in-pen weights could be collected in a way that does not restrict access to feed. Body weights taken without

withholding feed and water can vary throughout the day due to patterns of feed and WI for each individual animal (Zinn, 1990). In addition, weight measurements can be affected by movement of an animal on the scale and loss of digesta from the tract (Owens et al., 1995). Due to weight variation within a day and differences in precision of weights, it is important to have multiple measurements over an extended period of time.

Dry matter intake:

Efficiency of an animal production system is not only important from an economic stand point but is also important from a socio-environmental viewpoint (Hegarty et al., 2007). Consumers are concerned about the impact cattle have on the environment, thus making cattle more efficient will lower the impact they have on environment (Hegarty et al., 2007). For beef producers, feed costs represent a major economic input (Fan et al., 1995), and the efficiency of utilizing feed is different for each individual animal (Bailey et al., 1971; Garrett, 1971; Freeman, 1975). Elucidating these differences requires collection of individual-animal DMI.

Archer and Bergh (2000) recommend that DMI test length of 56 days for Afrikaner, Angus, Bonsmara and Hereford and 70-days for Simmental cattle. However, 35-days was recommended by Archer et al. (1997), Wang et al. (2006), and Retallick et al. (2017). Culbertson et al. (2015) and Cassady et al. (2016) recommended 42-day tests when looking at the beginning of the growing period and Cassady et al. (2016) recommended 35-days when looking at the end of the growing period. Clearly, dry matter intake can be accurately collected over a shorter time period than ADG, likely because DMI is measured daily. A shortened test length for DMI is beneficial because it allows more animals to be tested in one facility annually, which increases output from the system. Improvements in total beef

production efficiency could be made more rapidly with the ability to test more animals (Cassady et al., 2016), which drives the need to have cost-effective ways to test a greater number of animals. When ADG and DMI are collected simultaneously, a full 70 day test period is needed (Wang et al., 2006). However, when DMI and gain are decoupled, a shortened test period can be utilized for DMI (Wang et al., 2006). Average daily gain and DMI are collected together to be able to get measure of feed efficiency like residual feed intake. Residual feed intake is the difference between actual feed intake and expected feed intake (Koch et al., 1963). Estimated feed intake is calculated by regressing DMI on ADG and metabolic mid weight (Koch et al., 1963). Collecting ADG and DMI together is likely not necessary if ADG is assumed to be relatively consistent over the DMI collection period.

Genetic Parameter Estimates

As the importance of WI in production agriculture increases, we need to understand whether WI is a heritable trait and if selection can reduce WI in cattle. It is also key to understand the genetic and phenotypic relationships between WI and other production traits. Production trait in cattle are measures of performance and impact the amount of income that is generated. Greater knowledge of the amount of water cattle consume is important, and will allow the development and evaluation of water efficiency metrics.

Heritability estimates:

No estimates of heritability for WI have been reported for livestock, but there are estimates of heritability reported in mice. Bachmanov et al. (2002) reported a high heritability estimate for WI (0.69) and Ramirez and Fuller (1976) reported a moderate heritability estimate of 0.44. Bachmanov et al. (2002) utilized 28 different strands of mice, where individual WI was collected over a 4-day period, and Ramirez and Fuller (1976)

utilized heterogeneous mice, fully inbred, and partially inbred mice that had individual water intakes collected over 38 days.

Heritability estimates for DMI, ADG, residual feed intake (RFI) and feed conversion ratio (FCR) are reported in Table 1.1. Feed intake heritabilities range from 0.06 to 0.70, with an average pooled estimate of 0.40. Average daily gain has a moderate average heritability of 0.31 and ranges from 0.06 to 0.65. Residual feed intake has a moderate average heritability of 0.34 and ranges from 0.07 to 0.62. Heritability estimates for feed conversion ratio range from 0.06 to 0.46 and had an average of 0.23. The average heritability estimates were moderate for these traits, thus selection can be practiced to improve genetic merit for each of these traits. There is a large range in heritability estimates for all traits, suggesting large differences in genetic variance for these populations or breeds. There could also be differences due to the environment in which the cattle were reared. To reduce the amount of feed required for growth in feedlot cattle, it would be beneficial to improve FCR. However, genetic selections using ratio traits presents a challenge in prediction of change in the component traits for future generations (Arthur et al., 2001a).

Many carcass weight heritability estimates have been documented in the literature and are reported in Table 1.2. Heritability estimates where HCW was adjusted for either age or backfat thickness average 0.42 and 0.35, respectively. Morris et al. (1990) found that HCW adjusted for age resulted in higher heritability estimates than when adjusted for fat thickness (0.28 vs 0.17). The opposite result was reported by Devitt and Wilton (2001), which showed that fat adjusted HCW had higher heritability estimates than age adjusted (0.57 vs 0.47). In contrast, Shanks et al. (2001) found no difference in the heritability

estimate of HCW between the two adjustments. The difference between the two adjustments varied across studies (Utrera and Van Vleck, 2004).

Bouquet et al. (2010) reported that the heritability for live weight adjusted to 450 days of age is 0.54. Rib eye area heritability estimates in the literature range from 0.15 to 0.97 when heritability is adjusted to a constant age point and when adjusted to a constant weight ranged from 0.25 to 0.57. Lee et al. (2000) reported heritability estimates for REA for age (0.17) and backfat (0.18) adjusted analyses. However, Shanks et al. (2001) found that REA adjusted for backfat thickness had a slightly higher heritability estimate (0.29) when compared to age adjusted REA (0.26). Heritability estimates for BFAT range from 0.30 to 0.94 (Table 1.2), suggesting that genetic gain can be achieved through selection. Heritability estimates were similar when adjusted for different covariates and analyzed within the same study. Literature estimates for MARB when adjusted to a constant age ranged from 0.08 to 0.88, with the average being 0.45. When YG was adjusted to a constant age heritability estimates ranged from 0.24 to 0.85.

Genetic correlations:

Genetic correlations between FI and ADG in the scientific literature range from -0.54 to 0.87, with an average of 0.78 (Berry and Crowley 2013). Koch et al. (1963) reported smaller genetic correlation between ADG and FI (-0.54) and Grion et al. (2014) reported larger genetic correlations (0.87). Koch et al. (1963) observed variability in genetic correlation between ADG and FI estimates depending on the location, suggesting there may be some genotype by environmental interaction. The strong positive genetic correlation between FI and ADG suggests that selection to decrease feed intake to reduce feed costs (Arthur et al., 2001a) will also reduce gain. Average daily gain had negative

genetic correlation with feed conversion ratio of -0.62 with a range of -0.89 to 0.75 (Berry and Crowley, 2013). Arthur et al. (2001a) suggested that selecting for decrease FCR may reduce the amount of feed required for growth but could also lead to increase in mature BW which raises the cost of maintenance in breeding programs. Residual feed intake and ADG have small genetic correlation of 0.02 and ranges from -0.15 to 0.53 (Berry and Crowley, 2013). Due to the near non-existing correlation between RFI and ADG, selection for improved feed efficiency using RFI would have minimal effect on increasing mature body size in the cow herd compared to using FCR (Arthur et al., 2001a).

Feed intake has a moderate, positive average correlation of 0.39 with feed conversion ratio (Berry and Crowley, 2013). Mao et al. (2013) reported a low negative genetic correlation between FI and FCR -0.02 and positive estimates reported by Arthur et al. (2001a), and Arthur et al. (2001c) of 0.31 and 0.57, respectively. Selecting for decreased F/G ratio may reduce the amount of feed required for growth but could also lead to increases in mature BW, which raises the cost of maintenance in breeding programs (Arthur et al., 2001a). Previous literature has reported a wide range of genetic correlations between residual feed intake and FCR (-0.69, Koch et al., 1963; 0.66, Arthur et al., 2001a; 0.23, Archer et al., 2002; 0.41, Robinson and Oddy, 2004). The wide range of genetic correlations between RFI and FCR suggests that selecting to improve RFI could increase or decrease FCR. The average genetic correlation between the feed efficiency traits averaged 0.75 and ranged from -0.21 to 0.93.

Hot carcass weight has a high genetic correlation with REA (0.66, Cundiff et al., 1964; 0.678, Lamb et al., 1990; 0.42, Devitt and Wilton 2001). Rib eye area is expected to have a strong positive genetic correlation with HCW because REA is an indicator of

carcass muscling, which is a factor in total carcass weight (Devitt and Wilton, 2001). A low positive genetic correlation was observed between HCW and BFAT (0.15, Devitt and Wilton, 2001; 0.283, Lamb et al., 1990; 0.15, Cundiff et al., 1964; -0.06, Wilson et al., 1993; -0.05, Moser et al., 1997). The positive genetic correlation suggested by Devitt and Wilton, (2001), Lamb et al. (1990), and Cundiff et al. (1964) would suggest that selecting for increased HCW would increase the amount of fat on the animals. However, the negative genetic correlation reported by Wilson et al. (1993) and Moser et al. (1997) would suggest the opposite that selecting for increase HCW would decrease the amount of fat on the animals. The genetic correlation estimates for HCW and BFAT in Wilson et al. (1993) were from an Angus population, whereas Moser et al. (1997) used Brangus-sired animals. Lamb et al. (1990) reported a high, positive genetic correlation between HCW and MARB 0.569 and Devitt and Wilton (2001) reported a negative genetic correlation of -0.32 between HCW and MARB. Due to a wide range of genetic correlations reported in previous literature between HCW and BFAT as well as HCW and MARB, selecting cattle using a selection index in improve these traits would be the most beneficial. Lamb et al. (1990) reported a high, positive genetic correlation between REA and MARB (0.57) whereas Devitt and Wilton (2001) reported a moderate, negative correlation (-0.37).

Rib eye area is a part of the USDA YG calculation (Koch et al., 1982), and would be expected to have a high correlation with YG. Koch et al. (1982) reported a genetic correlation of 0.53 between REA and YG. Koch et al. (1982) reported a genetic correlation between BFAT and YG of -0.74 and Lamb et al. (1990) reported a much weaker genetic correlation of 0.184. Back fat thickness is also used to calculate USDA YG, so it would be expected to have a high correlation with YG. Based on the high genetic correlation

between BFAT and YG, it would be expected that BFAT would be a useful predictor of YG (Koch et al., 1982).

Phenotypic correlations:

Bachmanov et al. (2002) reported a phenotypic correlation between feed intake (FI) and WI in mice of 0.65. Physiological differences exist between cattle and mice due to the fact that cattle are ruminants and mice are monogastrics. There is also a vast difference in body size, which leads to differences in maintenance requirements (Demment and Van Soest, 1985). The positive correlation between FI and WI in mice may be due to their mutual dependency on body size, but it might involve another mechanism that is linked to FI and WI (Bachmanov et al., 2002).

Dry matter intake has a moderate to strong, positive phenotypic correlation with ADG (0.41 Arthur et al. 2001a; 0.42, Archer et al., 2002; 0.66, Nkrumah et al., 2004; 0.71, Robinson and Oddy, 2004; 0.63, Groin et al., 2014). The positive phenotypic correlation between DMI and ADG suggest that as cattle consume more feed they will gain faster. Residual feed intake is highly correlated with feed intake with an average of 0.66 (Berry and Crowley, 2013), larger and smaller estimates ranging from 0.42 (Robinson and Oddy, 2004) to 0.77 (Nkrumah et al., 2004). The strong phenotypic correlation between DMI and RFI suggests that cattle with lower DMI will also have lower RFI thus being more feed efficient. Phenotypic correlations between DMI and FCR ranged from -0.57 to 0.049 (Arthur et al., 2001a, Archer et al., 2002, Nkrumah et al., 2004, and Robinson and Oddy, 2004). Cattle that consume less feed will also have a decrease in the amount of feed required for growth, due to positive correlation between DMI and FCR (Arthur et al., 2001a and Robinson and Oddy, 2004). However, a negative phenotypic correlation between DMI

and FCR reported Archer et al. (2002) and Nkrumah et al. (2004) would suggest the opposite.

Previous literature reported low to high, negative phenotypic correlations between ADG and FCR (-0.74, Arthur et al. 2001a; -0.04 Archer et al., 2002; -0.63, Nkrumah et al., 2004; -0.08, Robinson and Oddy, 2004). Cattle that have higher gains will also tend to have lower FCR (more efficient). Residual feed intake is phenotypically uncorrelated with ADG by definition (Berry and Crowley, 2013), with larger and smaller estimates ranging from -0.06 (Arthur et al., 2001a) to 0.04 (Archer et al., 2002). Residual feed intake is generated at the phenotypic level and is thus phenotypically independent of its regressors when calculated using least squares regression (Berry and Crowley, 2013). Residual feed intake has a moderate, positive phenotypic correlation with FCR averaging 0.39 and ranging from -0.62 to 0.76 (Berry and Crowley, 2013). Advancements in technologies to measure feed consumption and animal performance using automated individual animals feeding systems could increase the accuracy of measuring these traits, and could explain some of the variation observed in correlations reported between traits.

Hot carcass weight has a high, positive phenotypic correlation with REA of 0.46, 0.579, and 0.53 (Cundiff et al., 1964, Lamb et al., 1990, and Devitt and Wilton 2001), thus heavier muscled animals also weigh more. Phenotypic correlations were small between HCW and BFAT values of 0.095, -0.007, and -0.004 have been reported by Lamb et al. (1990), Cundiff et al. (1964), and Devitt and Wilton (2001), respectively. Changes in HCW could result in minimal changes in BFAT, due to the small phenotypic correlation between HCW and BFAT. Lamb et al. (1990) and Devitt and Wilton (2001) reported positive phenotypic correlations between HCW and MARB (0.190 and 0.15, respectively)

suggesting heavier cattle also have more marbling. Devitt and Wilton (2001) reported REA and MARB (0.04) to be uncorrelated where Lamb et al. (2001) reported a small, positive correlation between REA and MARB (0.19). Rib eye area has a weak, positive phenotypic correlation with BFAT of 0.095 (Lamb et al., 2001). Cattle that have heavier carcass and larger REA will also tend to have more MARB. Marbling has a small, positive phenotypic correlation with BFAT and YG of 0.25 and 0.201, respectively (Lamb et al., 1990). Lamb et al. (1990) observed for phenotypic correlation between BFAT and YG of 0.276. Back fat is a component trait in the YG calculation and would be expected to be positively correlated with YG (Lamb et al., 1990).

Conclusion

Water is an essential and economically important nutrient that can be a limiting resource in some environments. Changes in the environment, population growth, competition from other agricultural enterprises, and wildlife impact the amount of high-quality water that is available to be utilized for animal production. Depending on the time of year, cattle consume an average of 19.0 to 37.14 liters of water per day; it has been reported that milking dairy cows could consume more than 100 liters a day. There has been limited study of water consumption in beef cattle through measuring individual water intakes while housed in a group setting, which would contribute greater understanding of WI and its effect on performance and efficiency. However, the largest contributor to the water footprint of animal production comes from the feed they consume (98.05), where a very small portion comes from drinking water (0.8%; Mekonnen and Hoekstra, 2012). While making changes in direct water consumption of beef cattle will not dramatically

change the overall water footprint of beef production, it should help producers manage on-farm water concerns, especially during drought.

Prediction equations have been developed to predict daily WI for individual animals that may also help producers manage on-farm water resources when they are scarce. These prediction equations account for a variety of different factors including dry matter intake, temperature, solar radiation, relative humidity, wind speed, and precipitation. Even though studies have already been conducted to develop prediction equations using pen water intake data, no studies have determined the number of days that are needed to collect accurate water intake phenotypes and only one study has developed prediction equations for water intake utilizing data on individual animals. The Beef Improvement Federation (BIF, 2016) has set guidelines for the number of days necessary to accurately measure ADG, DMI, residual feed intake and feed conversion ratio, but no guidelines exist for WI. Average daily gain and feed intake require a 70 d test period but DMI can be collected over a shorter test duration of 35 d. To make genetic progress in selecting cattle for WI, genetic parameters need to be estimated for WI in cattle. Heritability has been estimated in mice, where it is moderately to highly heritable. The relationship between WI other economically relevant traits must also be established to make sure that selecting to decrease water intake will not have negative impacts on other economically relevant production traits.

References

- Adams, R. M., B. H. Hurd, S. Lenhart, and N. Leary. 1998. Effects of global climate change on agriculture: an interpretative review. *Clim. Res.* 11:19-30
- Appuhamy, J. A. D. R. N., J. V. Judy, E. Kebreab, and P. J. Kononoff. 2016. Prediction of drinking water intake by dairy cows. *J. Dairy. Sci.* 99:7191-7205
- Arias, R. A. and T. L. Mader. 2011. Environmental factors affecting daily water intake on cattle finished in feedlots. *J. Anim. Sci.* 89:245-251
- 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. *J. Anim. Sci.* 75:2024-2032
- Archer, J. A. and L. Bergh. 2000. Duration of performance test for growth rate, feed intake, and feed efficiency in four biological types of beef cattle. *Lives. Prod. Sci.* 65:47-55
- Archer, J. A., A. Reverter, R. M. Herd, D. L. Johnston, and P.F. Arthur. 2002. Genetic variation in feed intake and efficiency of mature beef cow and relationships with postweaning measurements. In: *Proc 7th World Congr. Genet. Appl. Livest. Prod.* Montpellier, France
- 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. *Aust. J. Agric. Res.* 44:361-369
- Arthur, P. F., J. A. Archer, D. J. Johnson, 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. *J. anim. Sci.* 79:2805-2811

- Arthur, P. F., J. A. Archer, D. J. Johnson, R. M. Herd, E. C. Richardson, and P. F. Parnell. 2001b. Response to selection for net feed intake in beef cattle. *Proc. Assoc. Adv. Anim. Breed. Genet.* 14:135-138
- Arthur, P. F., G. Renand, and D. Krauss. 2001c. Genetic and phenotypic relationships among different measures of growth and feed efficiency in young Charolais bulls. *Livest. Prod. Sci.* 68:131-139
- Backmanov, A. A., D. R. Reed, G. K. Beauchamp, and M. G. Todoff. 2002. Food intake, water intake, and drinking spout side preference of 28 mouse strains. *Behav. Genet.* 32:435-443
- Bailey, C. M., W. R. Harvey, J. E. Hunter, and C. R. Torell. 1971. Estimated direct and correlated response to selection for performance traits in closed Hereford lines under different types of environments. *J. Anim. Sci.* 33:541
- Barkhouse, K. L., L. D. Van Vleck, L. V. Cundiff, M. Koohmaraie, D. D. Lunstra, and J. D. Crouse. 1996. Prediction of breeding values for tenderness of market animals from measurements on bulls. *J. Anim. Sci.* 74: 2612–2621
- Barwick, S. A., M. L. Wolcott, D. J. Johnson, H. M. Burrow and M. T. Sullivan. 2009. Genetics of steer daily and residual feed intake in two tropical beef genotypes, and relationships among intake, body composition, growth and other post-weaning measures. *Anim. Prod. Sci.* 49:351-366
- Beckett, J. L. and J. W. Oltjen. 1993. Estimation of the water requirement for beef production in the United States. *J. Anim. Sci.* 84:3415-3420
- Beede, D. K. and R. J. Collier. 1986. Potential nutritional strategies for intensively managed cattle during the thermal stress. *J. Anim. Sci.* 71:543-554

- Benyscheck. 1981. Heritabilities for growth and carcass traits estimated from data on Herefords under commercial conditions. *J. Anim. Sci.* 53:49-56
- Berry, D. P. and J. J. Crowley. 2013. Cell Biology Symposium: Genetics of feed efficiency in dairy and beef cattle. *J. Anim. Sci.* 91:1594-1613
- BIF. 2016. Guidelines for uniform beef improvement program. Beef Improvement Federation. Ninth edition. Raleigh, NC
- Bishop, S. C., J. S. Broadbent, R. M. Kay, I. Rigby and A. V. Fisher. 1992. The performance of Hereford x Friesian offspring of bulls selected for lean growth rate and lean food conversion efficiency. *Anim. Prod.* 54:23-30
- Bouquet, A. M. N. Fouilloux, G. Renand, and F. Phocas, 2010. Genetic parameters for growth, muscularity, feed efficiency, and carcass traits of young beef bulls. *Livest. Sci.* 129:38-48
- Brew, M. N., R. O. Myer, M. J. Hersom, J. N. Carter, M. A. Elzo, G. R. Hansen, and D. G. Riley. 2011. Water intake and factors affecting water intake of growing beef cattle. *Livest. Sci.* 140:297-300
- Brown, A. H., Jr., J. J. Chewning, A. B. Johnson, W. C. Lee, and C. J. Brown. 1991. Effects of 84-, 112- and 140-day postweaning feedlot performance tests for beef bulls. *J. Anim. Sci.* 69: 451-461
- Brown, A. H., Jr., Z. B. Johnson, J. J. Chewning, and C. J. Brown. 1988. Relationship among absolute growth rate, relative growth rate and feed conversion during postweaning feedlot performance tests. *J. Anim. Sci.* 66:2524-2529
- Cardot, V., Y. Le Roux, and S. Jurjanz. 2008. Drinking behavior of lactating dairy cows and prediction of their water intake. *J. Dairy. Sci.* 91:2257-2264

- Cassady, C. J., T. L. Felix, J. E. Beever, D. W. Shike, and National Program for Genetic Improvement of Feed Efficiency in Beef Cattle. 2016. Effects of timing and duration of test period and diet type on intake and feed efficiency of Charolais-sired cattle. *J. Anim. Sci.* 94:4748-4758
- Crews, D. H. Jr., E. J. Pollak, R. L. Weaver, R. L. Quaas, and R. J. Lipsey. 2003. Genetic parameters for carcass traits and their live animal indicators in Simmental cattle. *J. Anim. Sci.* 81:1427–1433
- Crowley, J. J., M. McGee, D. A. Kenny, D. H. Crews Jr., R. D. Evans and D. P. Berry. 2010. Phenotypic and genetic parameters for different measures of feed efficiency in different breed of Irish performance teste beef bulls. *J. Anim. Sci.* 88:885-894
- Culbertson, M. M., S. E. Speidel, R. K. Peel, R. R. Cockrun, M. G. Thomas, and R. M. Enns. 2015. Optimum measurement period for evaluating feed intake traits in beef cattle. *J. Anim. Sci.* 93:2482-2487
- Cundiff, L. V., D. Chambers, D. F. Stephens, and R. L. Willham. 1964. Genetic analysis of some growth and carcass traits in beef cattle. *J. Anim. Sci.* 23:1133-1138.
- Cundiff, L. V., K. E. Gregory, R. M. Koch, and G. E. Dickerson. 1971. Genetic relationships among growth and carcass traits of beef cattle. *J. Anim. Sci.* 33:550-555
- Demment, M. W., and R. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist.* 125:641-672

- Devitt, C. J. B., and J. W. Wilton. 2001. Genetic correlation estimates between ultrasound measurement on yearling bulls and carcass measurements on finished steers. *J. Anim. Sci.* 79:2790-2797
- Dunn, R. J., W. T. Magee, K. E. Gregory, L. V. Cundiff, and R. M. Koch. 1970. Genetic parameters in straightbred and crossbred beef cattle. *J. Anim. Sci.* 31:656–663
- Durunna, O. N., F. D. N. Mujibi, L. Goonewardena, 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. *J. Anim. Sci.* 89:158-167
- Durunna, O. N., G. Plastow, F. D. N. Mujibi, J. Grant, J. Mah, J. A. Basarab, E. K. Okine, S. S. Moore, and Z. Wang. 2011b. Genetic parameters and genotype x environment interaction for feed efficiency traits in steers fed grower and finisher diets. *J. Anim. Sci.* 89:158-167
- Elzo, M. A., D. D. Johnson, G. C. Lamb, T. D. Maddock, R. O. Myer, D. G. Riley, G. H. Hansen, J. G. Wasdin, and J. D. Driver. 2010. Heritabilities and genetic correlations between postweaning feed intake, growth, and ultrasound traits in a multibreed Angus-Brahman cattle population in the subtropics. In: Proc 9th World Congr. Genet. Appl. Livest. Prod. Leipzig, Germany, p. 203-207
- Fan, L. Q., D. R. C. Bailey, and N. H. Shannon. 1995. Genetic parameter estimation of postweaning gain, feed intake, and feed efficiency for Hereford and Angus bulls fed two different diets. *J. Anim. Sci.* 73:365-372
- Franklin, C. L., W. V. Thayne, W. R. Wagner, L. P. Stevens, and E. K. Inskeep. 1987. Factors affecting gain of beef bull consigned to a central test station. Bulletin 693. Agricultural and Forestry Experiment Station. West Virginia Univ., Morgantown

- Freeman, A. E. 1975. Genetic variation in nutritional of dairy cattle. National Academy of Science, Washington DC. P 19
- Garett, W. N. 1971. Energetic efficiency of beef and dairy steers. *J. Anim. Sci.* 32:451
- Gengler, N., C. Seutin, F. Boonen, and L. D. Van Vleck. 1995. Estimation of genetic parameters for growth, feed consumption, and conformation traits for double-muscled Belgian blue bulls performance-tested in Belgium. *J. Anim. Sci.* 73:3269-3273
- Glaze, J. B., Jr., and R. R. Schalles. 1995. Selection response and genetic parameter estimation for feed intake, gain, and feed conversion. <http://krex.k-state.edu/dspace/handle/2097/4876> (Accessed March 3, 2018)
- Graham, J. F., B. K. Knee, A. J. Clark, and G. A. Kearney. 1999. The potential to shorten the feeding period when measuring the net feed conversion efficiency of cattle using an automated feeding and weighing systems. *Proc. Adv. Anim. Breed. Genet.* 13:488-491
- Gregory, K. E., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and M. Koohmaraie. 1994. Breed effects, retained heterosis, and estimates of genetic and phenotypic parameters for carcass and meat traits of beef cattle. *J. Anim. Sci.* 72:1174–1183
- Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1995. Genetic and phenotypic (co)variances for growth and carcass traits of purebred and composite populations of beef cattle. *J. Anim. Sci.* 73:1920–1926
- Groin, A. L., M. E. Z. Mercadante, J. N. G. Cyrillo, S. F. M. Bonilha, E. Magnani, and R. H. Branco. 2014. Selection for feed efficiency traits and correlated genetic responses in feed intake and weight gain of Nellore cattle. *J. Anim. Sci.* 92:955-965

- Hassen, A., D. E. Wilson, and G. H. Rouse. 1999. Evaluation of carcass, live, and real-time ultrasound measures in feedlot cattle: I. Assessment of sex and breed effects. *J. Anim. Sci.* 77:273–282
- Hegarty, R. M., J. P. Goopy, R. M. Herd, and B. McCorkell. 2007. Cattle selected for lower residual feed intake have reduced daily methane production. *J. Anim. Sci.* 85:1479-1486
- 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. *Livest. Prod. Sci.* 63:111-119
- Hicks, R. B., F. N. Owens, D. R. Gill, J. J. Martin, and C. A. Strasia. 1988. Water intake by feedlot steers. *Okla. Anim. Sci. Rep. Mr.* 125-208
- 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. *Livest. Sci.* 99:11-118
- Hoque, M. A., M. Hosono, T. Oikawa, and K. Suzuki. 2009. Genetic parameters for measures of energetic efficiency of bulls and their relationship with carcass traits of field progeny in Japanese Black cattle. *J. Anim. Sci.* 87:99-106
- Inoue, K., M. Kobayahi, N. Shoji, and K. Kato. 2011. Genetic parameters for fatty acid composition and feed efficiency traits in Japanese Black cattle. *Animal.* 5:987-994
- IOM (Institute of Medicine). 2005. Dietary reference intakes for water, Potassium, Sodium, Chloride, and Sulfate. *Natl. Acad. Press, Washington, DC*

- Ittner, N. R., C. F. Kelly, and H. R. Guilbert. 1951. Water consumption of Hereford and Brahman cattle and the effect of cooled drinking water in hot climate. *J. Anim. Sci.* 10:742-751
- Jensen, J., I. L. Mao, B. B. Andersen, and P. Madsen. 1991. Genetic parameters of growth, feed intake, feed conversion, and carcass composition of dual-purpose bulls in performance testing. *J. Anim. Sci.* 69:931-939
- Kemp, R. A. 1990. Relationships among test length and absolute and relative growth rate in central bull tests. *J. Anim. Sci.* 68:624-629
- Kemp, D. J., W. O. Herring, and C. J. Kaiser. 2002. Genetic and environmental parameters for steer ultrasound and carcass traits. *J. Anim. Sci.* 80:1489-1496
- Koch, R. M. 1978. Selection in beef cattle III. Correlated response of carcass traits to selection for weaning weight, yearling weight and muscling score in cattle. *J. Anim. Sci.* 47:142-150
- Koch, R. M. L. V. Cundiff, and K. E. Gregory. 1982. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. *J. Anim. Sci.* 55:1319-1329
- Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22:486-494
- Korver, S. E., A. M. van Eekelen, H. Vos, G. J. Nieuwhof, and J. A. M. van Arendonk. 1991. Genetic parameters for feed intake and feed efficiency on growing dairy heifers. *Livest. Prod. Sci.* 29:49-59

- Lamb, M. A., O. W. Robison, and M. W. Tess. 1990. Genetic parameters for carcass traits in Hereford bulls. *J. Anim. Sci.* 68:64–69
- Lee, J. W., S. B. Choi, J. S. Kim, J. F. Keown, and L. D. Van Vleck. 2000. Parameter estimates for genetic effects on carcass traits of Korean native cattle. *J. Anim. Sci.* 78:1181–1190
- Loneragan, G. H., J. J. Wagner, D. H. Gould, F. B. Garry, and M. A. Thoren. 2001. Effects of water sulfate concentration on performance, water intake, and carcass characteristics of feedlot steers. *J. Anim. Sci.* 79:2941-2948
- Lui, M. F., and M. Makarechian. 1993a. Factors influencing growth performance of beef bulls in test station. *J. Anim. Sci.* 71:1123-1127
- Lui, M. F., and M. Makarechian. 1993b. Optimum test period and associations between standard 140-day test period and shorter test periods for growth rate in station test beef bulls. *J. Anim. Breed Genet.* 110:312-317
- Mader, T. L., M. S. Davis, and T. Brown-Brandl. 2006. Environmental factors influencing heat stress in feedlot cattle. *J. Anim. Sci.* 84:712-719
- MacNeil, M. D., L. V. Cundiff, C. A. Dinkel, and R. M. Koch. 1984. Genetics correlations among sex-limited traits in beef cattle. *J. Anim. Sci.* 58:1171–1180
- MacNeil, M. D., D. R. Bailey, J. J. Urick, R. P. Gilbert, and W. L. Reynolds. 1991. Heritabilities and genetic correlations for postweaning growth and feed intake of beef bulls and steers. *J. Anim. Sci.* 69:3183–3189
- MacNeil, M. D., D. N. Lopez-Villalobos, and S. L. Northcutt. 2011. A prototype national cattle evaluation for feed intake and efficiency of Angus cattle. *J. Anim. Sci.* 89:3917-3923

- Mao, F., L. Chen, M. Vinsky, E. Okine, Z. Wang, J. Basarab, D. H. Crews Jr., C. Li. 2013. Phenotypic and genetic relationships of feed efficiency with growth performance, ultrasound, and carcass merit traits in Angus and Charolais steers. *J. Anim. Sci.* 91:2067-2076
- Mekonnen, M. M., and A. Y. Hoekstra. 2012. A global assessment of the water footprint of farm animal products. *Ecosystems* 15:401-415
- Melin, M., H. Wiltorsson, and L. Norell. 2005. Analysis of feeding and drinking patterns of dairy cows in two cow traffic situations in automatic milking system. *J. Dairy. Sci.* 88:71-85
- Meyer, U., M. Everinghoff, D. Gadeken, and G Flachowsky. 2004. Investigations on the water intake of lactating dairy cows. *Livest. Prod. Sci.* 90:117-121
- Meyer, U. W. Stahl, and G. Flachowsky. 2006. Investigation on the water intake of growing bulls. *Livest. Sci.* 130:186-191
- Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: Synthesis.* Island Press. Washington
- Morris, C. A., R. Baker, A. Carter, and S. Hickey. 1990. Evaluation of eleven cattle breeds for crossbred beef production: Carcass data from males slaughtered at two ages. *Anim. Prod.* 50:79-92
- Morris, C. A. Cullen, N. G. and D. G. McCall. 1999. Genetic and phenotypic relationships among carcass measurements in beef cattle. *N. Z. J. Agric. Res.* 42:415-421
- Morrison, S. R. 1983. Ruminant heat stress: Effect on production and means of alleviation. *J. Anim. Sci.* 67:1594-1600

- Moser, D. W., J. K. Bertrand, I. Misztal, L. A. Kriese, and L. L. Benyshek. 1998. Genetic parameter estimates for carcass and yearling ultrasound measurements in Brangus cattle. *J. Anim. Sci* 76:2542–2548
- Mujibi, F. D. N., J. D. Nkrumah., O. N. Durunna, P. Stothard, J. Mah, Z. Wang, J. Basarab, G. Plastow, D. H. Crews Jr., and S. S. Moore. 2011. Accuracy of genomic breeding values for residual feed intake in crossbred beef cattle. *J. Anim. Sci.* 88:3353-3361
- Nardone, A., B. Ronchi, N Lacetera, M.S. Ranieri, and U. Bernabucci. 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livest. Prod.* 130:57-69
- Nephawe, K. A., L. V. Cundiff, M. E. Dikeman, J. D. Crouse, L. D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score of cows, and carcass traits of their steer relatives. *J. Anim. Sci.* 82:647–653
- 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. 2007. Genetic and phenotypic relationships of serum leptin concentration with performance, efficiency of gain, ultrasound and carcass merit of feedlot cattle. *J. Anim. Sci.* 85:2382-2390
- NOAA. 2018. Drought-February. <https://www.ncdc.noaa.gov/sotc/drought/>. Accessed April 18, 2018
- NRC. 2000. Nutrient Requirements of Beef Cattle. 7th rev. ed. Natl. Acad. Press. Washington, DC

- Okanishi, T., S. Masayuki, K. Tomohiro, O. Kenji, and F. Mukai. 2008. Genetic analysis of residual feed intakes and other performance test traits of Japanese Black cattle from revised protocol. *J. Anim. Sci.* 79:291-296
- Owens, F. N., D. R. Gill, D. S. Secrist and S. W. Coleman. 1995. Review of some aspects of growth and development of feedlot cattle. *J. Anim. Sci.* 73:3152-3172
- Parker, D. B., L. J. Perino, B. W. Auermann, and J. M Sweeten 2000. Water use and conservation at Texas high plains beef cattle feedyards. *Appl. Eng. Agric.* 16:77-82
- Pariacote, F., L. D. Van Vleck, R. E. Hunsley. 1998. Genetic and phenotypic parameters for carcass traits of American Shorthorn beef cattle. *J. Anim. Sci.* 76:2584–2588
- Ramirez, I. and J. L. Fuller. 1976. Genetic influence on water and sweetened water consumption in mice. *Physiol. Behav.* 16:163-168
- Ragsdale, A. C., H. J. Thompson, D. M. Worstell, and S. Brody. 1953. The effect of humidity on milk production and composition, feed and water consumption and body weight in cattle. *Res. Bul.* 521. Mo. Agr. Exp. Sta., University of Missouri, Columbia
- Retallick, K. J., J. M. Bormann, R. L. Weaber, M. D. MacNeil, H. L. Bradford, H. C. Freetly, K. E. Hales. D. W. Moser, W. M. Snelling. R. M. Thallman, and L. A. Kuehn. 2017. Genetic variance and covariance and breed differences for feed intake and average daily gain to improve feed efficiency in growing cattle. *J. Anim. Sci.* 95:1444-1450
- Reynolds, W. L., J. J. Urick, D. A. Veseth, D. D. Kress, T. C. Nelsen, and R. E. Short. 1991. Genetic parameters by son-sire covariances for growth and carcass traits of Hereford bulls in a nonselected herd. *J. Anim. Sci.* 69:1000–1007

- Riley, D. G., C. C. Chase Jr., S. W. Coleman, and T. A. Olson. 2014. Evaluation of the Criollo breed Romosinuano as purebred and crossbred cows with Brahman and Angus in Florida: I. Reproduction and parturition. *J. Anim. Sci.* 92:1902-1910. doi:10.2527/jas2013-7279
- Robinson, D. L. and V. H. Oddy. 2004. Genetic parameters for feed efficiency, fatness, and muscle area and feeding behavior of feedlot finished beef cattle. *Livest. Prod. Sci.* 90:255-270
- Rolf, M. M., J. F. Taylor, R. D. Schnabel, S. D. McKay, M. C. McClure, S. L. Northcutt, M. S. Kerley, and R. L. Weaber. 2010. Impact of reduce marker set estimation of genomic relationship matrices of genomic selection for feed efficiency in Angus cattle. *BMC Genet.* 11:24-33
- Rolfe, K. M., W. M. Snelling, M. K. Nielsen, H.C. Freetly, C. L. Ferrell, and T. G. Jenkins. 2011. Genetic and phenotypic parameter estimates for feed intake and other traits in growing beef cattle, and opportunities for selection. *J. Anim. Sci.* 89:3452-3459
- Rosegrant, M. W., X. Cai, and S. A. Cline. 2002. Global water outlook to 2020, Averting an impending crisis, A 2020 vision for food, agriculture, and the environment initiative. International Food Policy Research Institute/International Water Management Institute, Washington, D. C. U.S.A/ Colombo, Sri Lanka
- 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. *Can. J. Anim. Sci.* 84:177-185
- Sexson, J. L., J. J. Wagner, T. E. Engle. and J. Eickhoff. 2012. Predicting water intake by yearling feedlot steers. *J. Anim. Sci.* 90:1920-1928

- Shanks, B. C., M. W. Tess, D. D. Kress, and B. E. Cunningham. 2001. Genetic evaluation of carcass traits in Simmental-sired cattle at different slaughter end points. *J. Anim. Sci.* 79:595–604
- Shelby, C. E., W. R. Harvey, R. T. Clark, J. R. Quesenberry, and R. R. Woodward. 1963. Estimates of phenotypic and genetic parameters in ten years of Miles City R.O.P. steer data. *J. Anim. Sci.* 22:346–353
- Splan, R. K., L. V. Cundiff, M. E. Dikeman, L. D. Van Vleck. 2002. Estimates of parameters between direct and maternal genetic effects for weaning weight and direct genetic effects for carcass traits in crossbred cattle. *J. Anim. Sci.* 80:3107–3111
- Suguin, B., P. Rowlinson, M. Steele, A. Nefzaoui (Eds.). 2008. The consequence of global warming for agriculture and food population. In *Proc International Conf. Livestock and Global Climate Change*. p 9-11
- Swiger, L. A., and L. N. Hazel. 1961. Optimum length of feeding period in selecting for gain of beef cattle. *J. Anim. Sci.* 20:189-194
- Thornton, P. K., J. van de Steeg, A. Notenbaert, and M. Herrero. 2009. The impacts of climate change on livestock and livestock systems in developing countries: A review of what we know and what we need to know. *Agric. Syst.* 101:113-127
- USDA. 2012. U.S. drought 2012: Farm and food impacts. [Http://www.ers.usda.gov/topics/in-the-nes/us-drought-2012-farm-and-food-impacts.aspx/#livestock](http://www.ers.usda.gov/topics/in-the-nes/us-drought-2012-farm-and-food-impacts.aspx/#livestock). Accessed: April 4, 2015
- Utrera, A. R., and L. D. Van Vleck. 2004. Heritability estimates for carcass traits of cattle: a review. *Genet. Molec. Resear.* 3:380-394

- Van Arendonk, J. A. M., G. J. Nieuwhof, H. Vos, and S. Korver. 1991. Genetic aspects of feed intake and efficiency in lactation dairy heifers. *Livest. Prod. Sci.* 71:1721-1729
- Van der Westhuizen, R. R., J. Van der Westhuizen, and S. J. Schoeman. 2004. Genetic variance components for residual feed intake and feed conversion ratio and their correlation with other production traits in beef bulls. *South Afr. J. Anim. Sci.* 54:257-264
- Van Vleck, L.D., A. F. Hakim, L. V. Cundiff, R. M. Koch, J. D. Crouse, and K. G. Boldman. 1992. Estimated breeding values for meat characteristics of crossbred cattle with an animal model. *J. Anim. Sci.* 70:363–371
- Veseth, D. A., W. L. Reynolds, J. J. Urick, T. C. Nelsen, R. E. Short, and D. D. Kress. 1993. Paternal half-sib heritabilities and genetic, environmental, and phenotypic correlation estimates from randomly selected Hereford cattle. *J. Anim. Sci.* 71:1730–1736
- 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
- Wheeler, T. L., L. V. Cundiff, R. M. Koch, J. D. Crouse. 1996. Characterization of biological types of cattle (Cycle IV): carcass traits and longissimus palatability. *J. Anim. Sci.* 74:1023–1035
- Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2001. Characterization of biological types of cattle (Cycle V): carcass traits and longissimus palatability. *J. Anim. Sci.* 79:1209–1222

- Williams, Y. J., J. E. Pryce, C. Grainger, W. J. Wales, N. Linden, M. Porker, and B. J. Hayes. 2011. Variation in residual feed intake in Holstein Friesian dairy heifers in southern Australia. *J. Dairy. Sci.* 94:4715-4726
- Wilson, D. E., R. L. Willham, S. L. Northcutt, G. H. Rouse. 1993. Genetic parameters for carcass traits estimated from Angus field records. *J. Anim. Sci.* 71:2365–2370
- Winchester, C. F., and M. J. Morris. 1956. Water intake rates of cattle. *J. Anim. Sci.* 15:722-740
- Zinn, D. W., R. M. Durham, and H. B. Hedrick. 1970. Feedlot and carcass grade characteristics of steers and heifers as influenced by days on feed. *J. Anim. Sci.* 31:302-306

Table 1.1 Heritability estimates (SE) for average daily gain (ADG), feed intake (FI), residual feed intake (RFI), and feed conversion ratio (FCR) in growing animals published within the scientific literature.

ADG	FI	RFI	FCR	Reference
0.35	0.62	0.62	0.42	Archer et al., (1997)
0.41	0.59	0.44	0.31	Arthur et al. (1997)
0.28	0.39	0.39	0.29	Arthur et al. (2001a)
0.34	0.48	0.39	0.46	Arthur et al. (2001b)
0.41	0.48	0.43	0.31	Arthur et al. (2001c)
0.34	0.49	0.24		Barwick et al. (2009)
0.20	0.51	0.38		Barwick et al. (2000)
0.48	0.37		0.19	Bergh et al. (1992)
0.48	0.06		0.46	Bishop et al. (1992)
	0.30	0.26	0.30	Bouquet et al. (2010)
	0.48	0.45	0.23	Bouquet et al. (2010)
0.36			0.14	Brown et al. (1988)
0.33			0.13	Brown et al. (1988)
		0.30		Crews et al. (2003)
		0.26		Crews et al. (2003)
0.30	0.49	0.45	0.30	Crowley et al. (2010)
0.06	0.30	0.19	0.07	Durunna et al. (2011)
0.17	0.43	0.36	0.26	Durunna et al. (2011)
	0.21	0.14	0.18	Elzo et al. (2010)
0.43	0.27	0.23	0.35	Fan et al. (1995)
0.16	0.18	0.07	0.08	Fan et al. (1995)
0.55	0.58		0.16	Gengler et al. (1995)
0.25	0.24		0.14	Glaze and Schalles (1995)
0.38	0.31	0.16	0.17	Herd and Bishop (2000)
0.20	0.34	0.24	0.15	Hoque et al. (2006)
	0.36	0.49	0.38	Hoque et al. (2006)
	0.70	0.22	0.11	Inoue et al. (2011)
0.37	0.26		0.27	Jensen et al. (1991)
0.65	0.64			Koch et al. (1963)
0.30	0.56		0.18	Korver et al. (1991)
0.26	0.36	0.18		MacNeil et al. (2011)
0.28	0.41	0.29		Mujibi et al. (2011)
0.59	0.54	0.18	0.41	Knrumah et al. (2007)
0.26	0.33	0.14	0.14	Okanishi et al. (2008)
0.22	0.43			Retallick et al (2017)
0.23	0.27	0.52	0.06	Robinson and Oddy (2004)
0.09	0.14	0.38		Rolf et al. (2010)
0.26	0.40	0.19	0.27	Rolfe et al. (2011)
0.35	0.44	0.31	0.37	Schenkel et al. (2004)
0.27	0.46	0.27	0.37	Van Arendonk et al. (1991)
0.37			0.34	Van der Westhuzen et al. (2004)
0.22	0.17			Williams et al. (2011)

Table 1.2 Estimates of heritability for carcass traits reported in the scientific literature categorized by end point

Adjustment	CW	BFAT	LEA	MARB	YG	Reference	
Constant age				0.40		Barkhouse et al. (1996)	
	0.48	0.52	0.40	0.47		Benyshek (1981)	
	0.48	0.46	0.54			Crews et al. (2003)	
			0.43	0.73		Cundiff et al. (1964)	
	0.56	0.50	0.41	0.31		Cundiff et al. (1971)	
	0.47	0.45	0.35			Devitt and Wilton (2001)	
		0.94	0.02	-0.15		Dunn et al. (1970)	
		0.30		0.52		Gregory et al. (1994)	
	0.23	0.25	0.22	0.48		Gregory et al. (1995)	
	0.33	0.14	0.15			Hassen et al. (1999)	
	0.37	0.07	0.18			Hoque et al. (2002)	
	0.48	0.45	0.42			Kemp et al. (2002)	
			0.34	0.49	0.78		Kim et al. (1998)
	0.68	0.68	0.28	0.34		Koch (1978)	
	0.43	0.41	0.56	0.40		Koch et al. (1982)	
				0.17	0.08		Lee et al. (2000)
	0.44						MacNeil et al. (1984)
			0.52				MacNeil et al. (1991)
	0.28	0.03	0.30				Morris et al. (1990)
	0.48		0.42				Morris et al. (1999)
	0.59	0.27	0.39				Moser et al. (1998)
	0.52	0.57	0.65	0.59	0.53		Nephawe et al. (2004)
	0.6	0.46	0.97	0.88	0.54		Pariacote et al. (1998)
	0.33		0.01				Reynolds et al. (1991)
	0.32	0.26	0.12				Shanks et al. (2001)
	0.57	0.24	0.26				Shelby et al. (1963)
	0.49	0.58	0.60	0.58	0.49		Splan et al. (2002)
			0.62	0.43			Van Vleck et al. (1992)
	0.38		0.51	0.31			Veseth et al. (1993)
	0.15	0.56	0.65	0.73	0.76		Wheeler et al. (1996)
0.33	0.84	0.69	0.57	0.85		Wheeler et al. (2001)	
0.31	0.26	0.32	0.26			Wilson et al. (1993)	
		0.43	0.40	0.73		Brackelsberg et al. (1971)	
Constant fat thickness	0.57		0.52	0.30		Devitt and Wilton (2001)	
	0.39	0.24	0.53	0.16		Elzo et al. (1998)	
	0.31	0.24	0.28	0.33	0.24	Lamb et al. (1990)	
	0.44	0.37	0.29			Morris et al. (1990)	
	0.33		0.29	0.13		Shanks et al. (2001)	

**Chapter 2 - Test Duration of Water Intake, Average Daily Gain, and Dry
Matter Intake in Beef Cattle**

ABSTRACT

Water is an essential nutrient, but the effect it has on performance generally receives little attention. There are few systems and guidelines for collection of water intake phenotypes in beef cattle, which makes large-scale research on water intake a challenge. The Beef Improvement Federation has established guidelines for feed intake and average daily gain tests, but no guidelines exist for water intake. The goal of this study was to determine the test duration necessary for collection of accurate water intake phenotypes. To facilitate this goal, individual daily water intake (WI) and feed intake (FI) records were collected on 578 crossbred steers for a total of 70 d using an Insentec system at the Oklahoma State University Willard Sparks Beef Research Unit. Steers were fed in 5 groups and were individually weighed every 14 days. Within each group, steers were blocked by body weight (low and high) and randomly assigned to 1 of 4 pens containing approximately 30 steers per pen. Each pen provided 103.0 m² of shade and included an Insentec system containing 6 feed bunks and 1 water bunk. Steers were fed a constant diet across groups and dry matter intake was calculated using the average of weekly percent dry matter within group. Average feed and water intakes for each animal were computed for increasingly large test durations (7, 14, 21, 28, 35, 42, 49, 56, 63 and 70 d), and ADG was calculated using a regression formed from body weights (BW) taken every 14 d (0, 14, 28, 42, 56, and 70 d). Intervals for all traits were computed starting from both the beginning (d 0) and the end of the testing period (d 70). Pearson and Spearman correlations were computed for phenotypes from each shortened test period and for the full 70-d test. Minimum test duration was determined when the Pearson correlations were greater than 0.95 for each trait. Our results indicated that minimum test

duration for WI, DMI, and ADG were 35, 42, and 70 d, respectively. No comparable studies exist for WI; however, our results for FI and ADG are consistent with those in the literature. Although further testing in other populations of cattle and areas of the country should take place, our results suggest that WI phenotypes can be collected concurrently with DMI, without extending test duration, even if following procedures for decoupled intake and gain tests.

INTRODUCTION

Water is an essential nutrient that contributes to livestock production and health (Thornton et al., 2009), but measurement of water intake on individual animals has received fairly little attention in the recent scientific literature. Growing competition between human consumption, crop production, wildlife, and livestock has led to concerns about the availability of water in some regions of the world (World Economic Forum, 2017). Additionally, consumer concerns related to beef sustainability and environmental resource usage have increased in recent years (Nardone et al., 2010). These issues necessitate a systematic and accurate method for the collection of water intake phenotypes in beef cattle to determine heritability as well as the impact of water intake on beef production.

Accurate phenotypic data is essential for any genetic study. Obtaining accurate data for DMI and WI on individual animals requires collection of daily performance measures over a period of time. The Beef Improvement Federation (BIF, 2016) guidelines recommend a 70-d minimum test duration for ADG and a 45-d minimum test duration for feed intake. For ADG, research by Franklin et al. (1987) suggests 112 d, Lui and Makarechian (1993) suggests 84 d, Archer et al. (1997) and Wang et al. (2006)

suggest that a 63 to 70-d test duration is adequate. Recommendations for DMI are shorter at around 35 d (Archer et al., 1997; Wang et al., 2006; Culbertson et al., 2015; Cassady et al., 2016; and Retallick et al., 2017). Decoupling the collection of feed intake and ADG has been proposed by Retallick et al. (2017), which suggests the use of post-weaning ADG as a substitute for gain and collection of feed intake separately. This would allow a shortened test duration. While the importance of standardized tests for production traits such as ADG and DMI has previously been established, there are no established guidelines for collection of water intake phenotypes in beef cattle. The objective of this study was to determine the required test duration to accurately collect water intake phenotypes.

MATERIALS AND METHODS

Study Design

Water and feed intakes were collected using an Insentec system (Hokofarm Group, The Netherlands) at the Willard Sparks Beef Research Center located at Oklahoma State University in Stillwater, OK. This Insentec system consisted of 1 water bunk and 6 feed bunks per pen. The facility contained four pens, with each pen providing 11.27 by 31.85 m (358.95 m²) of space, 103.0 m² of which was covered. The Roughage Intake Control (RIC) management software utilized by the system calculates water and feed intake by subtracting the starting and ending weights of the bunks while simultaneously collecting additional data, such as the duration of each visit. Additional information on system specifications, accuracy, and specificity of the Insentec system can be found in Allwardt et al. (2017) and Chapinal et al. (2007).

Daily water intakes (WI) and as-fed feed intakes (FI) were collected on 578 crossbreed steers over a three-year period. All animal procedures were approved by the Institutional Animal Care and Use Committee at Oklahoma State University (protocol AG13-18) in accordance with Federation of Animal Science Societies (FASS, 2010) guidelines. Steers were fed in five different groups across different seasons: group 1 (n = 117) from May 2014 to August 2014, group 2 (n = 116) from November 2014 to January 2015, group 3 (n = 118) from May 2015 to July 2015, group 4 (n = 105) from June 2016 to August 2016, and group 5 (n = 123) from January 2017 to March 2017. Within each group, steers were blocked by body weight (BW) (low and high) and randomly assigned to one of four pens, each containing approximately 30 steers per pen.

Before entry into the test facility, each animal received a plastic tag for identification and a passive half-duplex radio frequency eID (Allflex USA Inc., Dallas-Fort Worth, TX) placed in the left ear. All groups were fed a growing diet throughout the study that consisted of 15% cracked corn, 51.36% wet corn gluten feed Sweet Bran[®] (Cargill Corn Milling, Dalhart, Texas), 28.44% prairie hay, and 5.20% supplement on a dry matter basis. Diet samples were taken weekly for dry matter collection, and a portion of each sample collected was composited and analyzed for nutrient content. The average percent dry matter was 74.02%, 73.70%, 73.11%, 73.24%, and 70.04% for groups 1, 2, 3, 4, and 5, respectively, which was used to convert FI to DMI. The mean gross energy of composited samples was 4,524.6 cal/g on a dry matter basis. Steers fed in groups 1-3 were managed using a slick bunk feed call procedure (slick), and steers fed during groups 4 and 5 had access to *ad libitum* (adlib) feed intake. Regardless of the feed management protocol, all steers had *ad libitum* access to water. Intakes were collected over a 70-d

period following a 21-d acclimation period to be in accordance with standard test duration guidelines for feed intake and BW gain published by the Beef Improvement Federation (BIF, 2016). Individual BW was collected at the beginning and end of the testing periods, and every 14 d during the test. Body weights were not recorded on d 42 for group 2 because of equipment malfunction. The Insentec system has been validated for both accuracy of feed and water intake collection (Chapinal et al., 2007; Allwardt et al., 2017) and restriction of water intake (Allwardt et al., 2017).

To ensure data quality, feed and water intake records were filtered for bunk starting weight, ending weight, and duration of time in the system. Start and end weight parameters were set to filter out records with unreasonable starting and ending weights, such as large negative values or weights that were significantly larger than the bunk capacity. Intake visits that were less than 5 s were removed. Water intake data collected on days where *ad libitum* water intake was not achieved, such as weigh dates or incidences of equipment malfunction, were treated as missing to maintain data quality. In groups 1-3, daily feed intakes were treated as missing on days where animals were removed from their pens (such as weigh dates) or for equipment malfunctions. Feed intakes were also treated as missing on days that *ad libitum* intake was not achieved for groups 4 and 5.

Phenotypic Data

Individual daily FI was converted to daily DMI using the following equation

$$DMI_{di} = FI_{di} \times DM\%_g$$

where DMI_{di} is the DMI for animal i on day d , FI_{di} is the feed intake for animal i on day d , and $DM\%_g$ is the mean dry matter percentage for the ration fed to group g expressed as a decimal.

Because BW will be affected by rumen fill and other environmental factors, a linear regression of individual observed BW against days on test was used to calculate ADG to better account for these differences. The regression was as follows:

$$BW_{id} = b_0 + ADG_i x_d + e_{id}$$

where BW_{id} is the observed body weight of animal i measured on day d of the test period, b_0 is the estimate of the initial body weight of each animal at the start of the test period, ADG_i is the estimated ADG for animal i , x_d is the test day d of the study, and e_{id} is the residual error. Summary statistics for phenotypic data (ADG, DMI, and WI) are presented in Table 1.

Average WI and DMI for each animal were computed for increasingly longer test periods in 7-d increments starting on day one and increasing until the full data set (forward) was utilized (F7, F14, F21, F28, F35, F42, F49, F56, F63, and 70 d). Feed and WI were also calculated starting from the end of the test period (d-70, reverse) using the same approach (R7, R14, R21, R28, R35, R42, R49, R56, R63, and 70 d). Each individual animal had to have a minimum of 3 days of intake records within each window to be considered for analysis. Similarly, ADG for each animal was also computed for increasingly longer test periods in 14 d intervals to correspond with the BW data available in both the forward (F14, F28, F42, F56 and 70 d) and reverse direction (R14, R28, R42, R58, and 70 d). Means and standard deviations for WI, DMI, and ADG were estimated for each shortened test period within each group, management type, and across

all data using the MEANS procedure of SAS 9.4 (SAS Institute Inc., Cary, NC, USA). Phenotypic (Pearson and Spearman) correlations were also estimated for each shortened test duration compared to the full 70-d test period and the fisher option within the CORR procedure of SAS 9.4 (SAS Institute Inc., Cary, NC, USA) was used to test whether correlations were significantly different from 1. Previous work by Archer et al. (1997) and Wang et al. (2006) set a less stringent level of 0.90 for Spearman correlations to determine if a shortened test duration for DMI and ADG were acceptable. In this study, minimum recommended test duration for water intake was determined when Pearson correlations were greater than 0.95, in accordance with the level used for the BIF guidelines (BIF, 2016). Spearman correlations were utilized to determine the amount of re-ranking, or differences in order from highest to lowest intakes, between individuals when test length differed.

RESULTS AND DISCUSSION

ADG Test Duration

Means and their corresponding standard deviations for each subset analyzed are shown in Table 2, and illustration of means for all animals are presented Fig. 1 panel A. Little variation was observed in ADG as test duration increases. For all groups, as test duration increases, variation decreases for ADG. However, the means for ADG vary within group. Mean ADG for groups 2 and 5 were observed to have decreasing BW gain as test duration increased. When examining Groups 3 and 4, ADG increased through the middle of the testing period and then decreased throughout the remainder of the test. Group 1 exhibited variation in ADG throughout the test period. Differences in mean ADG between groups could be at least partially attributed to differences in temperature

observed for each group. Growth is only maximized during a narrow thermal neutral range. When environmental conditions are not ideal, energy and nutrients are diverted away to maintain eutheria, which can decrease performance (O'Brien et al., 2010). The cooler temperatures during the latter part of the feeding period for groups 3 could have required the animals to put more energy towards maintenance and less toward gain. Birkelo et al. (1991) and Mader (2003) showed a decrease in ADG for finished cattle fed during the winter as compared to those fed during the summer. Ames and Ray (1983) explained that during times of cold stress, maintenance energy requirements increase linearly as temperature decreases. Rate of feed consumption increases in cattle as temperature decreases, but this usually doesn't compensate for the increase in maintenance energy requirements (Ames and Ray, 1983). Increases in maintenance energy requirements during heat stress ($THI > 74$; Mader et al. 2006) are attributed to increased energy expenditure for heat loss through panting and sweating (Wheelock et al., 2010), which could potentially result in lower ADG. During times when heat load increases, cattle decrease feed intake to lessen heat production, which may also affect ADG during those times (Ames and Ray, 1983).

Pearson and Spearman correlations for subsets of the 70-d test period are shown for individual groups, feed management groups, and for data combined across groups in Table 3. Graphical representations of these correlations are presented in Fig. S1. As expected, as test duration increases, Spearman and Pearson correlations also increase, regardless of whether the calculations are made starting at the beginning of the test (F14-F70) or from the end (R14-R70). Within group, there are differences in the degree of increase in correlation as test duration increases. The majority of the groups showed large

increases in their correlations with the addition of another data point when the number of days on test were low. Genetic correlations are for a shortened ADG test period tend to be high reported by previous scientific literature (Archer et al., 1997 and Thallman et al. 2018). These data indicate that the test duration for collection of ADG is likely a minimum of 70 d, which is generally consistent with estimates in the literature and the BIF guidelines (BIF, 2016). Slight differences were observed in Pearson and Spearman correlations for the slick bunk and *ad libitum* feeding groups, with both Pearson and Spearman correlations being lower at the earliest time points for the slick bunk groups. Despite these differences, data from both management types and the data combined across groups suggests a 70-d feeding period is necessary to measure ADG.

Recommendations for ADG test duration in the literature are 112 d (Franklin et al., 1987), 84 d (Lui and Makarechian, 1993), 70 d (Archer et al., 1997), and 63 d (Wang et al., 2006). The data from Wang et al. (2006) may have supported a shorter test duration because they used more frequent (weekly) BW measurements instead of every 14-d (the present study and Archer, 1997) or every 28-d (Franklin et al., 1987; Lui and Makarechian, 1993). We did not have a test period longer than 70 d for comparison because the experiment was designed to follow the BIF guidelines for ADG and DMI test duration. Thus, even though the Pearson and Spearman correlations are approaching our threshold of 0.95 (especially in the forward analysis) at 56 d, it is impossible to say definitively whether our correlations would have surpassed 0.95 on d 70 if we had employed a longer testing period.

DMI Test Duration

Means and their corresponding standard deviations for subsets and the full 70-d test period are shown in Table 4 and illustration of mean DMI for all animals is presented in Fig. 1 panel B. As expected, when test duration increased (F7-F70), DMI increased and the variation decreased for all the groups except for group 4. In contrast, DMI for group 4 decreased as the test duration increased. Hahn (1999) showed that as temperature continuously exceeds 25°C, cattle exhibit a decrease in feed consumption. Cattle experiencing heat stress have reduced intake and a nonlinear increase in maintenance energy requirements, which can lead to reduced performance (Ames and Ray, 1983). Temperatures in Group 4 exceeded 25°C for 61-d out of the 70-d test. Even though intakes decreased for Group 4, the standard deviation decreased as test duration increased, similar to the other groups. When test duration is evaluated starting at the end of the test period (R7-R70), DMI tends to increase slightly and then have a slight decline for the rest of the test period for most of the groups. When data is combined across groups and analyzed starting at the end of the test, DMI increases slightly from d 7 to 35 and then there is a slight decrease in DMI from d 35 to 70.

Pearson and Spearman correlations for subsets of the 70-d test period are shown in Table 5 and illustrated graphically in Fig. S2. Based on the Pearson correlations, minimum test duration for DMI would be 42 d. However, if the last 42-d of the test period are considered rather than the first, the correlations consistently do not meet the 0.95 threshold (0.949) until 49 d of data are included. If re-ranking of individuals is important, then the Spearman correlations may be the preferred metric. In this analysis of DMI, correlations were the same for both forward and reverse analyses. For the slick

bunk managed cattle, the Pearson correlation exceeded the 0.95 threshold at d 42 in the forward direction and d 49 in the reverse direction, which was identical to the result derived from using all of the data combined. The adlib fed cattle met the Pearson correlation threshold of 0.95 at F42 and R35, similar to results presented by Cassady et al. (2016). Wang et al. (2006) reported Pearson (0.929) and Spearman (0.931) correlations for DMI over 35 d using a GrowSafe system, which were slightly lower than in the present study. Pearson and Spearman correlations for DMI surpassed 0.95 at 49 d in the Wang et al. (2006) study. Wang et al. (2006) also evaluated percent change in residual variation as test duration increased and determined that past 35 d, change in percent variation was less than 1%. Archer et al. (1997) reported a phenotypic correlation of 0.73 for a 35-d test duration, and at 49-d correlations surpassed 0.95. It is important that data on traits that are included in breeding objectives are accurately collected. Archer et al. (1997) wanted to determine if a shortened test duration would impact the efficiency of selection for DMI and determined that a shortened test duration of 35 d would not impact the efficiency of selection. The authors determined that test durations for DMI greater than 35 d would have very little improvement on accuracy of selection based on observing only a 0.04 gain in efficiency of selection when going from 35 to 70 d. Culbertson et al. (2015) reported that Pearson and Spearman correlations surpassed the 0.95 threshold at 42-d. Comparing results from ADG and DMI, it is likely that taking daily feed intake measurements provides more information to accurately calculate DMI, which in turn reduces test duration. Increased test duration for ADG may also be necessary to account for differences in rumen fill over time, when collecting measurements with more frequently is not feasible or practical. For group 1, the Pearson

and Spearman correlations do not improve as rapidly after day 21 as the other groups. The rate of increase in the Pearson and Spearman correlations decreases between 35 to 42 d for group 3. This could be influenced by changes in weather during the feeding period for group 3. The first 35 d of the test duration were 6°C cooler and averaged 7 cm more rain than the last 35 days. These changes in weather could have had an impact on DMI during the first week of hot and sunny weather, thus affecting the correlations. This is evident as all the other groups exhibited increased correlations as test durations moved closer to the full 70-d test period.

The Beef Improvement Federation guidelines (BIF, 2016) suggest a 45-d shortened test duration for feed intake, which is consistent with the results from our analysis. Normally, feed intake and gain are collected simultaneously and the test period for animals is determined by collection of gain data so feed conversion ratios can be calculated (Retallick et al., 2017). There is potential to decouple the collection of feed intake and gain by collecting feed intake phenotypes through a shortened test duration and using another measure of gain, such as post weaning ADG (Retallick et al., 2017). Post weaning ADG is determined by dividing the difference between weaning weight and yearling weight by the number of days elapsed between the two measurements (Retallick et al., 2017). However, to use this approach, both weaning and yearling weights must be available. Retallick et al. (2017) reported a genetic correlation between test ADG and post weaning ADG of 0.5 and 0.88 for steers and heifers, respectively. Using post weaning ADG would allow for feed intake to be collected within a shortened 35-d test, while still providing high quality data for genetic evaluation. As an alternative to post weaning ADG, BW collected only at two time points (before and after the intake test)

could be used to meet the 70 d suggested length; regardless, BW while on test can be used in a multiple trait approach with post weaning gain and test intake as suggested by Thallman et al. (2018). This approach could potentially also be applied to phenotypes for water intake, provided that the required test duration is similar.

WI Test Duration

Means and their corresponding standard deviations for water intake for subsets and the entire 70-d test period are shown in Table 6, and illustration of means for all animals is presented in Fig. 1 panel B. As test duration increases for groups 1, 2, 3, and 5, the amount of water consumed increases numerically. Water consumption would be expected to increase as animals increase in size and BW during the testing period. In addition, groups 1 and 3 likely increase their water consumption due to a 1.5°C (group 1) and 6°C (group 3) increase in temperature from the first 35 d to the last 35 d. As ambient temperature rises, animals become more dependent upon peripheral vasodilation and water evaporation to increase heat loss and keep body temperature from rising (Berman et al., 1985), which could result in greater water requirements. In group 4, water intake peaks around d 28 to d 42, then decreases through the end of the test period. The results for WI differ when comparing calculations from the beginning (F7-F70) and end of the test (R7-R70), most likely because of the impact of temperature variation (21.6 to 31.9°C) on water intake, in addition to the impact of body mass. For the shortest test duration in the reverse analyses, cattle BWs are heavier, as animals are largest at the end of the test. For the summer groups (1, 3 and 4), temperature increased from the start of the trial until the end of the test period. The winter groups (2 and 5) were extremely variable, and temperatures fluctuated from around 15°C at the start of the trial to -1°C (group 2) and

25°C (group 5). WI for groups 1 and 2 decreased from R7 to R70. Group 5 mean intakes were similar from R7 to R49, with a slight decrease in water intake after R56.

The first 7-d of the study for groups 1, 4, as well as for data combined across groups, had larger standard deviations among animals within a group than groups 2, 3 and 5. As the test duration increased for group 1 and 4, the variation in water intake among animals within each group decreased. As test duration increases (F7-F70), variation among each group tends to decrease. However, as test duration increases in the reverse direction, only small changes in variation are observed as cattle spend more days on test. Greater variation is seen for the shorter test durations in the summer groups (1, 3, and 4) than the winter groups (2 and 5). This is likely due to weather factors influencing the variation in WI within the summer groups. Winter group steers experienced varying degrees of cold stress whereas steers fed during the summer experienced varying degrees of heat stress, which can have an impact on WI. Summer groups experienced a different number of days when THI exceeded 74 during the 70-d trial period (group 1, 38 d; group 3, 32 d; and group 4, 62 d).

Pearson and Spearman correlations for subsets and the full 70-d test period are presented in Table 7 and graphically illustrated in Fig. S3. Although variation exists within individual groups, the Pearson correlations for data combined across all groups indicate that a minimum of 35 d of data is necessary for collection of accurate WI phenotypes. Cattle that were managed with the slick bunk feed protocol required a slightly longer test duration of 42 d, regardless of whether the analysis was conducted from the beginning or end of the test. However, results from the *ad libitum* fed groups indicated that a shorter test duration of 21 d would be acceptable. Spearman correlations

for each group follow the same pattern as the Pearson correlations, except for the Spearman correlations in the reverse analysis, which did not meet the threshold of 0.95 until 42 d. For cattle fed during the summer (groups 1, 3, and 4), the first half of the test period was during May and June and the second half of the test took place during July and into August. The first half of the test tended to be slightly cooler (24.57°C, 20.24°C, and 27.33°C, for groups 1, 3, and 4, respectively) than in the second half of the test period (25.49°C, 26.46°C, and 28.79°C, for groups 1, 3, and 4, respectively). The temperature changes were likely a contributing factor to the observation that cattle consumed less water and intakes were less variable in the first half of the test period as compared to the last half of the test period.

For WI, the Pearson correlation threshold of 0.95 is exceeded by 35 d, regardless of whether the values were calculated from the beginning or end of test (0.966 and 0.95 for F35 and R35, respectively). Unlike DMI, the Spearman correlations are slightly lower at the same number of days (F35=0.947 and R35=0.943) and do not exceed the threshold of 0.95. This difference indicates that there is more re-ranking of individuals for WI than for DMI at the same test length threshold. Thus, if reranking of individuals is a concern, the test period should likely be extended to at least 42-d. Increasing this threshold is not problematic, as it is unlikely that animals would be undergoing a water intake test that was not concurrent with a feed intake test, which would generally be at least 42 to 45 d.

CONCLUSION

The results from the current study suggest 70 d and 42 d test durations are required for accurate collection of ADG and DMI phenotypes, respectively. This recommendation is similar to several studies previously published in the scientific literature. This analysis

also suggests that WI can be collected over a 35 to 42-d test. Results for DMI and WI indicate that both phenotypes can be collected simultaneously with a shortened test duration of 42 d, which would not interfere with the potential for decoupling feed intake and gain performance tests. These results were generated using data that spans a variety of seasons and animals from a variety of backgrounds. However, they are calculated using data from a single facility; thus, these results should be evaluated in other locations or results should be combined in a meta-analysis of multiple datasets as they become available to make a final recommendation on WI test length. Concurrent collection of both WI and DMI phenotypes allows more cost-effective phenotypic data collection, and increases the utility of feed intake tests by collecting an additional phenotype for the same cost, provided the facility has the capability to collect WI

REFERENCES

- Allwardt, K., C. Ahlberg, A. Broocks, K. Bruno, A. Taylor, S. Place, C. Richards, C. Krehbiel, M. Calvo-Lorenzo, U. DeSilva, D. VanOverbeke, R. Mateescu, C. Goad, and M.M Rolf. 2017. Technical Note: Validation of an automated system for monitoring and restricting water intake in group-housed beef systems. *J. Anim. Sci.* doi:10.2527/Jas2017.1593
- Ames, D. R., and D. E. Ray. 1983. Environmental manipulation to improve animal productivity. *J. Anim. Sci.* 57(Suppl. 2):209. doi:10.2527/animalscsi1983.57Supplement_2209x
- 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. *J. Anim. Sci.* 75:2024-2032. doi:10.2527/1997.7582024x
- Berman, A., Y. Folman, M. Kaim, M. Mamen, Z. Herz, D. Wolfenson, A. Arieli, and Y. Graber. 1985. Upped critical temperature and forced ventilation effects for high-yielding dairy cows in a subtropical climate. *J. Dairy Sci.* 68:1488-1495. doi:10.3168/jds.S0022-0302(85)80987-5
- Birkelo, C. P., D. E. Johnson, and H. P. Phetteplace. 1991. Maintenance requirements of beef cattle as affected by season on different planes of nutrition. *J. Anim. Sci.* 69:1214-1222. doi:10.2527/1991.6931205x
- Cassady, C. J., T. L. Felix, J. E. Beaver, D. W. Shike, and National Program for Genetic Improvement of Feed Efficiency in Beef Cattle. 2016. Effects of timing and duration of test period and diet type on intake and feed efficiency of Charolais-sired cattle. *J. Anim. Sci.* 94:4748–4758. doi:10.2527/jas.2016-0633

- Chapinal, N., D. M. Veira, D. M. Weary, and M. A. G. von Keyserlingk. 2010. Technical Note: Validation of a system for monitoring individual feeding and drinking behavior and intake in group-housed cattle. *J. Dairy. Sci.* 90:5732-5736. doi: 10.3168/jds.2007-0331
- Culbertson, M. M., S. E. Speidel, R. K. Peel, R. R. Cockrum, M. G. Thomas, and R. M. Enns. 2015. Optimum measurement period for evaluating feed intake traits in beef cattle. *J. Anim. Sci.* 93:2482-2487. doi:10.2527/jas2014-8364
- BIF. 2016. Guidelines for uniform beef improvement program. Beef Improvement Federation. Ninth edition. Raleigh, NC
- Federation of Animal Science Societies (FASS). 2010. Guide for the Care and Use of Agricultural Animal in Research and Teaching. http://aaalac.org/about/Ag_Guide_3rd_ed.pdf responses of Cattle to thermal heat loads
- Franklin, C. L., W. V. Thayne, W. R. Wagner, L. P. Stevens, and E. K. Inskeep. 1987. Factors affecting gain of beef bulls consigned to a central test station. Bulletin 693. Agricultural and Forestry Experiment Station. West Virginia Univ., Morgantown
- Hahn, G. L. 1999. Dynamic responses of Cattle to thermal heat loads. *J. Anim. Sci.* 77(Suppl 2):10-20. doi:10.2527/1997.77suppl_210x
- Lui, M. F., and M. Makarechian. 1993. Factors influencing growth performance of beef bulls in test station. *J. Anim. Sci.* 71:1123-1127. doi:10.2527/1993.7151123x
- Mader, T. L. 2003. Environmental stress in confined beef cattle. *J. Anim. Sci.* 81:E110-E119. doi:10.2527/2003.8114_suppl_2E110x

- Mader, T. L., M. S. Davis, and T. Brown-Brandl. 2006. Environmental factors influencing heat stress in feedlot cattle. *J. Anim. Sci.* 84:712-719. doi:10.2527/2006.843720x
- Nardone, A., B. Ronchi, N Lacetera, M.S. Ranieri, and U. Bernabucci. 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livest. Prod.* 130:57-69. doi:10.1016/j.livsci.2010.02.011
- O'Brien, M. D., R. P. Rhoads, S. R. Sanders, G. C. Duff, and L. H. Baumgard. 2010. Metabolic adaptations to heat stress in growing cattle. *Domestic Animal Endocrinology.* 38:86-94. doi:10.1016/j.domaniend.2009.08.005
- Retallick, K. J., J. M. Bormann, R. L. Weaver, M. D. MacNeil, H. L. Bradford, H. C. Freetly, K. E. Hales. D. W. Moser, W. M. Snelling. R. M. Thallman, and L. A. Kuehn. 2017. Genetic variance and covariance and breed differences for feed intake and average daily gain to improve feed efficiency in growing cattle. *J. Anim. Sci.* 95:1444-1450. doi:10.2427/jas.2016.1260
- Thallman, R. M., L. A. Khuen, W. M. Snelling, K. J. Retallick, J. M. Bormann, H. C. Freetly, K. E. Hales, G. L. Bennett, R. L. Weaver, D. W. Moser, and M. D. MacNeil. 2018. Reducing the period of data collection for intake and gain to improve response to selection for feed efficiency in beef cattle. *J. Anim. Sci.* doi:10.1093/jas/skxx077
- Thornton, P. K., J. van de Steeg, A. Notenbaert, and M. Herrero. 2009. The impact of climate change on livestock and livestock systems in developing countries: A review of what we know and what we need to know. *Agric. Syst.* 101:113-127. doi:10.1016/j.agsy.2009.05.002
- 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.
doi:10.2527/jas.2005-715

Wheelock, J. B., R. P. Rhoads, M. J. VanBaale, S. R. Sanders, and L. H. Baumgard. 2010.
Effects of heat stress on energetic metabolism in lactating Holstein cows. *J. Dairy.
Sci.* 93:644-655. doi: 10.3168/jds.2009-2635

World Economic Forum. 2017. The Global Risks Report 2017. World Economic Forum.
12:1-78.

Table 2.1 Summary statistics for average daily gain, (ADG), dry matter intake (DMI), and water intake (WI) over the 70 d test period

Trait	Mean	Std ^a	Min	Max	CV% ^a
ADG, kg	3.41	0.82	0.90	5.61	24.0
DMI, kg	10.54	1.51	5.80	16.25	14.3
WI, kg	37.69	11.28	14.02	108.32	29.9

^aStd is the standard deviation and CV% is coefficient of variation reported as a percent

Table 2.2 Means (standard deviations) for a 70-d average daily gain (ADG, kg) test. Shorter test durations are subsets of the full 70-d test of the specified duration. Forward analyses begin at d 0 and reverse analyses begin at d 70.

Group	Period ^a	Test duration				
		14	28	42	56	70
1	Forward	2.94 (1.88)	3.21 (1.35)	2.88 (0.94)	3.21 (0.76)	3.06 (0.63)
	Reverse	1.51 (1.72)	3.18 (0.93)	3.00 (0.69)	3.06 (0.62)	3.06 (0.63)
2	Forward	4.12 (1.91)	3.93 (1.37)	3.93 (1.37)	3.95 (0.82)	3.83 (0.75)
	Reverse	3.14 (1.59)	3.14 (1.59)	3.75 (0.94)	3.78 (0.79)	3.83 (0.75)
3	Forward	2.56 (2.58)	3.82 (1.45)	3.64 (1.02)	3.42 (0.84)	3.22 (0.68)
	Reverse	2.45 (2.97)	2.60 (1.29)	2.63 (0.85)	3.15 (0.72)	3.22 (0.68)
4	Forward	2.49 (1.35)	3.31 (0.96)	3.37 (0.81)	3.06 (0.68)	2.79 (0.64)
	Reverse	1.84 (1.66)	1.79 (1.02)	2.22 (0.76)	2.69 (0.64)	2.79 (0.64)
5	Forward	6.02 (2.01)	4.76 (1.05)	4.31 (0.75)	4.08 (0.64)	4.04 (0.63)
	Reverse	4.67 (1.86)	3.87 (1.09)	3.67 (0.81)	3.54 (0.72)	4.04 (0.63)
All	Forward	3.67 (2.41)	3.83 (1.37)	3.63 (1.12)	3.56 (0.85)	3.41 (0.82)
	Reverse	2.76 (2.32)	2.95 (1.38)	3.08 (1.00)	3.26 (0.80)	3.41 (0.82)

^a Forward-records were split into the first F14, F28, F42, F56, and F70 days of the test duration, reverse-records were split into the last R14, R28, R42, R56, and R70 days of the test duration.

Table 2.3 Pearson and Spearman correlations for each shortened test duration and the full 70 d test period for ADG (kg).

Group ^a	Direction ^b	Analysis	Test duration (d)				
			14	28	42	56	70
1	Forward	Pearson	0.465	0.711	0.822	0.885	1.0
		Spearman	0.396	0.726	0.781	0.929	1.0
	Reverse	Pearson	0.123	0.495	0.635	0.892	1.0
		Spearman	0.262	0.509	0.632	0.895	1.0
2	Forward	Pearson	0.375	0.601	0.601	0.943	1.0
		Spearman	0.360	0.562	0.562	0.934	1.0
	Reverse	Pearson	0.393	0.393	0.730	0.929	1.0
		Spearman	0.430	0.430	0.748	0.909	1.0
3	Forward	Pearson	0.303	0.566	0.760	0.885	1.0
		Spearman	0.266	0.527	0.731	0.876	1.0
	Reverse	Pearson	0.118	0.404	0.636	0.880	1.0
		Spearman	0.190	0.371	0.599	0.849	1.0
4	Forward	Pearson	0.600	0.707	0.834	0.932	1.0
		Spearman	0.541	0.661	0.819	0.927	1.0
	Reverse	Pearson	0.424	0.583	0.827	0.953	1.0
		Spearman	0.418	0.552	0.815	0.957	1.0
5	Forward	Pearson	0.296	0.574	0.857	0.913	1.0
		Spearman	0.290	0.559	0.831	0.910	1.0
	Reverse	Pearson	0.515	0.657	0.827	0.937	1.0
		Spearman	0.472	0.602	0.804	0.930	1.0
Slick	Forward	Pearson	0.431	0.617	0.720	0.930	1.0
		Spearman	0.419	0.623	0.722	0.924	1.0
	Reverse	Pearson	0.276	0.389	0.713	0.919	1.0
		Spearman	0.384	0.389	0.798	0.912	1.0
Adlib	Forward	Pearson	0.700	0.775	0.879	0.949	1.0
		Spearman	0.736	0.770	0.860	0.940	1.0
	Reverse	Pearson	0.702	0.808	0.907	0.940	1.0
		Spearman	0.732	0.812	0.913	0.934	1.0
All	Forward	Pearson	0.549	0.673	0.759	0.934	1.0
		Spearman	0.563	0.684	0.768	0.935	1.0
	Reverse	Pearson	0.458	0.579	0.795	0.912	1.0
		Spearman	0.531	0.578	0.798	0.905	1.0

^aSlick-cattle managed with slick bunk feed protocol, adlib-cattle had access to *ad libitum* feed, all-all groups were combined

^b Forward-records were split into the first F14, F28, F42, F56, and F70 days of the test duration, reverse-records were split into the last R14, R28, R42, R56, and R70 days of the test duration.

Table 2.4 Means (standard deviations) for a 70-d dry matter intake (DMI, kg) test. Shorter test durations are subsets of the full 70 d test of the specified duration. Forward analyses begin at d 0 and reverse analyses begin at d 70.

Group	Item ^a	Day of test									
		7	14	21	28	35	42	49	56	63	70
1	Forward	7.8 (2.4)	8.5 (2.2)	9.1 (2.0)	9.5 (1.9)	9.6 (1.7)	9.7 (1.6)	9.8 (1.6)	9.9 (1.5)	10.0 (1.5)	10.1 (1.4)
	Reverse	10.4 (1.4)	10.6 (1.3)	10.7 (1.3)	10.6 (1.3)	10.6 (1.3)	10.5 (1.3)	10.5 (1.4)	10.5 (1.4)	10.3 (1.4)	10.1 (1.4)
2	Forward	8.2 (2.1)	8.6 (2.0)	8.9 (2.0)	9.2 (1.9)	9.5 (1.8)	9.7 (1.8)	10.0 (1.8)	10.2 (1.7)	10.2 (1.7)	10.2 (1.7)
	Reverse	10.9 (1.8)	10.4 (1.8)	10.8 (1.7)	10.9 (1.7)	11.0 (1.7)	10.9 (1.7)	10.8 (1.7)	10.6 (1.7)	10.4 (1.7)	10.2 (1.7)
3	Forward	9.5 (2.2)	9.5 (2.1)	9.7 (2.0)	9.8 (2.0)	9.9 (1.7)	9.7 (1.7)	9.8 (1.7)	10.0 (1.6)	10.0 (1.5)	10.0 (1.5)
	Reverse	10.4 (1.4)	10.4 (1.3)	10.5 (1.3)	10.6 (1.4)	10.2 (1.3)	10.2 (1.4)	10.2 (1.4)	10.2 (1.4)	10.1 (1.5)	10.0 (1.5)
4	Forward	11.2 (1.3)	11.1 (1.2)	10.6 (1.0)	10.7 (1.1)	10.6 (1.0)	10.7 (1.0)	10.8 (1.0)	10.7 (1.0)	10.7 (0.9)	10.6 (0.9)
	Reverse	9.8 (1.0)	10.1 (1.0)	10.2 (0.9)	10.4 (1.0)	10.6 (1.0)	10.6 (1.0)	10.6 (0.9)	10.5 (0.9)	10.5 (0.9)	10.6 (0.9)
5	Forward	10.6 (1.4)	10.7 (1.3)	10.9 (1.2)	11.0 (1.2)	11.2 (1.2)	11.3 (1.2)	11.5 (1.2)	11.6 (1.2)	11.7 (1.2)	11.7 (1.2)
	Reverse	11.9 (1.6)	12.0 (1.5)	12.2 (1.4)	12.3 (1.4)	12.2 (1.4)	12.1 (1.3)	12.0 (1.3)	11.9 (1.3)	11.8 (1.3)	11.7 (1.2)
All	Forward	9.4 (2.3)	9.7 (2.1)	9.8 (1.9)	10.0 (1.8)	10.2 (1.7)	10.2 (1.6)	10.4 (1.6)	10.5 (1.6)	10.5 (1.5)	10.5 (1.5)
	Reverse	10.7 (1.6)	10.8 (1.6)	10.9 (1.5)	11.0 (1.5)	10.9 (1.5)	10.9 (1.5)	10.8 (1.5)	10.7 (1.5)	10.6 (1.5)	10.5 (1.5)

^a Forward-records were split into the first F7, F14, F21, F28, F35, F42, F49, F56, F63, and F70 days of the test duration, reverse-records were split into the last R7, R14, R21, R28, R35, R42, R49, R56, R63, and R70 days of the test duration

Table 2.5 Pearson and Spearman correlations for each shortened test duration and the full 70 d test period for DMI (kg).

Group ^a	Direction ^b	Analysis	Day of test									
			7	14	21	28	35	42	49	56	63	70
1	Forward	Pearson	0.709	0.777	0.855	0.902	0.941	0.963	0.983	0.991	0.997	1.0
		Spearman	0.747	0.809	0.866	0.903	0.940	0.959	0.979	0.988	0.997	1.0
	Reverse	Pearson	0.699	0.781	0.852	0.868	0.893	0.914	0.947	0.968	0.992	1.0
		Spearman	0.734	0.793	0.856	0.879	0.905	0.918	0.947	0.966	0.990	1.0
2	Forward	Pearson	0.782	0.828	0.883	0.921	0.951	0.967	0.983	0.990	0.998	1.0
		Spearman	0.812	0.848	0.899	0.922	0.953	0.966	0.981	0.989	0.997	1.0
	Reverse	Pearson	0.821	0.840	0.891	0.913	0.937	0.953	0.972	0.985	0.997	1.0
		Spearman	0.839	0.840	0.886	0.902	0.928	0.945	0.972	0.986	0.996	1.0
3	Forward	Pearson	0.832	0.892	0.916	0.935	0.958	0.975	0.986	0.993	0.998	1.0
		Spearman	0.815	0.894	0.915	0.924	0.950	0.969	0.984	0.992	0.998	1.0
	Reverse	Pearson	0.805	0.813	0.869	0.906	0.915	0.938	0.968	0.986	0.996	1.0
		Spearman	0.812	0.825	0.877	0.909	0.917	0.938	0.966	0.982	0.994	1.0
4	Forward	Pearson	0.797	0.868	0.899	0.929	0.955	0.969	0.985	0.992	0.998	1.0
		Spearman	0.747	0.842	0.885	0.924	0.952	0.965	0.984	0.992	0.997	1.0
	Reverse	Pearson	0.810	0.872	0.899	0.927	0.955	0.961	0.977	0.987	0.996	1.0
		Spearman	0.841	0.894	0.919	0.940	0.961	0.967	0.976	0.987	0.994	1.0
5	Forward	Pearson	0.770	0.840	0.881	0.908	0.942	0.966	0.981	0.988	0.997	1.0
		Spearman	0.734	0.826	0.856	0.890	0.927	0.951	0.972	0.982	0.995	1.0
	Reverse	Pearson	0.786	0.867	0.923	0.945	0.955	0.966	0.982	0.991	0.997	1.0
		Spearman	0.793	0.889	0.922	0.941	0.955	0.960	0.976	0.988	0.996	1.0
Slick	Forward	Pearson	0.721	0.803	0.863	0.905	0.941	0.967	0.983	0.991	0.998	1.0
		Spearman	0.736	0.813	0.865	0.901	0.938	0.966	0.982	0.990	0.997	1.0
	Reverse	Pearson	0.776	0.809	0.872	0.896	0.905	0.928	0.957	0.977	0.994	1.0
		Spearman	0.794	0.818	0.876	0.897	0.907	0.929	0.958	0.976	0.993	1.0
Adlib	Forward	Pearson	0.584	0.664	0.831	0.886	0.931	0.952	0.975	0.988	0.997	1.0
		Spearman	0.536	0.622	0.797	0.860	0.916	0.938	0.964	0.982	0.995	1.0

All	Reverse	Pearson	0.832	0.890	0.919	0.940	0.956	0.966	0.979	0.985	0.996	1.0
		Spearman	0.835	0.892	0.908	0.929	0.947	0.958	0.973	0.980	0.994	1.0
	Forward	Pearson	0.750	0.810	0.878	0.915	0.947	0.968	0.983	0.991	0.998	1.0
		Spearman	0.745	0.806	0.876	0.911	0.946	0.966	0.981	0.991	0.997	1.0
	Reverse	Pearson	0.803	0.856	0.893	0.919	0.935	0.949	0.968	0.981	0.995	1.0
		Spearman	0.806	0.858	0.889	0.916	0.931	0.947	0.967	0.978	0.994	1.0

^aSlick-cattle managed with slick bunk feed protocol, adlib-cattle had access to *ad libitum* feed, all-all groups were combined

^b Forward-records were split into the first F7, F14, F21, F28, F35, F42, F49, F56, F63, and F70 days of the test duration, reverse-records were split into the last R7, R14, R21, R28, R35, R42, R49, R56, R63, and R70 days of the test duration

Table 2.6 Means (standard deviations) for a 70-d water intake (WI, kg) test. Shorter test durations are subsets of the full 70 d tests of the specified duration. Forward analyses begin at d 0 and reverse analyses begin at d 70.

Group	Item ^a	Day of test									
		7	14	21	28	35	42	49	56	63	70
1	Forward	31.8 (9.7)	34.5 (8.9)	35.5 (8.4)	37.4 (8.4)	38.5 (8.4)	38.6 (8.3)	39.1 (7.9)	39.3 (7.8)	40.1 (7.9)	40.6 (8.1)
	Reverse	45.6 (11.9)	45.4 (10.6)	43.9 (9.6)	43.6 (9.3)	42.7 (8.9)	42.7 (8.8)	42.7 (8.7)	42.1 (8.6)	41.4 (8.3)	40.6 (8.1)
2	Forward	24.7 (7.1)	24.6 (6.5)	24.7 (6.4)	25.2 (6.3)	25.7 (6.1)	26.3 (6.2)	26.3 (6.0)	26.3 (5.8)	26.6 (5.6)	27.3 (5.4)
	Reverse	33.7 (12.4)	30.1 (10.7)	29.5 (7.4)	29.1 (6.3)	29.1 (5.9)	28.8 (5.7)	28.4 (5.7)	28.0 (5.6)	27.6 (5.5)	27.3 (5.4)
3	Forward	27.9 (7.1)	28.0 (6.7)	27.6 (6.3)	28.5 (6.3)	31.2 (6.3)	32.3 (6.2)	34.6 (6.5)	35.5 (6.6)	36.3 (6.7)	35.9 (6.6)
	Reverse	33.5 (7.7)	37.7 (8.5)	39.9 (8.3)	41.2 (8.3)	41.0 (8.2)	41.0 (8.0)	39.4 (7.5)	37.9 (7.0)	36.8 (6.8)	35.9 (6.6)
4	Forward	44.9 (9.3)	48.4 (11.2)	51.3 (12.9)	51.6 (13.4)	53.9 (14.5)	53.2 (14.3)	52.6 (13.9)	53.0 (14.3)	52.4 (14.1)	51.5 (13.8)
	Reverse	44.0 (12.9)	45.6 (12.4)	49.0 (14.3)	48.9 (13.5)	49.2 (13.5)	51.4 (14.5)	51.8 (14.7)	52.3 (14.8)	52.2 (14.4)	51.5 (13.8)
5	Forward	29.2 (5.2)	29.8 (4.9)	30.9 (4.9)	31.6 (4.9)	32.9 (5.0)	33.4 (4.9)	33.9 (4.9)	34.2 (4.9)	34.5 (4.8)	34.7 (4.8)
	Reverse	36.6 (6.5)	36.4 (5.5)	36.5 (5.3)	36.8 (5.3)	36.6 (5.2)	36.8 (5.2)	36.4 (5.1)	35.9 (5.0)	35.2 (4.8)	34.7 (4.8)
All	Forward	31.4 (10.3)	32.7 (11.2)	33.6 (12.1)	34.5 (12.2)	36.0 (12.7)	36.3 (12.2)	37.0 (11.8)	37.3 (11.9)	37.7 (11.7)	37.7 (11.3)
	Reverse	38.5 (11.6)	38.9 (11.3)	39.6 (11.3)	39.7 (11.0)	39.5 (11.3)	39.9 (11.5)	39.5 (11.6)	39.0 (11.7)	38.3 (11.6)	37.7 (11.3)

^a Forward-records were split into the first F7, F14, F21, F28, F35, F42, F49, F56, F63, and F70 days of the test duration, reverse-records were split into the last R7, R14, R21, R28, R35, R42, R49, R56, R63, and R70 days of the test duration

Table 2.7 Pearson and Spearman correlations for each shortened test duration and the full 70 d test period for water intake (WI, kg).

Group ^a	Direction ^b	Analysis	Day of test									
			7	14	21	28	35	42	49	56	63	70
1	Forward	Pearson	0.635	0.733	0.821	0.881	0.927	0.955	0.978	0.988	0.996	1.0
		Spearman	0.591	0.696	0.778	0.837	0.899	0.943	0.973	0.985	0.995	1.0
	Reverse	Pearson	0.831	0.888	0.913	0.922	0.935	0.954	0.973	0.984	0.996	1.0
		Spearman	0.848	0.883	0.903	0.917	0.936	0.955	0.970	0.982	0.994	1.0
2	Forward	Pearson	0.722	0.794	0.838	0.879	0.906	0.920	0.927	0.935	0.981	1.0
		Spearman	0.612	0.735	0.799	0.836	0.871	0.885	0.900	0.911	0.975	1.0
	Reverse	Pearson	0.448	0.462	0.652	0.783	0.889	0.932	0.964	0.984	0.995	1.0
		Spearman	0.452	0.461	0.647	0.777	0.871	0.916	0.957	0.981	0.994	1.0
3	Forward	Pearson	0.727	0.787	0.806	0.823	0.906	0.946	0.972	0.986	0.998	1.0
		Spearman	0.706	0.775	0.799	0.822	0.907	0.945	0.973	0.986	0.997	1.0
	Reverse	Pearson	0.766	0.850	0.905	0.935	0.942	0.953	0.978	0.989	0.997	1.0
		Spearman	0.795	0.851	0.915	0.938	0.950	0.957	0.977	0.988	0.997	1.0
4	Forward	Pearson	0.822	0.887	0.944	0.967	0.985	0.989	0.994	0.997	0.999	1.0
		Spearman	0.867	0.914	0.945	0.957	0.979	0.987	0.992	0.996	0.998	1.0
	Reverse	Pearson	0.879	0.940	0.967	0.973	0.982	0.988	0.992	0.996	0.999	1.0
		Spearman	0.845	0.927	0.956	0.961	0.971	0.978	0.989	0.996	0.999	1.0
5	Forward	Pearson	0.835	0.868	0.895	0.923	0.947	0.967	0.983	0.991	0.996	1.0
		Spearman	0.819	0.848	0.889	0.924	0.951	0.964	0.979	0.990	0.996	1.0
	Reverse	Pearson	0.694	0.863	0.910	0.919	0.940	0.966	0.982	0.992	0.997	1.0
		Spearman	0.634	0.833	0.886	0.907	0.935	0.962	0.979	0.989	0.995	1.0
Slick	Forward	Pearson	0.705	0.805	0.845	0.879	0.935	0.957	0.977	0.984	0.995	1.0
		Spearman	0.669	0.783	0.818	0.858	0.928	0.955	0.977	0.984	0.995	1.0
	Reverse	Pearson	0.686	0.818	0.902	0.931	0.945	0.958	0.980	0.991	0.998	1.0
		Spearman	0.638	0.800	0.904	0.936	0.953	0.963	0.982	0.991	0.998	1.0
Adlib	Forward	Pearson	0.894	0.930	0.960	0.975	0.986	0.991	0.995	0.997	0.999	1.0

		Spearman	0.932	0.947	0.960	0.970	0.980	0.987	0.993	0.996	0.998	1.0
	Reverse	Pearson	0.827	0.919	0.960	0.965	0.975	0.986	0.991	0.996	0.999	1.0
		Spearman	0.665	0.829	0.914	0.926	0.944	0.972	0.987	0.995	0.999	1.0
All	Forward	Pearson	0.830	0.892	0.921	0.941	0.966	0.977	0.988	0.992	0.997	1.0
		Spearman	0.793	0.858	0.876	0.903	0.947	0.966	0.983	0.989	0.997	1.0
	Reverse	Pearson	0.712	0.822	0.920	0.933	0.950	0.970	0.985	0.994	0.999	1.0
		Spearman	0.639	0.792	0.899	0.923	0.943	0.963	0.982	0.993	0.998	1.0

^aSlick-cattle managed with slick bunk feed protocol, adlib-cattle had access to *ad libitum* feed, all-all groups were combined

^bForward-records were split into the first F7, F14, F21, F28, F35, F42, F49, F56, F63, and F70 days of the test duration, reverse- records were split into the last R7, R14, R21, R28, R35, R42, R49, R56, R63, and R70 days of the test duration

Figure 2.1 Panel A - Mean average daily gain (ADG) for all animals throughout the 70 d test, Panel – B Mean average daily water intake (WI) and average daily dry matter intake (DMI) throughout the 70 d test

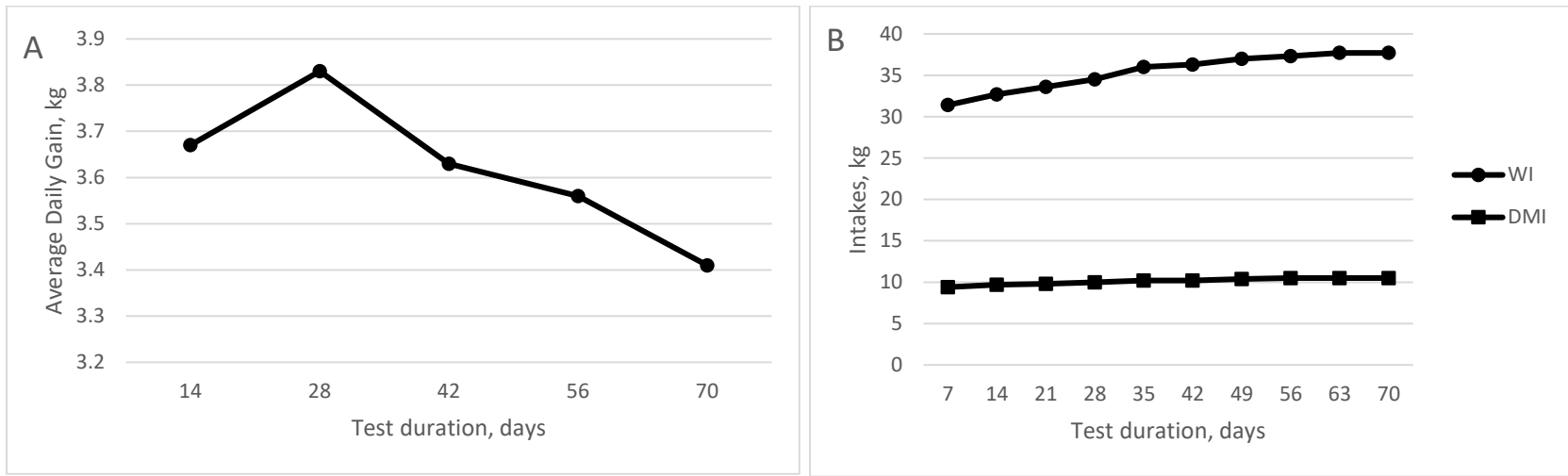


Figure 2.2 Panel A - Pearson correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Forward), Panel B - Pearson correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Reverse), Panel C - Spearman correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Forward), Panel D - Spearman correlations between average daily gain (ADG) calculated during shortened test periods and the full 70 d test (Reverse)

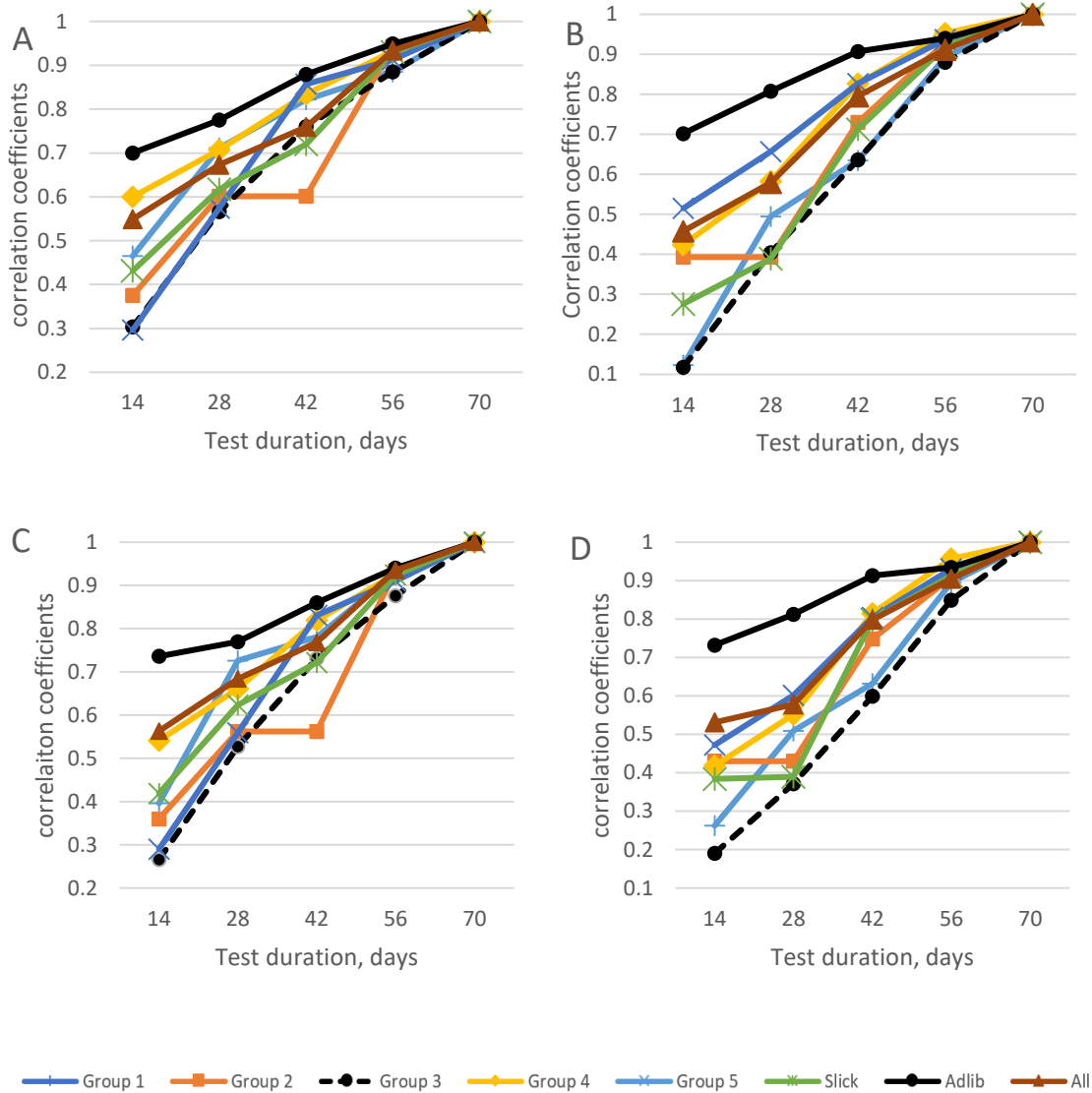


Figure 2.3 Panel A - Pearson correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Forward), Panel B - Pearson correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Reverse), Panel C - Spearman correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Forward), Panel D - Spearman correlations between dry matter intake (DMI) calculated during shortened test periods and the full 70 d test (Reverse)

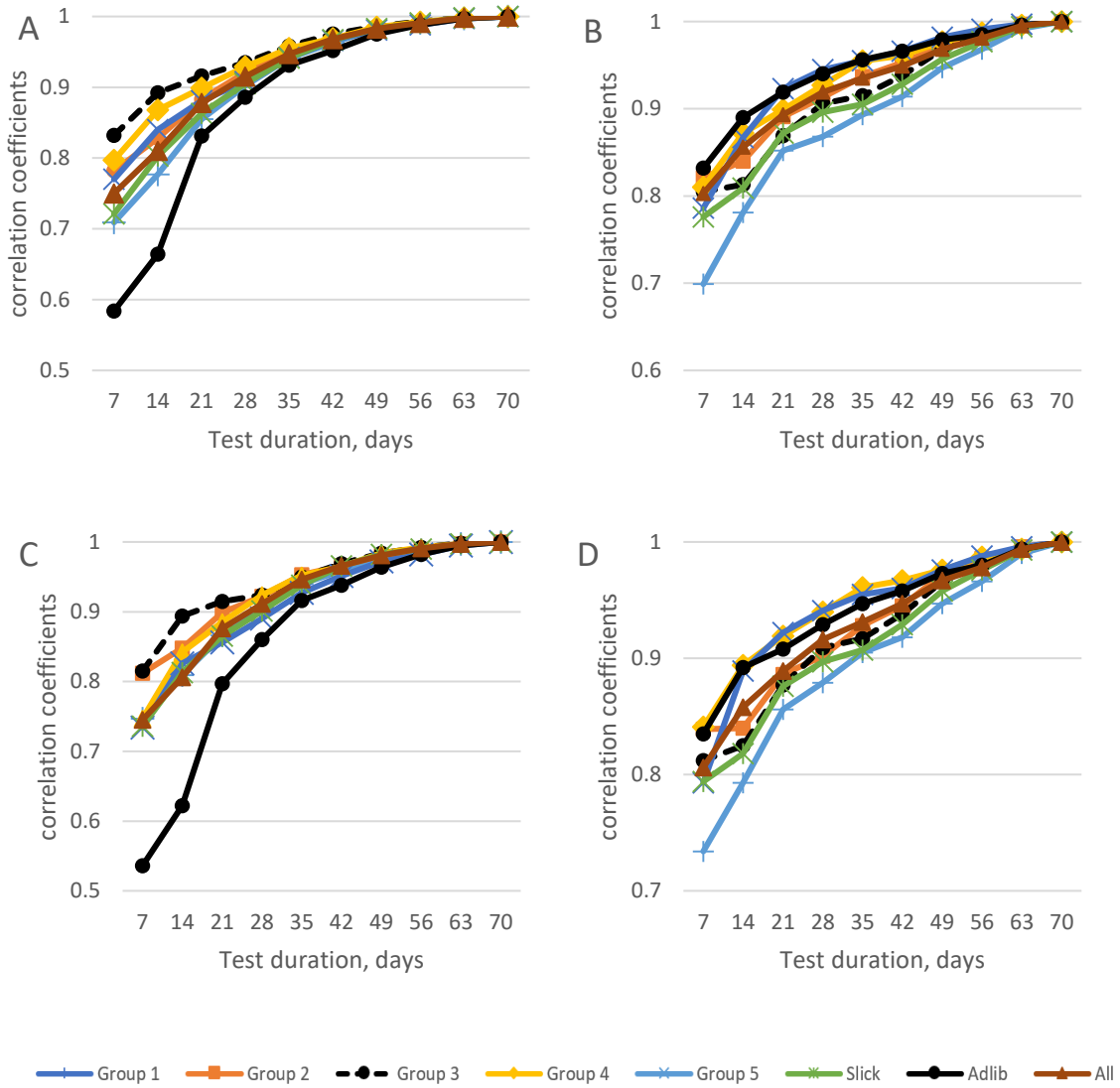
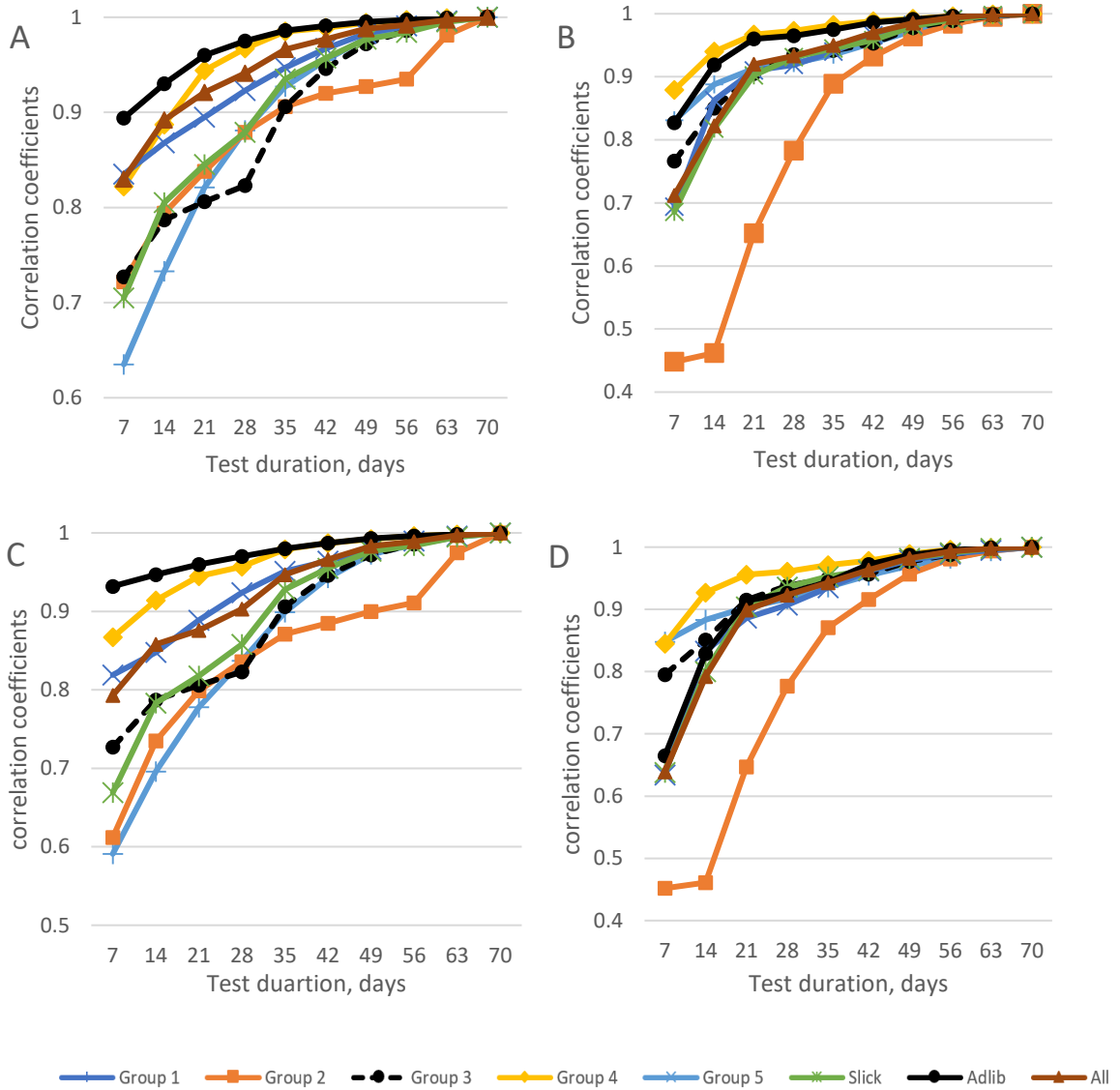


Figure 2.4 Panel A - Pearson correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Forward), Panel B - Pearson correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Reverse), Panel C - Spearman correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Forward), Panel D - Spearman correlations between water intake (WI) calculated during shortened test periods and the full 70 d test (Reverse)



**Chapter 3 - Environmental Effects on Water Intake and Water Intake
Prediction in Growing Beef Cattle**

ABSTRACT

Water is an essential nutrient, but there are few recent studies that evaluate how much water individual beef cattle consume and how environment impacts an individual's water intake. Most studies have focused on pen intakes allocated to individual animals. Thus, the objective of this study was to evaluate the impact of environmental parameters on individual-animal water intake across different seasons and develop prediction equations to estimate water intake, including within different environments and management protocols. Individual daily feed intake (FI) and water intake (WI) records were collected on 579 crossbred steers over 70-d. Steers were fed in five groups over a three-year period from May 2014 to March 2017. Individual weights were collected every 14 days and weather data was retrieved from the Oklahoma Mesonet's Stillwater station. Differences between water intake as a percent of body weight (WI%) were analyzed, accounting for average temperature (TAVG), relative humidity (HAVG), solar radiation (SRAD), and wind speed (WSPD). Seasonal (summer vs winter) and management differences (*ad libitum* vs slick bunk) were examined. Regression analysis was utilized to generate a water intake prediction equation. There were significant ($p < 0.05$) differences in WI between all groups when no environmental parameters were included in the model. Although performance was more similar after accounting for all differences in weather factors, significant ($p < 0.05$) seasonal and feed management differences were still observed, but were less than 0.75% of a steer's body weight. The best linear predictors of daily water intake were dry matter intake (DMI), metabolic weights (MWTs), TAVG, SRAD, HAVG, and WSPD. Slight differences in coefficient of determination were observed for summer (0.34), winter (0.39), *ad libitum* (0.385), slick bunk (0.41), and across

all seasons and bunk management (0.40). Based on the moderate R^2 values for the WI prediction equation, individual daily WI can be predicted with reasonable accuracy based on the environmental conditions that are present, MWTS, and DMI consumed, but substantial variation exists in individual animal WI that are not accounted for by the models.

Key words: Water Intake, Beef Cattle, Water Prediction, Insentec

INTRODUCTION

Water is a key nutrient that aides in temperature regulation, growth, digestion, metabolism and excretion (NRC, 2000). More knowledge about how animals respond to environmental changes, especially how climate change might affect water intake (WI) would be useful (Mader, 2003). Understanding how weather changes impact cattle water intake will allow producers to better manage water resources. This can be particularly important in the summer, when cattle exposed to high heat loads can have their thermal equilibrium disrupted, due to the key role of water in maintaining thermal equilibrium (Arias and Mader, 2011). The Livestock Weather Safety Index (LWSI; LCI 1970) has established benchmark levels for heat stress and use the temperature-humidity index (THI) to quantify environmental conditions. The THI equation used by LWSI only contains temperature and humidity as reported by Thom (1959) and NOAA (1976). However, later work by Mader et al., (2006) showed that temperature and humidity were not the only factors that affect heat stress. Mader et al. (2006) suggested that solar radiation (SRAD) and wind speed (WSPD) were also important factors to evaluating heat stress in cattle.

Having the ability to accurately predict WI could allow producers to better manage water resources and ensure adequate water availability. Winchester and Morris (1958) developed a method to predict WI by using ratios of WI to DMI at specific temperature thresholds. To build upon Winchester and Morris's (1958) prediction equation, Arias and Mader (2011) examined how temperature differences during the summer and winter effect WI for cattle managed in a commercial feedlot setting and used this data to develop (WI) prediction equations for summer, winter and an overall model that includes average temperature (TAVG), SRAD, dry matter intake DMI, WSPD, average humidity (HAVG), and precipitation. Sexson et al. (2012) developed an equation to predict WI in feedlot cattle using high, low, and average relative humidity, low and high temperature, high, low and average sea level pressure, WSPD, body weight, previous day high temperature, and metabolic body weight. Parker et al., (2000), Arias and Mader (2011) and Sexson et al. (2012) utilized pen (WI), and no contemporary studies have developed water intake prediction equations utilizing individual animal feed and water intake. The objective of this study is to characterize the impact of environmental conditions on water intake for individual animals and develop prediction equations for water intake utilizing both season and bunk management protocols.

MATERIALS AND METHODS

Phenotypic data

Over a three-year period, 38,543 daily feed and water intake records were collected using an Insentec system (Hokofarm Group, The Netherlands) in Stillwater, Oklahoma. Steers (n=578) were crossbred or commercial Angus and fed in 5 feeding groups. Data were collected on each group using a 70-d feed and gain intake test (BIF, 2016). The timing

of trials allowed collection of data across different seasons: group 1 (n=117) from May 2014 to August 2014, group 2 (n=116) from November 2014 to January 2015, group 3 (n=118) from May 2015 to July 2015, group 4 (n=105) from June 2016 to August 2016, and group 5 (n=123) from January 2017 to March 2017. Groups 2 and 5 were considered winter groups and the remainder were considered summer groups.

The facility contains four separate pens that comprise both shaded (103.0 m²) and unshaded (255.9 m²) areas. The barn is open on the south, has an automated curtain on the north side and roll up doors on the east and west side. The doors and curtain were opened during the summer to add ventilation and were closed during the winter.

All groups were fed the same growing diet throughout the study that is approximately 4,524.6 cal/g on a dry matter basis (Allwardt et al. 2017). The percent dry matter was 74.02%, 73.70%, 73.11%, 73.24%, and 70.04% for groups 1, 2, 3, 4, and 5, respectively. Steers fed in groups 1-3 were managed using a slick bunk feed call procedure and steers fed during groups 4 and 5 had access to *ad libitum* feed intake. Regardless of the feed management protocol, all steers had access to *ad libitum* water. To insure data quality, feed and water intake records were filtered as outlined by Allwardt et al. (2017). Briefly, data was filtered for start and end weights, bunk visit duration, equipment malfunction, and weigh days to ensure that all records were reasonable and *ad libitum* conditions were achieved, where necessary. Because of the requirement for *ad libitum* feed intake in groups 4 and 5, feed intakes were also treated as missing in these groups on days that *ad libitum* intake was not achieved.

Individual body weights were collected every 14 d. The average daily gain (ADG) for each animal was obtained by regressing body weight over time to account for differences in fill.

Individual daily weights (dWT) were calculated by:

$$dWT_{ij} = \text{Intercept} + \text{ADG} * \text{day}_d$$

where:

dWT_{id} =Individual daily weights i^{th} individual on the j^{th} day, and

day_d = the d^{th} day weights were taken

Each daily WI measure was converted to WI as a percent of body weight (WI%) by dividing daily WI by dWT. Reporting WI as a percent of body weight for each individual daily measure roughly accounts for the difference in size of individuals. All animal procedures were approved by the Institutional Animal Care and Use Committee at Oklahoma State University (protocol AG13-18) in accordance with Federation of Animal Science Societies (FASS, 2010) guidelines.

Environmental Data

Weather data were obtained from the Stillwater station of the Oklahoma Mesonet (Brock et al., 1995) for the study dates. Data downloaded from Mesonet were daily maximum, minimum, and average temperature and relative humidity, average daily wind speed, and total daily solar radiation (daily accumulation of solar radiation), which were generated from measurements taken every 5 minutes throughout the day. Mesonet measures air temperature and relative humidity at 1.5 m above ground using a thermistor-sortion probe (Brock et al., 1995). Solar radiation is measured using a silicon photodiode-type pyranometer that is mounted on a separate tripod at 1.75 m (Brock et al., 1995). Wind speed and direction were measured using a R. M. Young m5103 model probe that was

mounted 10 m high (Brock et al., 1995). Daily minimum and maximums were determined for each 24-hour period starting at 12:00 AM and ending at 11:59 PM. Temperature-humidity index (THI) was calculated using the equation reported by Mader et al., (2006)

Statistical Analysis

Analyses in this study were based on consumed water only; water from feed was not included. To determine the appropriate variables to include in subsequent analyses, several variables and combinations of variables were tested to maximize the fit of a regression model (R^2). This was performed using the selection option in PROC Reg of SAS 9.4. Variables that were tested for the prediction model were DMI, MWTS, minimum temperature, maximum temperature, TAVG, minimum relative humidity, maximum relative humidity, HAVG, SRAD, WSPD, and THI. The variables to use in subsequent predictions were determined by the model that had the largest coefficient of determination with the smallest number of factors included. For an additional factor to be added to the analysis, a larger coefficient of determination was needed (defined as 1%) in order to keep the final models as simple and user-friendly as possible. Water intake was used to develop prediction equations instead of WI% because MWTS was included in the model. The simplest linear prediction model with the best fit included the following:

$$DWI = b_0 + b_1 DMI + b_2 dMWTS + b_3 TAVG + b_4 HAVG + b_5 SARD + b_6 WSPD$$

where b_0 is the intercept value, b_1 is the coefficient for DMI, b_2 is the coefficient for dMWTS, b_3 is the coefficient for TAVG, b_4 is the coefficient for HAVG, b_5 is the coefficient for SRAD, and b_6 is the coefficient for WSPD.

Effect of Environmental Conditions on Water Intake

Cattle drink different amounts of water during different seasons, which reflects differences in magnitude of weather variables (Arias and Mader, 2011). A better understanding of WI requirements for cattle at different time points during the year and how intake is affected by changes in different weather variables is needed. Summary statistics for the weather conditions in each group were calculated using the means procedure in SAS 9.4. Pair wise comparisons were made between all groups using the general linear model procedure in SAS 9.4 to determine any differences between TAVG, HAVG, SRAD, and WSPD that were experienced between each feeding period.

Various models including the weather factors selected previously were fitted to better understand the effect weather factors have on water intake as a percent of body weight (WI%). Steers were fed during different seasons and years, so environmental factors varied for each group. Model 1 was the baseline model that did not include any weather data, which was used to quantify the differences in raw intakes between groups, and was constructed as follows:

$$WI\%_{ijk} = \text{group}_i + \text{group}(\text{pen})_{i(j)} + e_{ijk}$$

where:

$WI\%_{ijk}$ = Daily water intake as a percent of body weight for the k^{th} individual from i^{th} group and the j^{th} pen,

group_i = The i^{th} group where $i=1-5$,

$\text{group}(\text{pen})_{i(j)}$ = the j^{th} pen nested within the i^{th} group

e_{ijk} = random residual

Significance of each individual factor was first ascertained by adding each individual weather variable to model 1 in 5 separate univariate repeated measures analyses, and each

was fitted using a first order auto regressive covariance structure using PROC GLIMMIX in SAS 9.4. Weather factors that were added to the model were TAVG, HAVG, SRAD and WSPD. Then, to account for environmental differences between the feeding groups, each environmental factor was added to model 1 as a covariate in a step-wise fashion until every available factor had been included. The order for addition of weather factors was determined based on the size of the F statistic of each single factor model, with the highest F value added to the model first. Once all weather factors had been included, the full model was as follows:

$$WI\%_{ijk} = \text{group}_i + \text{group}(\text{pen})_{i(j)} + \text{SRAD} + \text{TAVG} + \text{HAVG} + \text{WSPD} + e_{ijk}$$

Where:

$WI\%_{ijklmno}$ = Daily water intake as a percent of body weight for the k^{th} individual from i^{th} group, the j^{th} pen,

group_i = The i^{th} group where $i=1-5$,

$\text{group}(\text{pen})_{i(j)}$ = the j^{th} pen nested within the i^{th} group

SRAD = the covariate of solar radiation

TAVG = the covariate of average daily temperature

HAVG = the covariate of average daily relative humidity

WSPD = the covariate of average daily wind speed

e_{ijk} = random residual

For each model, contrasts were constructed to determine the effect of feed management (slick bunk in groups 1-3 vs *ad libitum* in groups 4 and 5) and season (summer for groups 1, 3, and 4 vs winter in groups 2 and 5), the interaction between bunk management and season (summer slick bunk in groups 1 and 3 versus summer *ad libitum* in group 4 and

winter slick bunk for group 2 vs winter *ad libitum* in group 5). Differences between groups, seasons, and bunk management were considered significant at the $p \leq 0.05$ level.

Cross Validation

A five-fold cross validation was performed to determine whether there were systematic differences between groups that would limit our ability to combine data across groups for analysis. For the cross validation, a prediction equation was developed using DMI, MWTS, TAVG, HAVG, SRAD, and WSPD data from 4 of the 5 groups and used to predict the intakes for steers in the fifth group. Thus, predictions in the fifth group were generated independently of the training population. Correlations between predicted and actual intakes were computed to determine how similar the predicted water intakes were to the observed water intakes.

Water Intake Prediction Equation

Simple linear regression analysis was performed for each variable used in the linear prediction model using the regression procedure in SAS 9.4. The general model fit was as follows:

$$DWI = b_0 + b_1 \text{Variable}$$

where b_0 is the intercept value, b_1 is the coefficient for a specific weather variable, and Variable is a general term to denote the individual regression analyses fit for DMI, dMWTS, TAVG, HAVG, SRAD, and WSPD.

These univariate analyses were conducted for each set of data available (all, summer, winter, slick bunk, and *ad libitum*).

Finally, WI prediction equations were developed using the weather variables identified previously for all the data, for only slick bunk management, for only *ad libitum*

feed availability, for only winter groups, and for only summer groups. To validate the overall prediction equation, the equation was utilized to predict DWI in an independent group of animals not utilized in the development of the equation (group 6). Group 6 cattle were fed the same ration and managed similarly to the previous 5 groups. They were allowed access to *ad libitum* feed and water and were fed from September 2017 to November 2017. Predictions from the equation developed in this study were also compared to values calculated from prediction equations developed by Winchester and Morris (1965) and Arias and Mader (2011). Predictions from the current study were not compared to DWI predictions by Sexson et al. (2012) because daily high sea level pressure was not available.

RESULTS AND DISCUSSION

Environmental Variables

A summary of environmental conditions for each group are presented in Table 3.1. Significant differences in average temperatures were detected across the summer groups (group 1 and 3, $P = 0.0382$); group 1 and 4, $P = 0.0002$; and group 3 and 4, $P < 0.0001$). All summer groups were fed from May to August, and temperatures ranged from 13.07 to 31.93°C. The winter groups (group 2 and 5) had significantly ($P < 0.0001$) different average daily ambient temperatures which ranged from -7.10 to 25.25°C. Even though groups 2 and 5 are both considered winter groups, data was collected during different months. Group 2 was fed November to January where group 5 was fed from January to March. Unsurprisingly, there were significant temperature ($P < 0.0001$) differences between summer and winter groups. Group 4 experienced the highest average temperature (28.06°C) and group 2 experienced the lowest average temperature (4.03 °C).

Even though the three summer groups were fed at roughly the same time of year, there were still significant differences in HAVG detected between groups 1 and 3 ($P = 0.0447$) and groups 3 and 4 ($P = 0.0012$). However, there were no differences in HAVG observed between groups 1 and 4 ($P = 0.2095$). The HAVG during the winter groups was significantly different ($P = 0.0003$). Unlike temperature, not all winter and summer groups experienced differences in HAVG, but significant differences were noted between some summer and winter groups (1 and 5, $P = 0.0001$; 2 and 3, $P = 0.0301$; 3 and 5, $P < 0.0001$; and 4 and 5, $P = 0.0103$). Group 3 cattle experienced the highest HAVG (75.71%) and group 5 experienced the lowest HAVG (63.00%).

For the summer groups (1, 3, and 4), there were no significant differences in SRAD except between groups 3 and 4 ($P = 0.0147$). Differences in SRAD were observed between the winter groups ($p < 0.0001$). As would be expected, SRAD significantly higher in the summer groups when compared to the winter groups (1 vs 2; $P < 0.0001$, 1 vs 5; $P < 0.0001$, 2 vs 3; $P < 0.0001$, 2 vs 4; $P < 0.0001$, 3 vs 5; $P < 0.0001$, and 4 vs 5; $P < 0.0001$). Similar to TAVG, group 4 cattle experienced the highest SRAD (24.08 MJ/m²) and group 2 steers experienced the lowest (7.89 MJ/m²).

Fewer differences between groups were noted for WSPD. The only significant differences observed were between summer and winter groups: 1 and 5 ($P = 0.0334$), 2 and 4 ($P = 0.0426$), 3 and 5 ($P = 0.0219$), and 4 and 5 ($P < 0.0001$). Cattle fed during winter group 5 experienced the highest wind speed (12.72 km/h) and group 4 cattle experienced the lowest (10.18 km/h).

Effect of Environmental Variables on Water Intake

Different seasons have varying TAVG, HAVG, SRAD, and WSPD which impacts the degree of WI% that an animal consumes. Single-factor models for each weather variable were analyzed to determine the order of importance for each variable. All weather variables had a significant ($P < 0.0001$) effect on WI% when analyzed as single factors. All factors had the same P-value, so the F-statistic was used to determine relative importance of each variable. Surprisingly, SRAD (F-value = 2040.01) had the highest F-statistic, even though cattle had access to shade. Average temperature (F-value = 1420.10) was determined to have the second most significant effect on WI%, followed by relative humidity (F-value = 1347.09) and WSPD (F-value = 95.22).

Baseline Model

Differences in WI% are shown in Table 2. WI% was significantly different ($P < 0.05$) between all groups, except for groups 1 and 4, when no environmental factors are included in the model. Group 4 steers consumed the most water per unit of body size, which may be because they experienced the highest TAVG and SRAD (Table 3.1). Cattle fed during group 4 consumed 0.75% ($P = 0.3376$), 56.5% ($P < 0.0001$), 25.1% ($P < 0.0001$), and 28.0% ($P < 0.0001$) more water than groups 1, 2, 3 and 5, respectively. Group 2 steers consumed the lowest amount per unit body weight, which was 55.4% ($P < 0.0001$), 25.1% ($P < 0.0001$), and 22.3% ($P < 0.0001$) less than group 1, 3, and 5 respectively, likely due to the fact that group 2 steers experienced the lowest TAVG and SRAD (Table 3.1). Group 3 steers drank 24.2% ($P < 0.0001$) less water than group 1 and 2.3% ($P < 0.0305$) more than group 5. Differences in WI% among the groups could be attributed to animals attempting to regulate body temperature by reducing heat load (Beede and Collier, 1986). Increases in

WI could be attributed to the animals relying on peripheral vasodilation and water evaporation to regulate body temperature (Berman et al., 1985).

Seasonal effects were observed, and steers fed during the summer months had significantly ($P < 0.0001$) higher WI% than steers fed during the winter, with summer steers drinking, on average, about 2.34% of their body weight more than steers in the winter. Understanding how WI% differs between seasons can be beneficial to producers, allowing them to provide ample water for cattle to maximize performance and minimize heat stress. This would be especially beneficial at times when there might be a shortage in the quality or quantity of water (like during a drought), thus allowing for better management of water resources. Bunk management also had an impact on WI%. Steers that had access to *ad libitum* feed drank significantly more water (0.87% of body weight; $P < 0.0001$) than steers managed under a slick bunk protocol. This result is different from Mader and Davis (2004), which reported no difference in WI between *ad libitum* (39.35 liters/d) and slick bunk management (41.18 liters/d) using pen water intakes allocated to individual animals over an 82 d feeding period. Differences in WI% were also found when examining the interaction between bunk management and season. Cattle that were on a slick bunk management protocol and fed during the summer drank significantly less (1.13% of body weight; $P < 0.0001$) than *ad libitum* steers fed during the summer. The same trend followed for cattle fed during the winter that were on the slick bunk management protocol, who drank significantly less (0.77% of body weight ; $P < 0.0001$) than their *ad libitum* counterparts. Differences between slick and *ad libitum* feed intake in the winter groups was significant, but of a smaller magnitude than in the summer (0.77% of body weight vs 1.13% of body weight), which is to be expected given that intakes in the

summer are generally higher. Significant differences were noted between seasons, feed management, and their interaction, and ranged from 0.77% to 2.34% of body weight. These differences indicate that specific predictions equations for seasons and management protocols may be advantageous when trying to predict WI.

Solar Radiation

SRAD was added to baseline model and results are reported in column 4 of Table 2. Significant differences in WI% were detected between all of the groups ($P < 0.0001$), except between group 1 and 4 ($P = 0.5641$), but the magnitude of the differences were generally smaller and intakes were more similar across groups after accounting for SRAD (Figure 1). Group 1 steers consumed the most water, rather than group 4. Group 1 steers drank 33.9% ($P < 0.0001$), 24.4% ($P < 0.0001$), 0.49% ($P < 0.5641$), and 16.4% ($P < 0.0001$) more water than groups 2, 3, 4, and 5 respectively. Group 2 steers still had the lowest WI%, consuming 7.7% ($P < 0.0001$), 33.3% ($P < 0.0001$), and 15.1% ($P < 0.0001$) less than group 3, 4, and 5 respectively. Steers in group 3 consumed 23.8% ($P < 0.0001$) and 6.9% ($P < 0.0001$) less water than group 4 and 5, respectively. Group 4 animals consumed 15.8% ($P < 0.0001$) more water than group 5 animals. Interestingly, when solar radiation was added to the model, it did cause some re-ranking between groups (group 1 and group 4, and group 3 and group 5). Group 3 cattle had lower intakes than the other summer groups, and are more similar to the winter groups (group 2 and 5) than the other summer groups, despite the fact that the SRAD is similar to the other summer groups. Significant differences in SRAD were not observed between the three summer groups except between groups 3 and 4 (Table 3.1); however, fewer differences in WI% were observed between the summer groups when SRAD was included in the model. Because

cattle had access to shade, they may not have experienced the full effect of SRAD differences between each group. The amount of time that cattle spent in the shade has not been quantified in this study but, anecdotally, cattle fed during the winter months tended to spend less time in the barn, thus getting more exposure to SRAD. The amount of exposure to SRAD can affect the temperature of surfaces animals come into contact with as well as directly impact body temperature, particularly in dark-hided cattle (Mader et al., 2006). Cattle of different hide colors also absorb SRAD at different rates, with black-hided cattle absorbing the most and white-hided cattle absorbing the least (Silanikove, 2000). Arp et al. (1983) reported that, due to relative absorptivity and emissivity differences between black-haired and white-haired cattle, that surface body temperature of black-haired cattle can be up to 21°C greater than white-haired cattle. Group 5 steers were the only group with all black-hided cattle and even though they experienced lower temperatures than the summer groups, their surface body temperature could have been a lot higher, which could have contributed to greater WI%. Even with differences in exposure to SRAD between seasons and potential differences in use of shade (or lack thereof), SRAD is clearly an important predictor of WI% in this study. The impact of SRAD also reinforces the impact of shade as an important mitigator of heat stress in beef cattle (Mader et al., 1999). However, previous research has shown that providing shade for cattle does not always improve performance (Brown-Brandl et al., 2005). The ability of cattle to acclimate and compensate for short-term losses in feed intake and gain caused by heat stress may be why increases in performances are not always seen in cattle with access to shade (Mader et al., 1999). Shade may not have been shown to consistently improve cattle performance,

but access to shade has been shown to lower core body temperature and respiration rate (Mittlöhner et al., 2001, Valtorta et al., 1997).

Seasonal differences were observed, with summer groups having higher WI% (1.34% of body weight; $P < 0.0001$) than cattle fed during the winter. However, the magnitude of the difference in WI% between summer and winter shrank by almost half when accounting for SRAD. Cattle that were managed with the slick buck protocol drank less (0.79% of body weight; $P < 0.0001$) than steers that had access to *ad libitum* feed. During the summer months, cattle that were managed with the a slick bunk protocol consumed less (0.96% of body weight; $P < 0.0001$) water as a unit of body weight than cattle that had access to *ad libitum* feed. An identical result was also found for cattle fed during the winter when comparing slick and *ad libitum* management (0.58% of body weight; $P < 0.0001$), although the magnitude of the difference shrinks in the winter as compared to the summer.

Average Daily Temperature

Both SRAD and TAVG were added to the baseline model and results are reported in column 5 of Table 2. Significant differences were detected in WI% between all groups ($P < 0.05$), except between groups 4 and 5 ($P = 0.8316$). Group 1 steers have the highest WI%. For the majority of groups, the difference in WI% decreased (Figure 1), with the exception of group 1 and 4. The increase between group 1 and 4 could be due to the interaction between TAVG and HAVG (Arias and Mader, 2011), which has not yet been included in the model. When SRAD was the only weather variable included in the model, there was not a significant difference between groups 1 and 4, but when TAVG is added, a significant ($P = 0.0008$) difference between the two groups is noted. Group 1 steers

consumed 11.2% ($P < 0.0001$), 24.2% ($P < 0.0001$), 3.2% ($P = 0.0008$), and 2.9% ($P = 0.0046$) more water than groups 2, 3, 4, and 5 respectively, which is likely due to the fact groups 1 and 4 have the highest TAVG with the least amount of variation (Table 3.1). The consistently higher TAVG for group 1 and 4 steers would suggest that steers in these groups experienced more days with heat stress. The NRC designates that thermoneutral conditions are between 15 and 25°C (NRC 1996). In this study, steers experienced 37 d, 0 d, 31 d, 61 d, and 1 d over 25°C for groups 1, 2, 3, 4, and 5, respectively. Group 2 steers drank 8.0% ($P < 0.0001$) and 8.4% ($P < 0.0001$) less than group 4 and 5 steers, respectively, but 11.5% ($P < 0.0001$) more than group 3, even though group 2 steers experienced the lowest TAVG and SRAD (Table 3.1). When both SRAD and TAVG are included in the model, group 3 cattle had the lowest WI%. Group 3 cattle consumed 20.4% ($P < 0.0001$) and 20.8% ($P < 0.0001$) less water than groups 4 and 5 respectively. Group 3 is the only summer group that experienced temperatures below 15 °C, which could cause cold stress, and have the fewest days above 25°C that could lead to heat stress when compared to the other summer groups. The wide range of temperatures (and generally cooler temperatures; Table 3.1) that were experienced by group 3 steers could be one reason why this group of cattle had lower intakes than the other summer groups (1 and 4). Group 4 steers drank 3% less than group 5, but this difference was not significant ($P=0.831$).

When accounting for TAVG, cattle fed during the winter tended to drink more than cattle fed during the summer, but intakes were not significantly different between seasons ($P = 0.2606$). However, significant differences remain for feed management ($P < 0.0001$). The magnitude of the difference in WI% between different bunk management protocols decreased with the addition of TAVG (0.68% vs 0.79% of body weight). The slick bunk

managed cattle consumed less WI% than cattle that had access to *ad libitum* feed. The interactions between feed management and season for the summer ($P < 0.0001$) and winter ($P < 0.0001$) groups were still significant. Cattle that had access to *ad libitum* feed drank more water than slick bunk cattle whether they were fed during the summer or winter. Water intake as a percent of body for slick bunk cattle fed during the summer was 0.65% of body weight lower than *ad libitum* steers ($P < 0.0001$). A slightly smaller difference was seen for cattle fed during the winter months (0.37% of body weight; $P < 0.0001$), with slick bunk managed steers consuming less than *ad libitum* steers. Steers that had access to *ad libitum* feed had higher WI%; however, the addition of TAVG reduced the difference between slick bunk managed cattle and *ad libitum* fed cattle, regardless of season.

Average Daily Relative Humidity

When the model described previously was augmented with the addition of HAVG, there were still significant ($P < 0.05$) differences in WI% between all groups (Table 2, column 6). Group 1 cattle still consume the most water per unit body weight, drinking 14.8% ($P < 0.0001$), 23.1% ($P < 0.0001$), 3.2% ($P = 0.0003$), and 6.4% ($P < 0.0001$) more water than group 2, 3, 4 and 5 respectively. Figure 1 shows that differences between groups decreased after the addition of HAVG. Solar radiation, TAVG, and HAVG are major contributing factors to heat stress (Mader et al., 2006), and heat stress can increase consumption of water. By accounting for differences in these three variables between groups, smaller differences in WI% would be expected. Group 2 cattle consumed 7.3% ($P < 0.0001$) more WI% than group 3, but 11.2% ($P < 0.0001$) and 7.9% ($P < 0.0001$) less WI% than group 4 and 5 respectively. The addition of HAVG to the model decreased the difference in WI between groups 2 and 3 from 11.5% to 7.3%. Group 3 cattle experienced

the highest HAVG and higher temperatures than group 2, which could explain this result. However, the difference between groups 2 and 4 increased by 3.2% with the addition of HAVG. The difference between groups 2 and 5 was similar to the previous model. Even though cattle in group 3 experienced a 7.11 unit higher HAVG than group 4, there was a small reduction in magnitude of the difference between group 3 and 4 (1.2%). The effect of HAVG on WI% is impacted by temperature. When cattle are exposed to higher temperatures, HAVG tends to have a greater effect on WI% (Arias and Mader, 2011). There was a slightly larger reduction in the magnitude of differences between groups 3 and 5 (5%). When accounting for HAVG, a 3.32% ($P = 0.0119$) increase in the difference between groups 4 and 5 was observed. Although relative humidity had less impact on WI% than temperature in this study, it still contributed to the heat load experienced by cattle. When humidity and ambient temperature rise, evaporative cooling effects decline as humidity reduces respiratory and surface evaporation, potentially resulting in cattle consuming more water to regulate body temperature during times of high heat load (Silanikove, 2000).

Seasonal differences were still significant after the addition of HAVG to the model, with summer cattle having a higher WI% than winter cattle (0.21% of body weight; $P = 0.0161$). Cattle that had access to *ad libitum* feed consumed more water (0.59% of body weight; $P < 0.0001$) than cattle managed with a slick bunk protocol. This trend is also true for the interaction between management protocol and season (summer $P < 0.0001$ and winter $P < 0.0001$). The magnitude of differences between management, season, and management by season were all less than 0.62% of body weight.

Average Daily Wind Speed

Wind speed was the final weather factor added to the model, and there were significant ($P < 0.05$) differences between WI% in all the groups (Table 2, column 7). Figure 1 shows additional reductions in differences between groups when all weather factors were added to the model. Group 1 cattle still consumed the most water per unit body weight, drinking 14.4% ($P < 0.0001$), 23.0% ($P < 0.0001$), 3.5% ($P = 0.0001$), and 6.0% ($P < 0.0001$) more water than group 2, 3, 4 and 5 respectively. The differences in WI% between group 1 and the other groups was similar to the previous model that did not account for WSPD (which was 14.8%, 23.1%, 3.2%, and 6.4% for groups 2, 3, 4, and 5, respectively). It is not surprising that minimal changes were observed when WSPD was added even though wind can aid in convection cooling (Morrison, 1983), since WSPD had the fewest significant differences between groups (Table 3.1). Group 2 cattle consumed 7.5% ($P < 0.0001$) more WI% than group 3, but 10.6% ($P < 0.0001$) and 7.9% ($P < 0.0001$) less WI% than group 4 and 5, respectively. Small reductions in WI% were observed between groups 3 and 4, 3 and 5, and 4 and 5 when WSPD was added to the model. The impact of WSPD on WI% may not have been as significant in this study, as cattle had access to the barn, which would limit the amount of wind exposure for the cattle. Minor differences in the amount of convection cooling that was possible in each group would be expected. Convection cooling is when cooler air comes in contact with a warmer body; thus a layer of air surrounding the body heats and is carried away with air movement (Silanikove, 2000). Wind speed can also impact evaporative cooling. Cattle use evaporative cooling to dissipate heat load (Morrison, 1983); however, this increases the need for cattle to consume water to maintain homeostasis (Arias and Mader, 2011). Evaporative cooling can also contribute to cold stress in the winter (Mader, 2003).

Seasonal differences were still significant with the addition of WSPD to the model with summer cattle having a higher WI% than winter cattle (0.18% of body weight; $P = 0.0396$). Even though there were significant differences between these groups, this study included over 38,000 records, which results in even small differences being detected as significant. This small difference suggests that after accounting for differences in weather, cattle fed during the summer and winter have similar levels of WI%. Differences that remain are likely due to individual animal genetic variation (including breed composition), that have not been accounted for in these models. Cattle that had access to *ad libitum* feed consumed more water (0.58% of body weight; $P < 0.0001$) than cattle managed with a slick bunk protocol. This trend is also true for the interaction between management protocol and season (summer $P < 0.0001$ and winter $P < 0.0001$). The magnitude of differences between management, season, and management by season were all less than 0.58% of body weight after accounting for all four environmental variables.

Water Intake Prediction

Cross validation

A fivefold cross validation was performed to determine whether it was appropriate to combine data across different groups to create a joint prediction model for WI. Correlations between the observed WI and predicted WI (model developed with the other 4 groups) were 0.53, 0.38, 0.61, 0.44, and 0.64 for groups 1, 2, 3, 4 and 5 respectively. Correlations were lowest for group 2 and group 4. Even though group 5, which was also a winter group, was included in the training set when predicting group 2, temperatures during group 5 were significantly warmer than group 2 (Table 3.1). Thus, correlations were likely lower when predicting group 2 because intakes were being predicted at temperatures

that were not reflected in the training set. Lower correlations for group 4 were likely due to differences in body weight. Group 4 steers were the heaviest, having an initial average start weight of 412.38 kg, compared to 321.53 kg, 333.87 kg, 367.04 kg, and 341.82 kg for groups 1, 2, 3, and 5, respectively, and thus, predictions were being made in this group on sizes of animals not well represented in the training. The other groups had relatively high correlations between predicted values and observed values given that environmental factors, body size, and breed composition differences were not accounted for in this analysis. Based on these results, data was combined across groups for further analysis and development of an overall prediction equation for WI.

Overall Prediction

Results from univariate analyses predicting DWI are shown in Table 3.3. When using data from all groups, DMI is positively ($P < 0.0001$) related to DWI. As steers consumed more feed, they also tended to consume more water. The current study, as well as Winchester and Morris (1956), Arias and Mader (2011), and Sexson et al. (2012), all showed a positive relationship between DWI and DMI in their prediction equations. However, the current study suggests a higher slope estimate (2.17) than Arias and Mader (1.03; 2011) and Sexson et al. (0.349; 2012). The prediction equation from Winchester and Morris (1958) is based on DMI at different temperature levels. Depending on the season, the relationship between DWI and DMI are known to differ. DWI generally increases and DMI generally decreases during the summer and the opposite occurs during the winter (Sexson et al., 2012). When differing relationships exist between DMI and DWI depending on the season, prediction of DWI from DMI can be inconsistent (Sexson et al., 2012). However, this relationship was not observed in the current study, as both DWI and DMI

have a positive relationship during both the summer and winter. DWI was also related to MWTS ($P < 0.0001$). Larger steers tended to consume more water, which is supported by Meyer et al. (2006), who found a similar result in a population of dairy cows.

Temperature was positively associated with DWI ($P < 0.0001$), as expected. As temperature increases past 25°C (as it did for 37d, 0d, 31d, 61d, and 1d in groups 1, 2, 3, 4, and 5, respectively), cattle begin to experience heat stress NRC (1996). Water can play a key role in regulating body temperature (Berman et al., 1985); thus, as cattle experience higher temperatures, they would be expected to consume more water. The result in this study is consistent with both Arias and Mader (2011), and Sexson et al. (2012), which showed that increases in temperature were associated with increases in DWI. In our study, for every 1-degree Celsius increase in temperature, there is an increase in DWI consumption of 0.65 kg, which is intermediate to previous literature estimates. Arias and Mader (2011) used maximum temperature (TMAX) in their prediction equation instead of TAVG, but reported that as TMAX increases by 1°C , DWI increased by 0.45 kg. Sexson et al. (2012) reported that an increase of 1°C in TAVG produces a 1.034 kg increase in DWI.

Cattle experiencing increases in HAVG during the feeding period had decreased ($P < 0.0001$) DWI. One way that cattle lose water is through respiration (Sexson et al., 2012). However, respiratory air is highly saturated with water, thus water losses through respiration are greater when humidity is low (Sexson et al. 2012). The amount of humidity in the air can also effect the rate of evaporative cooling processes (Morrison, 1983). Thus, cattle exposed to high HAVG would be expected to have a more difficult time dissipating heat through evaporative cooling. Arias and Mader (2011) found that HAVG did not

contribute to differences in DWI over all seasons. However, Sexson et al. (2012) also found that as HAVG increases, DWI decreases.

As outlined in Table 3.3, an increase in DWI consumption of 0.72 kg results from an increase of 1 MJ/m² in SRAD. Exposure to SRAD can increase body temperature, which can lead to increases in DWI to help regulate body temperature (Arias and Mader, 2011). Providing shade to cattle has been shown to reduce heat load up to 30% (Mader et al., 1999). Beede and Collier (1986) suggested that providing cattle with protection from SRAD is one of the most immediate and cost-effective ways to increase productivity in ruminants.

Increases in WSPD decreased ($P < 0.0001$) DWI, possibly because of increased air flow leading to evaporative cooling. Evaporative cooling is one of the most practical means to cool livestock in times of heat stress (Morrison, 1983). Mader et al. (1999) also suggested that increased WSPD leads to enhanced convection and evaporative cooling due to the increased air flow. Wind speed is more effective when HAVG is low, because as HAVG increases, evaporative cooling is limited (Mader et al., 2006)

Results from the multivariate analysis predicting WI are shown in Table 4. It is important to also analyze weather factors cumulatively in a single model to predict DWI, as there are interrelationships between the weather variables and their effects on DWI. The overall model explained 40% of the variation in daily WI when including DMI, MWTS, TAVG, HAVG, SRAD, and WSPD (Table 3.2). This is not comparable to Arias and Mader (2011), which explained 65% of the variation with their overall model, but is slightly higher than Sexson et al. (2012), which explained 32% of the variation in DWI. By utilizing pen intakes, Arias and Mader (2011) were able to capitalize on a larger sample size ($n=1,275$)

as compared to this study's smaller sample size (n=579). In addition, the use of pen intakes may improve model fit due to the fact that the data structure may mask individual differences between animals, which could contribute to greater overall variability in our dataset.

Average temperature and DMI were the most important predictors of DWI, and explained 19.4% and 12.4% of the variation respectively. The overall model developed by Arias and Mader (2011) included only three variables (DMI, SRAD, and TMIN), with minimum temperature (partial $R^2 = 0.56$) as the most key variable and DMI (partial $R^2=0.02$) as the least important variable. This result may be due to the fact that they utilized pen water and feed intakes extrapolated out to individual animals, which might have minimized the importance of DMI by masking individual differences between animals. DMI measurements on individual animals clearly assist in predicting DWI in this study where intakes are not averaged across a pen, leading to the increased importance of DMI in this model. Minimum temperature was established by Mader (2003) and Amundson et al. (2006) as an important measure of energy balance, primarily due to dissipation of heat during the night. The ability of animals to reduce heat load during the night may influence the amount of water cattle consume to help regulate body temperature. In the current study, TAVG was determined to be a better predictor of DWI than TMIN, and addition of TMIN did not substantially improve the model fit. Minimum temperature may not have been as useful in predicting DWI in the current study because TMIN may not have reached low enough values, especially during the summer feeding groups, to dissipate heat during the night. Arias and Mader (2011) reported that if TMIN doesn't reach below 12°C, that heat loss through convection and conduction methods may not be as successful. In the current

study, the night temperature reached below 12°C in the summer groups 1, 3 and 4 for only 0 d, 5 d, and 0 d, respectively.

To better explore differences in models published in the scientific literature and the one developed in this study, observed DWI from an independent group of animals (winter, *ad libitum*) was used to compare the overall model from this study to predicted DWI from models developed by Arias and Mader (2011) and Winchester and Morris (1965). The correlation between intakes predicted with the model developed in this study and observed DWI in the validation group was 0.49. The correlation between DWI predicted using the equation in Arias and Mader (2011) and observed DWI was similar at 0.51. The correlation of predicted intakes from Winchester and Morris (1965) and the observed intakes was also 0.49. The model from Arias and Mader (2011) likely has no advantage over the Winchester and Morris (1965) model because it accounts for other weather factors than just a measure of temperature. However, the current study includes more weather factors and still did not do numerically as well as Arias and Mader (2011). The Arias and Mader (2011) prediction equation was developed from pen intakes instead of individual intakes. Arias and Mader (2011) utilized 1,275 animals to develop their DWI prediction equations where Winchester and Morris (1956) utilized approximately 50 head. Using more records to develop prediction equations should create more robust equations that can predict over a wider range of intakes and weather variables. In addition, using a large number of animals fed in pens may be an advantage in this process, since predictions are generally focused on the average animal. Winchester and Morris (1956) collected individual WI over one to two-week intervals, recording temperature and feed intake as well. Results from Ahlberg et al. (2017) indicate that a one to two-week collection period for DWI is too short to accurately

collect DMI using automated collection systems. Despite these factors, based on this validation, all models performed similarly ($R^2=0.49-0.51$) and the best equation could only explain 51% of the variation between predicted and actual DWI. This suggests that weather factors, body size, and DMI are not the only factors that contribute to variation in DWI. Differences in genetic merit for DWI and individual-animal variation in response to thermal stresses could be part of why the correlations were not higher.

Overall prediction models are beneficial during times that do not easily fit into a specific time period like summer or winter. However, these models are only as robust as the data that they were trained on. Thus, if predicting DWI on animals of different size, composition, or in different environmental conditions to the training data, the prediction of DWI will not be as reliable. This can also happen if sudden weather events take place that expose animals to weather factors that are extreme. As an example, prediction of DWI during extremely cold subzero temperatures might result in very low to even negative estimates of DWI if temperature is heavily weighted in a model. Some of these issues may be alleviated by using seasonal models, when they are available. In any case, overall or seasonal prediction models should be augmented with new data as it is collected (particularly on different classes of animals and in different locations that might have more extreme weather conditions) to improve WI predictions and all models should be compared utilizing independent data sets to determine the optimum prediction. Augmenting the current study's analysis with additional DWI records collected on different classes of animals and in other locations will make sure that the DWI prediction equation is robust enough to accurately predict DWI broadly over a variety of production scenarios.

Seasonal Models

Results from univariate analysis predicting DWI in summer and winter are shown in Table 3.3. The summer and winter univariate analyses follow the same trends as the overall data, but there are some differences in the magnitude of the effects on DWI. For the summer and winter data, DWI increases by 2.74 kg and 2.25 kg for every 1 kg increase in DMI, respectively. Interestingly, these values are larger than those observed when using all available data jointly. For the summer data, TAVG ($R^2 = 0.20$) explained more variation than in the winter data ($R^2 = 0.06$). Unsurprisingly, TAVG is more important to predicting DWI during the summer, likely due to the impact that TAVG can have on heat load and the relative lack of cold stress in this particular environment. Cattle fed during the summer time tend to experience higher TAVG and greater heat load than cattle fed during the winter. However, for the winter data, DMI (partial $R^2 = 0.29$) and MWTS (partial $R^2 = 0.20$) explained more variation than DMI (partial $R^2 = 0.16$) and MWTS (partial $R^2 = 0.10$) for summer groups. The variation explained by HAVG, SRAD, and WSPD were similar between the summer and winter data.

Results from the summer and winter multivariate analyses are shown in Table 3.4. The summer model, developed using data from group 1, 3 and 4, only explained 34% of the variation in DWI. Of the 6 variables that were included in the model, DMI (partial $R^2 = 0.155$) and TAVG (partial $R^2 = 0.137$) explained over 29.2% of the variability. Arias and Mader (2011) predicted daily WI during the summer months using DMI, solar radiation, and minimum temperature (TMIN) and explained 23% of the variation in DWI. Dry matter intake and a measure of temperature (TAVG vs TMIN) were key factors for predicting intakes during the summer in both studies. In this study, SRAD explains very little of the variation in the summer model (partial $R^2 = 0.000001$), whereas it was the major

contributor that explained the most variation in the summer model developed by Arias and Mader (2011; partial $R^2 = 0.14$). This may be because the steers in Arias and Mader (2011) did not have access to shade, whereas steers in this study had access to shade, and, anecdotally, the cattle appeared to spend a lot of time in the shade during the summer months, which limited their exposure to solar radiation. The inclusion of SRAD in a seasonal prediction equation when shade has been provided may not be as useful for predicting WI as it is for cattle that don't have access to shade. Sexson et al. (2012) also predicted DWI in yearling steers fed during the summer and developed a model that explained 32% of the variation in DWI, which is similar to this study. The model in Sexson et al. (2012) included 14 variables instead of the three and six variables included in the model for Arias and Mader (2011) and this study, respectively. Not only was the current daily maximum temperature included, but Sexson et al. (2012) also accounted for the previous daily maximum temperature as well as a quadratic effect of temperature. Previous day maximum temperature had a smaller impact than the current day maximum temperature (Sexson et al., 2012), possibly because steers had the ability to dissipate heat during the night. Sexson et al. (2012) also included high and average sea pressure in their prediction equation, although it had minimal impact (partial R^2 from 0.056 to 0.01). Increases in barometric pressure can reduce water vaporization in the lungs, which reduces water loss through respiration causing cattle to consume less water (IOM, 2005), but that effect did not appear to be a large contributor to variation in DWI in Sexson et al. (2012). The Sexson et al. (2012) model also differed from Arias and Mader (2011) and the current study's summer model because it didn't include DMI.

The winter model explained slightly more variation than the summer model (39%), which may be because DWI is more variable in the summer. This can be seen by the larger standard deviations of DWI observed during the summer groups (8.1 kg, 6.6 kg, and 13.8 kg for groups 1, 3, and 4, respectively) vs winter groups (5.4 kg and 4.8 kg for groups 2 and 5, respectively). Of the six factors included in the model, DMI ($R^2 = 0.291$) explains the overwhelming majority of the variation. Steers fed during the winter experienced only one day of heat stress between both groups and 132d of cold stress between both groups. Winchester and Morris (1956), Murphy et al. (1983) and Hicks et al. (1988) showed that DMI is a strong predictor of DWI. Bond et al. (1976) suggested that the ability to predict DWI from DMI is associated with the percent roughage in the diet, with DWI being more easily predicted from DMI when roughage content in the diet is higher. This could not be tested in this study as the same diet was used for all groups. Arias and Mader (2011) included six variables in their winter model ($R^2 = 0.23$), including DMI, SRAD, maximum temperature (TMAX), WSPD, HAVG, and precipitation. Maximum temperature (partial $R^2 = 0.05$), WSPD (partial $R^2 = 0.04$), HAVG (partial $R^2 = 0.07$), and precipitation (partial $R^2 = 0.05$) are the four variables that explain the majority of the variation in the Arias and Mader (2011) winter model. In our study, the environmental factors explained far less variation in DWI (~7%), with most of the emphasis placed on DMI. However, the Arias and Mader (2011) study was conducted when average temperatures were much colder (-2.0 °C vs 17.3 °C), and more humid (74.4% relative humidity vs 67.4%). Bedding was provided for some of the feed groups during the winter time for the Arias and Mader (2011), but no bedding was provided for the current study.

Ad libitum vs slick bunk management

Results from *ad libitum* and slick bunk univariate analyses are shown in Table 3.3. For the *ad libitum* data, MWTS, TAVG, and SRAD are the variables that drive DWI. However, for the slick bunk data, DMI, TAVG, and SRAD are the variables that explain the most variation in DWI. Although two of those factors are common between the management techniques, the estimates and coefficients of determination vary substantially.

Temperature and SRAD both play key roles in predicting DWI for both feed management prediction equations, likely because cattle fed during the summer that were managed under both *ad libitum* and slick bunk were exposed to heat stress (THI exceeding 74) for 38 d, 32 d and 62 d for groups 1, 3, and 4, respectively. High temperatures paired with high SRAD increase body temperature, which could result in cattle consuming more water to help regulate their body temperature (Berman et al., 1985). Dry matter intake is an important factor to predict DWI for cattle managed under a slick bunk protocol, and it has the highest coefficient of determination other than temperature. Under a slick bunk protocol some animals may have limited DMI, which could alter the relationship between DMI and DWI. On the other hand, MWTS are a more important factor for the *ad libitum* group, and the variation explained by DMI is much lower. Similar to the winter model, WSPD is not significant ($P=0.51$) in the slick bunk univariate analysis (Table 3.3), although it has a small, but significant effect in the *ad libitum* data.

Results from *ad libitum* and slick bunk multivariate analyses predicting DWI are shown in Table 3.4. The *ad libitum* model explained 41% of the variation in DWI and the slick bunk slightly less, at 39%. Of the six variables included in the *ad libitum* model, MWTS (partial $R^2 = 0.11$) and TAVG (partial $R^2 = 0.23$) explained about 34% of the variability in DWI. Unlike the seasonal models, using just two variables explains the

majority of the variation observed, with TAVG alone explaining 23% of the variation. The slick bunk model explained 39% of the variation in DWI and of the six variables that were included in the model, DMI (partial $R^2 = 0.15$) and TAVG (partial $R^2 = 0.19$) explained 34% of the variability. The slick bunk management model follows the same trend as the overall and summer models, with DMI and TAVG being the most important factors in predicting DWI. Relative humidity, SRAD and WSPD each explained approximately 3%, 0.4% and 0.1% of the variation, respectively, in the slick bunk model.

Temperature explains the most variation in both the *ad libitum* and slick bunk models, which is consistent with the importance of temperature in predicting DWI in the other models described in this study. In the *ad libitum* model, there was a slight negative estimate for MWTS; however, for the slick bunk model, the estimate is positive and substantially larger even though it contributes less to explaining variation in the data. Sexson et al. (2012) showed a positive association between DWI and body weight for animals 500 kg or less and a negative association with body weight when weight is greater than 500 kg. For the current study, many of the *ad libitum* fed steers started at a higher weight than the slick bunk steers, and likely spent more of the feeding period over the 500 kg threshold. The change in association between body weight and DWI is likely a result of the changes in composition of gain as cattle approach slaughter weights (Sexson et al., 2012). For the slick bunk model, DMI is an important driver of DWI, and DMI has the second highest coefficient of determination. On the other hand, MWTS explain more variation for the *ad libitum* fed group, and partial R^2 for DMI is much lower. Unlike the summer or winter prediction models, MWTS is the second most important factor when predicting DWI in the *ad libitum* model. Dry matter intake only explained 5% of the

variation in the *ad libitum* prediction model, but explains 15.5% of variation in the summer model, 29% in the winter, and 15% in the slick bunk model. This suggests that limiting the amount of dry matter available for consumption alters the relationship between DMI and DWI in some of the steers, leading to DMI and temperature driving the prediction of DWI in slick bunk steers. Conversely, the *ad libitum* fed steers do not have this restriction, and thus DWI is instead driven by size of the animal and temperature.

There are no DWI prediction equations for different feed management protocols previously published in the literature, so no direct comparisons between models can be made. Cattle utilized in the Sexson et al. (2012) prediction had access to *ad libitum* feed and the cattle utilized for Arias and Mader, (2011) study were a mixture of slick bunk managed and *ad libitum* managed cattle. Although Arias and Mader, (2011) had cattle managed with two different feed protocols, they did not develop separate equations for the different feed management strategies. Cattle fed in a feedlot setting are often managed with a slick bunk protocol. However, grazing breeding stock often have *ad libitum* access to forage, unless they are experiencing a shortage in feed resources due to drought or limit feeding hay and supplement during the winter. Having prediction equations that are specific to the type of feed management being practiced could allow producers to more accurately predict the water resources needed for their livestock.

CONCLUSION

Differences in WI% were observed between each group, which likely stem from a combination of environment, management, genetic background, and individual animal variation. The magnitude of the differences between groups decreased as different environmental factors were adjusted for in the data. After accounting for all environmental

parameters (SRAD, TAVG, HAVG, and WSPD) included in subsequent modeling efforts, significant differences were still observed across groups, with WI% ranging from 8.00 to 9.84 percent of body weight. Seasonal differences in WI% were also detected between cattle fed in the winter and summer (0.18% of body weight). Even though the seasonal differences detected were significant, a difference of 0.18% of body weight is reasonably small. Because of the large number of observations in the data set, small differences can be detected as significant that may not accurately represent the magnitude of differences in the underlying biology. Differences in feed management affected WI%, but the differences between steers that had access to *ad libitum* feed or steers managed with a slick bunk protocol were less than 1% of body weight when all environmental factors were accounted for in the model.

Water intake prediction equations were developed that included variables of DMI, MWTS, TAVG, HAVG, SRAD, and WSPD. The amount of variation explained by different models ranged from 0.34 to 0.41, with the summer model as the least predictive and *ad libitum* model as the most predictive. Slick bunk management makes DWI more difficult to predict and the relative importance of variables in these two models shifted depending on the feed management protocol. The prediction of DWI for steers that had access to *ad libitum* feed was the only prediction equation where MWTS was one of the two most important factors in predicting DWI. Weather factors have a significant effect on DWI and play a vital role in predicting DWI along with DMI and body size; however, individual animal variation in WI is an important factor that contributes to variation in WI that cannot be explained by current models.

REFERENCES

- Ahlberg, C. M., K. Allwardt, A. Brooks, K. Bruno, A. Taylor, C. Krehbiel, C. Richards, S. Place, U. DeSilva, D. VanOverbeke, R. Mateescu, and M. M. Rolf. 2017. Water Intake in Growing Beef Cattle. Kansas Agricultural Experiment Station Research Reports. Vol. 3: Iss. 1. doi.org/10.4148/2378-5977.1348
- Allwardt, K, C. Ahlberg, A. Brooks, K. Bruno, A. Taylor, S. Place, C Richards, M. Calvo-Lorenzo, U. DeSilva, D. VanOverbeke, R. Mateescu, C Goad, and M. Rolf. 2017. Technical note: Validation of an automated system for monitoring animal intake in group-housed beef steers. *J. Anim. Sci.*95:4213-4219. doi: 10.2527/jas.2017.1593
- Amundson, J. L., T. L. Mader, R. J. Rasby, and Q. S. Hu. 2006. Environmental effects on pregnancy rate of beef cattle. *J. Anim. Sci.* 84:3415-3420
- 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. *J. Anim. Sci.* 75:2024-2032. doi:10.2527/1997.7582024x
- Arias, R. A. and T. L. Mader. 2011. Environmental factors affecting daily water intake on cattle finished in feedlots. *J. Anim. Sci.* 89:245-251. doi:10.2527/jas.2010-3014
- Arp, S. C., F. N. Owens, S. L. Armbruster, and D. Schmidt. 1983. Effect of animal density, coat color and heat stress on performance of feedlot steers, Oklahoma Anim. Sci. Res. Rep. MP-114. Oklahoma State Univ. Exp. Stn., Stillwater, OK. P 79-81

- Beatty, S. T., A. Barnes, E. Taylor, D. Pethick, M. McCarthy, and S. K. Maloney. 2006. Physiological responses of *Bos taurus* and *Bos indicus* cattle to prolonged continuous heat and humidity. *J. Ani. Sci.* 84:972-985. doi:10.2527/2006.844986x
- Beckett, J. L. and J. W. Oltjen. 1993. Estimation of the water requirement for beef production in the United States. *J. Anim. Sci.* 71:818-826. doi:10.2527/1993.714818x
- Beede, D. K., and R. J. Collier. 1986. Potential nutritional strategies for intensively managed cattle during thermal stress. *J. Anim. Sci.* 62:543-554. doi:10.2527/jas1986.622543x
- Berman, A., Y. Folman, M. Kaim, M. Mamen, Z. Herz, D. Wolfenson, A. Arieli, and Y. Graber. 1985. Upped critical temperature and forced ventilation effects for high-yielding dairy cows in a subtropical climate. *J. Dairy Sci.* 68:1488-1495. Doi:10.3168/jds.S0022-002(85)80987-5
- BIF. 2016. Guidelines for uniform beef improvement program. Beef Improvement Federation. Ninth edition. Raleigh, NC
- Bond, J., T. S. Rumsey, and B. T. Weinland. 1976. Effect of deprivation and reintroduction of feed and water on the feed and water intake behavior of beef cattle. *J. Anim. Sci.* 43:873-878. doi:10.2527/jas1976.434873x
- Brock, F. V., K. C. Crawford, R. L. Elliott, G. W. Cuperus, S. J. Stadler, H. L. Johnson, and M. D. Eilts. 1995. The Oklahoma Mesonet: a technical overview. *J Atmos Ocean Technol* 12:5-19
- Brown-Brandl, T. M., R. A. Eigenberg, J. A. Nienaber, and G. L. Hahn. 2005. Dynamic response indicators of heat stress in shaded and non-shaded feedlot cattle, Part I:

- Analyses of indicators. *Biosystems. Engineering.* 90(4):451-462.
- Doi:10.1016/j.biosystemseng.2004.12.006
- IOM (Institute of Medicine). 2005. Dietary Reference Intakes for Water, Potassium, Sodium, Chloride, and Sulfate. Natl. Acad. Press, Washington. DC
- MA. 2005. The millennium ecosystem assessment. "Ecosystems and Human Wellbeing Scenarios, col 2", Island Press.
- <http://www.maweb.org/en/products.global.scenarios.aspx>
- Mader, T. L. 2003. Environmental stress in confined beef cattle. *J. Anim. Sci.* 81(E Suppl.):E110-E119. doi:10.2527/2003.8114_suppl_2E110x
- Mader, T. L., J. M. Dahlquist, G. L. Hahn, and J. B. Gaughan. 1999. Shade and wind barrier effects on summertime feedlot cattle performance *J. Anim. Sci.* 77:2065-2072. doi:10.2527/1999.7782065x
- Madar, T. L. and M. S. Davis. 2004. Effect of management strategies on reducing heat stress of feedlot cattle: Feed and water intake. *J. Anim. Sci.* 82:3077-3087. doi:10.2537/2004.82103077x
- Mader, T. L., M. S. Davis, and T. Brown-Brandl. 2006. Environmental factors influencing heat stress in feedlot cattle. *J. Anim. Sci.* 84:712-719. doi:10.2537/2006.843712x
- Meyer, U., M. Everinghoff, D Gadenken, and G. Flachowsky. 2004. Investigation on the water intake of lactating dairy cows. *Livestock Production Science.* 90:117-121. doi:10.106/j.livprodsci.2004.03.005
- Mitlöhner, F. M, J. L. Morrow, J. W. Dally, S. C. Wilson, M. L. Galyean, M. F. Miller, and J. J. McGlone. 2001. Shade and water misting effects on behavior, physiology,

- performance, and carcass traits of heat-stress feedlot cattle. *J. Anim. Sci.* 79:2327-2335. doi:10.2537/2001.7992327x
- Morrison, S. R. 1983. Ruminant heat stress: Effect on production and means of alleviation. *J. Anim. Sci.* 57:1594-1600. doi:10.2537/jas1983.5761594x
- Nardone, A., B. Ronchi, N Lacetera, M.S. Ranieri, and U. Bernabucci. 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livest. Prod.* 130:57-69. doi:10.106/j.livprodsci.2010.02.011
- NOAA. 2017. Drought-March. <https://www.ncdc.noaa.gov/sotc/drought/>. Accessed May 9, 2017
- NRC. 1996. *Nutrient Requirements of Beef Cattle*. 7th rev. ed. Natl. Acad. Press. Washington, DC
- NRC. 2000. *Nutrient Requirements of Beef Cattle*. 7th rev. ed. Natl. Acad. Press. Washington, DC. Rosegrant, M. W., X. Cai, and S. A. Cline. 2002. Global water outlook to 2020, Averting an impending crisis, A 2020 vision for food, agriculture, and the environment initiative. International Food Policy Research Institute/International Water Management Institute, Washington, D. C. U.S.A/ Colombo, Sri Lanka
- Sexson, J. L., J. J. Wagner, T. E. Engle, and J. Eirikhoff. 2012. Predicting water intake by yearling feedlot steers. *J. Anim. Sci.* 90:1920-1928. doi:10.2527/jas.2011-4307
- Silanikove, N. 2000. Effects of heat stress on the welfare of extensively managed domestic ruminants. *Livest. Prod. Sci.* 67:1-18. doi:10.1016/S0301-6226(00)00162-7
- Thornton, P. K., J. van de Steeg, A. Notenbaert, and M. Herrero. 2009. The impact of climate change on livestock and livestock systems in developing countries: A review

of what we know and what we need to know. *Agric. Syst.* 101:113-127.

doi:10.1016/j.agsy.2009.05.002

Valtorta, S. E., P. E. Leva, and M. R. Gallardo. 1997. Evaluation of different shades to improve dairy cattle well-being in Argentina. *International Journal Biometeorology.*

41:65-67. doi:10.1007/s00484005

Winchester. C. F., and M. J. Morris. 1956. Water intake rates of cattle. *J. Anim. Sci.* 15:722-740. doi:10.2527/jas1956.153722x

Table 3.1 Means, standard deviations, minimums (Min) and maximums (Max) for environmental variables observed during the feeding period for each group.

Variables^a	Group	Mean	Std	Min	Max
Temperature	1	25.03 ^b	3.13	17.33	30.85
	2	4.03 ^c	6.05	-7.10	17.86
	3	23.35 ^d	4.67	13.07	29.94
	4	28.06 ^e	2.52	21.63	31.93
	5	9.66 ^f	6.27	-1.35	25.25
Relative Humidity	1	71.33 ^b	10.05	47.52	95.84
	2	70.98 ^{b,c}	16.44	42.65	98.76
	3	75.71 ^d	10.91	52.98	96.52
	4	68.60 ^{b,c,e}	8.41	52.26	89.53
	5	63.00 ^f	16.25	23.51	99.92
Wind Speed	1	11.33 ^b	3.45	4.75	20.48
	2	11.50 ^{b,c}	4.61	3.11	22.10
	3	11.22 ^{b,c,d}	3.14	5.57	20.15
	4	10.18 ^{b,d,e}	2.90	3.51	17.64
	5	12.72 ^{c,f}	4.70	5.31	27.70
Solar Radiation	1	22.33 ^b	6.73	3.36	31.03
	2	7.89 ^c	4.55	1.58	15.40
	3	21.39 ^{b,d}	8.51	3.88	30.29
	4	24.08 ^{b,e}	5.24	6.35	31.01
	5	12.86 ^f	5.90	1.39	22.33

^aTemperature measured in °C, relative humidity measured as a percent, wind speed measured as kilometers per hour, and solar radiation measured as MJ/m²

^{bcd}^{ef}Differences in superscripts within each column and variable indicate significant differences between groups (P<0.05)

Table 3.2 LSMEANS for effect of environmental variables on mean water intake as a percent of mid-test body weight for cattle fed in different groups, seasons, and under different bunk management protocols. The baseline model with no environmental variables included was augmented with each additional weather variable in the table until all four variables were fit in the model

Group ^a	Season	Baseline	+Solar, MJ/m ²	+Temperature, °C	+Humidity, %	+Wind Speed, km/h
1	Summer	10.72 ^b	10.30 ^b	9.74 ^b	9.85 ^b	9.84 ^b
2	Winter	6.90 ^c	7.69 ^c	8.74 ^c	8.58 ^c	8.60 ^c
3	Summer	8.63 ^d	8.28 ^d	7.84 ^d	8.00 ^d	8.00 ^d
4	Summer	10.80 ^b	10.25 ^b	9.44 ^e	9.54 ^e	9.51 ^e
5	Winter	8.44 ^e	8.85 ^e	9.47 ^e	9.26 ^f	9.28 ^f
SP vs WP		2.34 ^{***}	1.34 ^{***}	-0.09	0.21 [*]	0.18 [*]
Slk vs AL		-0.87 ^{***}	-0.79 ^{***}	-0.68 ^{***}	-0.59 ^{***}	-0.58 ^{***}
SP Slk vs AL		-1.13 ^{***}	-0.96 ^{***}	-0.65 ^{***}	-0.61 ^{***}	-0.59 ^{***}
WP Slk vs AL		-0.77 ^{***}	-0.58 ^{***}	-0.37 ^{***}	-0.34 ^{***}	-0.34 ^{***}

^aSP includes intakes collected during the summer, WP includes intakes collected during the winter, Slk are groups under slick bunk management, AL are groups with *ad libitum* access to feed

^{bcd}^{ef}Differences in superscripts within each column indicate significant differences between groups (P<0.05)

*Significant difference between contrasts for each analysis (0.0001^{***}, 0.01^{**}, and 0.05^{*})

Table 3.3 Univariate regression analysis of each variable used for predicting water consumption (kg/d) of crossbred steers.

Variable	Slope estimate	SE	R ²	P-value
<i>All data</i>				
DMI, kg	2.17	0.029	0.12	<0.0001
MWTS, kg	0.61	0.008	0.13	<0.0001
Average Temperature, °C	0.65	0.006	0.21	<0.0001
Relative Humidity, %	-0.18	0.005	0.03	<0.0001
Solar Radiation, MJ/m ²	0.72	0.008	0.19	<0.0001
Wind Speed, km/h	-0.08	0.018	0.0005	<0.0001
<i>Summer</i>				
DMI, kg	2.74	0.042	0.16	<0.0001
MWTS, kg	0.59	0.011	0.10	<0.0001
Average Temperature, °C	1.74	0.023	0.20	<0.0001
Relative Humidity, %	-0.52	0.010	0.12	<0.0001
Solar Radiation, MJ/m ²	0.67	0.014	0.09	<0.0001
Wind Speed, km/h	-0.04	0.032	0.0001	<0.0001
<i>Winter</i>				
DMI, kg	2.25	0.028	0.29	<0.0001
MWTS, kg	0.53	0.009	0.20	<0.0001
Average Temperature, °C	0.39	0.013	0.06	<0.0001
Relative Humidity, %	-0.52	0.010	0.12	<0.0001
Solar Radiation, MJ/m ²	0.67	0.014	0.09	<0.0001
Wind Speed, km/h	-0.04	0.032	0.0001	0.2120
<i>Ad libitum</i>				
DMI, kg	1.62	0.058	0.05	<0.0001
MWTS, kg	0.66	0.014	0.14	<0.0001
Average Temperature, °C	0.76	0.010	0.26	<0.0001
Relative Humidity, %	-0.06	0.009	0.003	<0.0001
Solar Radiation, MJ/m ²	0.89	0.014	0.22	<0.0001
Wind Speed, km/h	-0.18	0.028	0.003	<0.0001
<i>Slick bunk</i>				
DMI, kg	2.15	0.033	0.15	<0.0001
MWTS, kg	0.48	0.011	0.08	<0.0001
Average Temperature, °C	0.58	0.008	0.19	<0.0001
Relative Humidity, %	-0.18	0.007	0.03	<0.0001
Solar Radiation, MJ/m ²	0.64	0.008	0.19	<0.0001
Wind Speed, km/h	0.02	0.023	0.00	0.5097

^aDMI=Dry matter intake, MWTS=mid metabolic body weight, TAVG=average daily temperature in Celsius, HAVG=average daily relative humidity as a percentage, WSPD=average daily wind speed in miles per hour, SRAD=average daily solar radiation as MJ/m²,

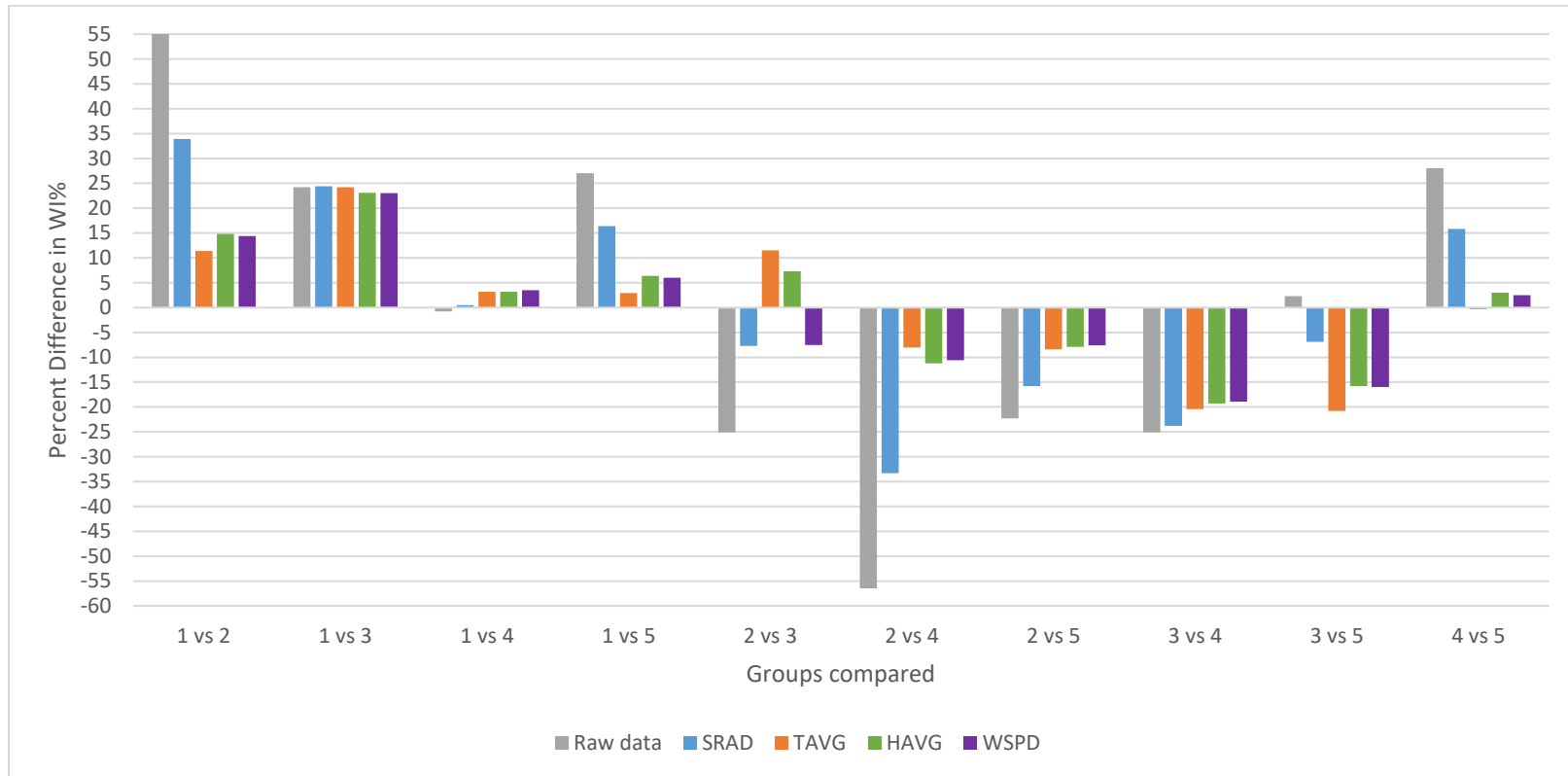
Table 3.4. Partial regression coefficients for daily water intake prediction models including environmental factors, DMI, and metabolic body weights.

Variable ^a	Overall		Summer		Winter		Slk ^b		Ad-lib ^b	
	Estimate	Partial R ²	Estimate	Partial R ²	Estimate	Partial R ²	Estimate	Partial R ²	Estimate	Partial R ²
Intercept	-4.18		-9.74		-4.24		-2.25		0.71	
DMI	2.00	0.124	2.32	0.155	1.76	0.290	1.86	0.15	2.63	0.05
MWTS	0.22	0.057	0.11	0.040	0.22	0.032	0.20	0.01	-0.009	0.11
TAVG	0.57	0.194	1.31	0.137	0.26	0.033	0.45	0.19	0.76	0.23
HAVG	-0.15	0.025	-0.17	0.006	-0.09	0.032	-0.14	0.03	-0.06	0.01
WSPD	-0.16	0.001	-0.27	0.003	-0.06	0.0006	-0.08	0.004	-0.11	0.01
SRAD	0.14	0.003	-0.03	0.000001	0.13	0.003	0.18	0.001	0.23	0.001
R²		0.40		0.34		0.39		0.39		0.41

^aDMI=Dry matter intake, MWTS=mid metabolic body weight, TAVG=average daily temperature in Celsius, HAVG=average daily relative humidity as a percentage, WSPD=average daily wind speed in miles per hour, SRAD=average daily solar radiation as MJ/m²

^bSlk are groups under slick bunk management, ab-lib are groups with *ad libitum* access to feed

Figure 3.1 Percent increase or decrease in water intake as a percent of body weight (WI%) within each group resulting from step-wise addition of weather variables to the model



Raw data= Baseline model which consisted of $WI\%_{ijk} = \text{group}_i + \text{group}(\text{pen})_{i(j)} + e_{ijk}$, SRAD=the addition of average daily solar radiation as MJ/m² to baseline model $WI\%_{ijk} = \text{group}_i + \text{group}(\text{pen})_{i(j)} + \text{SRAD} + e_{ijk}$, TAVG=The addition of average daily temperature in Celsius to the model $WI\%_{ijk} = \text{group}_i + \text{group}(\text{pen})_{i(j)} + \text{SRAD} + \text{TAVG} + e_{ijk}$, HAVG= the addition of average daily relative humidity as a percentage to the model $WI\%_{ijk} = \text{group}_i + \text{group}(\text{pen})_{i(j)} + \text{SRAD} + \text{TAVG} + \text{HAVG} + e_{ijk}$, WSPD=the addition of average daily wind speed in kilometers per hour to the model $WI\%_{ijk} = \text{group}_i + \text{group}(\text{pen})_{i(j)} + \text{SRAD} + \text{TAVG} + \text{HAVG} + \text{WSPD} + e_{ijk}$,

Chapter 4 - Characterization of Water Intake and Water Efficiency in Beef

Cattle

ABSTRACT

Substantial emphasis has recently been placed on feed efficiency in an effort to reduce production costs, but no emphasis has been placed on making cattle more water efficient due to lack of data. In the future, water may not be as readily available due to increases in competition from a growing human population, wildlife, and other agricultural sectors. Thus, the objective of this study was to calculate water efficiency metrics for cattle and evaluate their relationship to growth, feed intake, and feed efficiency. Individual daily feed intake (FI) and water intake (WI) records were collected on 578 crossbred steers over a 70-d test period. Animals with low water intake ate less feed, had lower gains, and were more water efficient (as defined by water to gain ratio, W/G, and residual water intake, RWI). However, the amount of water consumed by animals had minimal phenotypic relationship with feed efficiency (RFI, $R^2=0.1050$ and F/G ratio $R^2=0.0726$). Cattle that had low dry matter intake (DMI) consumed less water, had lower gains, had lower residual feed intake (RFI), and had higher feed to gain ratio (F/G). The level of feed consumed had minimal relationship with water efficiency. Water intake, W/G, RWI and average daily gain (ADG) had moderate heritability estimates of 0.39, 0.39, 0.37 and 0.37, respectively. High heritability estimates were observed for dry matter intake (DMI) and RFI (0.67 and 0.65, respectively). Feed to gain had a low heritability estimate of 0.16. Water intake had a strong positive genetic correlation with W/G (0.99) and RWI (0.88), thus selecting for decreased water intake would also make cattle more water efficient. The genetic correlation between WI and ADG was 0.05; thus, selecting for low WI cattle should have little effect on growth. There is a low to moderate genetic correlation between WI and DMI (0.34). Residual water intake has a positive genetic correlation with W/G ratio (0.89) and F/G ratio

(0.42) and is negatively genetically correlated with RFI (-0.57). Water to gain and F/G had a strong positive genetic correlation (0.68). Residual feed intake has a positive genetic correlation with W/G ratio (0.37) and F/G (0.88). Minimal antagonisms seem to be present between WI, and ADG, although selecting for decreased WI would likely have a small effect on ADG. Thus, care should be taken to ensure that unintended changes do not occur in DMI or ADG and incorporation of WI into a selection index would likely prove to be the most effective method for selection.

Key words: Water Efficiency, Beef Cattle, Water Intake

INTRODUCTION

Freshwater is approximately 2.5% of all water resources (Thornton et al., 2009), and water has often been viewed as an unlimited resource. More recently, water crises have been viewed as one of the top 5 likely global risks reported by the World Economic Forum (2017). It is predicted that in 2025, 64% of the world population will live in a water-deprived basin, compared to 38% in 2009 (Rosegrant et al., 2002). Effects of global warming on water availability could force the livestock sector to establish a new priority in production of animal products that require less water (Nardone et al., 2010).

Few studies have been conducted in beef cattle to examine how efficient cattle are at utilizing water. Currently, there are no heritability estimates in the scientific literature for water intake (WI) in beef cattle or other livestock animals. However, heritability estimates for water intake have been reported in mice. Bachmanov et al. (2002) and Ramirez and Fuller (1976) reported heritability estimates for WI of 0.69 and 0.44, respectively. Phenotypic correlations between WI and body weight (BW) were moderate

and positive (0.49; Bachmanov et al., 2002). Water intake also has a high, positive phenotypic correlation (0.65) with feed intake (FI) in mice (Bachmanov et al., 2002). However, beef cattle are ruminants, and it is unknown how heritability estimates of WI in ruminants will compare to those in monogastric species like mice.

Due to rising concerns about water availability in the future, it is important to understand the relationship between WI and other economically important traits like DMI and average daily gain (ADG). Thus, we must collect WI phenotypes, generate measures of water efficiency, and evaluate their relationships to other economically important production traits to determine if genetic antagonisms exist between these traits. Understanding the genetic relationship between WI and DMI, ADG, and efficiency traits is important. Other traits could be used as indicator traits to help predict WI. The objective of this study was to calculate water efficiency and evaluate the relationships between WI, water efficiency, DMI, feed efficiency, and ADG.

MATERIALS AND METHODS

Study Design

An Insentec system (Hokofarm Group, The Netherlands) at the Willard Sparks feedlot located at Oklahoma State University was utilized to collect daily water intake (WI) and feed intake (FI) on 578 crossbreed steers over a three-year period from May 2014 to March 2017. Steers were fed in 5 feeding groups that consisted of 3 summer groups (group 1, n=117, from May 2014 to August 2014; group 3, n=118, from May 2015 to July 2015, and group 4, n=105, from June 2016 to August 2016) and 2 winter groups (group 2, n=116, from November 2014 to January 2015 and group 5, n=123, from January 2017 to March 2017). This Insentec system consists of 1 water bunk and 6 feed bunks per pen, and bunks

were placed beneath a shade structure. Additional information on the facility structure and layout can be found in Ahlberg et al. (2018). Within each group, steers were blocked by weight (low and high) and randomly assigned to 1 of 4 pens, each containing approximately 30 steers per pen. Feed intake and WI records were filtered to maintain data quality using the procedures outlined in Allwardt et al. (2017). Briefly, start and end weights were filtered for appropriateness and filtered water and feed intakes were screened for length of visit, where very short visits (less than 5 s) and extremely long visits (greater than 3,600 s) were removed. Group 1-3 steers were managed using a slick bunk feed protocol and groups 4 and 5 had access to *ad libitum* feed during the 70-d test period. All animals had access to *ad libitum* water throughout the testing period.

Intakes were collected over a 70-day period following a 21-day acclimation to be in accordance with test length guidelines for DMI and weight gain published by the Beef Improvement Federation (BIF, 2016). During the testing period, body weights were collected every 14 days. All groups were fed the same growing diet throughout the 70-d test period that consisted of 15% cracked corn, 51.36% wet corn sweet bran, 28.44% prairie hay, and 5.20% supplement. Mean gross energy of composited samples was ~4,524.6 cal/g on a dry matter basis. Dry matter for the groups ranged from 70.04% to 74.02%. During the acclimation period cattle were implanted with Compudose (Elanco Animal Health, Greenfield, IN), an implant containing estradiol 17 β (E₂ β).

Two blood samples were collected on weigh days during the feeding period. Blood was drawn from the jugular vein of each animal and collected in 10 mL BD vacutainer tubes containing 1.5 mL of ACD as an anticoagulant. Whole blood was centrifuged to obtain white blood cells and DNA was extracted using a phenol:chloroform:isoamyl

alcohol extraction and ethanol precipitation. DNA samples were sent to GeneSeek (Lincoln, NE) for genotyping on the GeneSeek Genomic Profiler High-Density genotyping array (GGP HD150K). The GGP HD150K provides data on approximately 150,000 single nucleotide polymorphism (SNP) markers. Genotypes were filtered for quality control including for minor allele frequency less than 0.05, and SNP and animal call rate less than 0.90. All animal procedures were approved by the Institutional Animal Care and Use Committee at Oklahoma State University (protocol AG13-18) in accordance with Federation of Animal Science Societies (FASS, 2010) guidelines.

Phenotypic Data

Within each group, animals were assigned to either high, medium or low WI and DMI groups using K-means clustering with $k=3$. This methodology was chosen to more objectively establish intake groups and avoid arbitrarily ranking animals and assigning the top, middle, and bottom third of the data into each category. Cattle were assigned to WI and DMI categories to determine if the level of feed and water cattle consume has an effect on WI, DMI, ADG, and feed and water efficiency.

Average daily gain (ADG) for each individual was calculated over the 70-d period by regressing BW over time to account for differences in rumen fill. Mid-test weight was obtained by taking the ADG for each individual from the regression analysis, multiplying by 35 days, and adding it to the intercept for each individual. Mid-metabolic weights (MMWT) were obtained by taking the mid-test weight to the 0.75 power.

Efficiency measures

Water efficiency measures, including water to gain ratio (W/G) and residual water intake (RWI) were calculated for each group. Water to gain ratio was calculated as follows:

$$W/G = \frac{AWI}{ADG}$$

where WI is the average daily water intake (AWI) and ADG is the average daily gain over the 70-day test.

For each group, residual water intake (RWI) was calculated as follows:

$$RWI = AWI - eWI$$

where WI is the AWI and eWI is the expected WI calculated as follows:

$$eWI = b_0 + b_1DMI + b_2MMWT + e$$

where b_0 is the intercept, b_1 is the regression coefficient for average daily DMI and b_2 is the regression coefficient for (MMWT). Regression coefficients (b_i) were estimated within each group.

Feed efficiency measures, including feed to gain ratio (F/G) and residual feed intake (RFI) were calculated for each group. Feed to gain ratio (Koch et al., 1963) was calculated as follows:

$$F/G = \frac{DMI}{ADG}$$

Where DMI is the average daily dry matter intake and ADG for the 70-day test.

For each group, RFI (Koch et al., 1963) was calculated as follows:

$$RFI = DMI - eDMI$$

where DMI is the average daily dry matter intake and eDMI is the expected dry matter intake calculated as follows:

$$eDMI = b_0 + b_1ADG + b_2MMWT + e$$

where b_0 is the intercept, b_1 is the regression coefficient for ADG, and b_2 is the regression coefficient for (MMWT). Regression coefficients (b_i) were estimated for each group. Summary statistics for all traits are presented in Table 4.1.

Breed composition

Although breed composition of steers was unknown, cattle were visually evaluated before entering the trial period in an effort to exclude individuals that had *Bos indicus* ancestry because animals with *Bos indicus* influenced cattle are known to consume less water, especially in hot temperatures (Winchester and Morris, 1956; Brew et al., 2011). Breed composition was estimated utilizing each individual animal's genotypes within a regression framework developed by Chiang et al. (2010). Genotypes were coded as the number of copies of allele B (using the Illumina A/B genotype calls) divided by 2 (Kuehn et al., 2011) to scale the number of copies of allele B to be between 0 and 1, which places them on the same scale as the breed allele frequency estimates. The following model was used to predict breed composition:

$$y = Xb + e$$

where X is a 36,403 by 16 matrix of frequencies for allele B (36,403 allele frequencies for 16 breeds) and b is a vector of regression coefficients that represents the percentage of each breed for each individual animal in y, and e is a vector of random residuals. This methodology requires robust estimates of allele frequencies in a large number of breeds, so breed specific allele frequencies used were those calculated in Kuehn et al. (2011). Estimates for the percent of each of the 16 breeds were then summed for each individual animal. If the value was less than 1, the difference from 1 was assigned as other to account for the fact that there are more than 16 breeds represented in the United States that were

not represented in the available allele frequencies. Zeros were assigned for any small negative regression coefficients. Estimates that summed to greater than 1 were then scaled as follows:

$$\frac{1}{\sum \text{nonzero breed regression coefficients}} \times \text{each breed coefficient}$$

Figure 4.1 shows the mean percent of each breed observed in each group and across all groups. Because percentages for most breeds were low, estimates were grouped into biological types (British, Continental, *Bos indicus*, and dairy) and the mean percentages of each biological type for each group are presented in Fig 4.2. Despite visual selection against animals that have *Bos indicus* ancestry, a low level of *Bos indicus* ancestry was present in 3 of the 5 groups.

Statistical analysis

Summary statistics of phenotypic data for each group and level within group were calculated using SAS 9.4 System for Windows (SAS Institute Inc., Cary, NC, USA). Differences between low, medium, and high WI and DMI levels were analyzed for WI, DMI, W/G, F/G, RWI, and RFI using SAS 9.4 for each group and with data combined across groups. The following model was used for analyses of WI, DMI, ADG, W/G, F/G, RWI, and RFI measures for each individual group:

$$\text{Trait}_{ij} = \text{Intake level}_i + \text{SWT}_i + B_i + C_i + I_i + D_i + e_{ij}$$

where,

Trait_{ij} is the trait of interest (WI, DMI, ADG, RWI, RFI, W/G and F/G) for the ith intake level (WI or DMI) and the jth individual,

Intake_level_i is the ith intake level (low, medium, or high for WI or DMI),

SWT is the starting weight for the ith individual fitted as a covariate,

B is the percent of British breed composition for the i^{th} individual fitted as a covariate,
 C is the percent of continental breed composition for the i^{th} individual fitted as a covariate,
 I is the percent *Bos indicus* for the i^{th} individual fitted as a covariate,
 D is the percent dairy breed composition for the i^{th} individual fitted as a covariate, and
 e is the random residual.

For analyses of data combined across all groups, a fixed effect was added to the model to account for differences in feed management. Phenotypic correlations between all traits were estimated using SAS 9.4 System for Windows (SAS Institute Inc., Cary, NC, USA).

Genetic analyses were performed using single-step genomic BLUP (ssGBLUP; Aguilar et al., 2010; Christensen and Lund, 2010) and genetic (co)variance parameters were estimated using an average information restricted maximum likelihood (AIREML) algorithm incorporated into the BLUPF90 software package (Misztal et al., 2014). In ssGBLUP, the numerator relationship matrix that traditionally reflects average relatedness as defined by pedigree (A^{-1}), is replaced with the H^{-1} matrix, which is defined as follows:

$$H^{-1} = A^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & G^{-1} - A_{22}^{-1} \end{bmatrix}$$

where A^{-1} is the inverse of the numerator relationship matrix for all animals, G^{-1} is the inverse of the genomic relationship matrix for genotyped animals, and A_{22}^{-1} is the inverse of the numerator relationship matrix for genotyped animals (Aguilar et al., 2011). In this study, we did not have any animals with pedigree, only genomic relationships established by genotypes, so in this study H^{-1} is solely a function of G^{-1} . The genomic relationship matrix was calculated as $G=ZZ'/k$ based on the method provided by VanRaden (2008), where Z is the subtraction of P (allele frequencies expressed as difference from 0.5) from

M (matrix of marker alleles for each individual), and k is $2 \cdot \sum(p_i \cdot (1-p_i))$. Traits were fitted using the following bivariate linear animal models:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 b_1 \\ X_2 b_2 \end{bmatrix} + \begin{bmatrix} Z_1 u_1 \\ Z_2 u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_i is a vector of phenotypes for trait 1 or 2 (WI, DMI, ADG, RWI, W/G, RFI, and F/G), b_i is a vector of fixed effects for trait 1 and 2 (group and feed management) and covariates of start weight, percent British, percent continental, percent *Bos indicus*, and percent dairy were also fit in the model for each trait., X_i is an incidence matrix for each element in b_i for trait 1 and 2, u_i is a vector of additive direct genetic effects for trait 1 and 2, Z_i is an incidence matrix for u_i for trait 1 and 2, and e_i is a vector of random residuals for trait 1 and 2. Heritabilities and standard deviations were averaged for each trait across all the bivariate runs for the trait of interest. Residual (co)variance structure used was:

$$\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} I\sigma_{e1}^2 & I\sigma_{e1,e2} \\ I\sigma_{e2,e1} & I\sigma_{e2}^2 \end{bmatrix}$$

where the matrix I represents the identity matrix with dimension equal to the number of records for each trait. The genetic (co)variance structure was:

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} G\sigma_{u1}^2 & G\sigma_{u1,u2} \\ G\sigma_{u2,u1} & G\sigma_{u2}^2 \end{bmatrix}$$

where the G matrix is the genomic relationship matrix. As an alternative to standard errors, standard deviations were calculated for functions of (co)variances, thus calculations of phenotypic variance, heritability and genetic correlations were derived by repeated sampling of parameter estimates from the asymptotic multivariate normal distribution, based on methodology presented by Meyer and Houle (2013).

RESULTS AND DISCUSSION

Water Intake Levels

Differences in WI for low, medium, and high WI intake groups are presented in Table 4.2. There is a significant difference in WI between low, medium, and high levels within all groups and across groups. For all groups except for group 1, there is a smaller increase from low to medium WI levels (10.36 kg, 5.44 kg, 7.24 kg, 10.50 kg, and 5.45 kg for groups 1, 2, 3, 4, and 5, respectively) than from medium and high levels (9.41 kg, 12.71 kg, 16.41 kg, 30.05 kg, and 12.42 kg for groups 1, 2, 3, 4, and 5, respectively). Pairwise comparisons between low, medium and high WI are significantly different when all groups are combined. Group 3 was the only group where breed composition covariates had a significant impact on WI (British; $P=0.0135$, Continental; $P=0.0126$, *Bos indicus*; $P=0.334$, and Dairy; $P=0.0081$). We did not see a significant reduction in WI for *Bos indicus* breeds, likely because of the very small sample size present in this study.

There is a significant difference in DMI between low, medium, and high WI levels within all groups and when all data is combined, except between group 3 medium and high ($P = 0.2096$). As WI increases, cattle consume more feed. Larger increases in DMI are observed as cattle go from medium to high WI (1.93 kg, 2.11 kg, 1.52 kg, 0.90 kg, and 2.22 kg for groups 1, 2, 3, 4, and 5, respectively) as compared to moving from low to medium intake (0.85 kg, 1.13 kg, 1.10 kg, 0.45 kg, and 0.96 kg for groups 1, 2, 3, 4, and 5, respectively). Cattle that had low WI also consumed less feed than cattle with medium and high WI and cattle with medium WI consumed less feed than cattle with high WI when all groups are combined ($P < 0.0001$). For most mammals, water is consumed during or shortly

before or after feeding events, and in rats, food-related drinking accounts for approximately 70% of their daily WI (Kraly, 1983).

Animals that drank more water had significantly higher ADG within all groups and across all groups except for group 4 (Table 4.2; $P > 0.05$). Low WI cattle have decreased gains compared to high WI cattle, and this could affect days on feed (DOF), which could increase feed costs and narrow profit margins. Average daily gain and DMI have a moderate, positive phenotypic correlation (Berry and Crowley, 2013). As illustrated in Table 4.3, cattle with higher WI have higher DMI; thus, we would expect cattle with higher WI to have higher gains as a result of increased DMI. Langemeier et al. (1992) reported that improvements in ADG will reduce cost of gain, thus increasing profitability. Mark et al. (2000) found that ADG is more important for lighter weight placements because they are on feed for a longer period of time.

Residual water intake is significantly different ($P < 0.0003$) between WI levels within each group and across all groups. Low WI animals have more favorable RWI than animals that have medium or high WI. Low WI animals consume less water and utilize water more efficiently relative to their DMI and body size. Water quantity and quality is currently not limiting in beef production for many areas of the country. However, for producers that run cow-calf operations in dry climates or in areas where water quality is poor, water quantity and quality can be limiting. For many producers, dugouts and ponds only have a limited supply of water and drought can greatly reduce or eliminate these supplies entirely, rendering that pasture unfit for grazing. Some producers have developed pipelines to pump water from their well to tanks in pastures where cattle are grazing to help alleviate these issues. However, during drought, wells can run dry and producers may not

be able to provide water to their animals. One option is to haul water, which requires a good estimate of the herd's water requirements. In these situations, it would be beneficial to have cattle that have both low water consumption and are efficient at utilizing available water resources.

Residual feed intake has fewer differences between WI levels. However, low WI animals are the most feed efficient (lower RFI values) except for group 1 and 2, which were numerically more efficient, but not statistically different. Cattle with low and medium ($P=0.2619$) WI levels in group 2 had similar RFI values which were lower than high WI cattle. RFI was only different between low and high WI levels ($P = 0.0039$) for group 1 animals. Animals that are feed efficient and have low WI or high water efficiency are desirable. The relationship between feed efficiency and water consumption should also be assessed using genetic correlations to assess whether there are any genetic antagonisms present.

No differences in W/G were detected between low, medium, and high WI levels for cattle fed during the winter time (group 2 and 5). For the summer groups, significant differences in W/G between low and high WI levels were noted ($P = 0.0096$, $P = 0.0141$, and $P < 0.0001$ for groups 1, 3, and 4, respectively), where cattle that have low WI utilize less water per pound of gain. This is similar to the results for RWI, where low WI cattle were more efficient than high WI cattle. For group 4 and across all groups, animals with high WI levels required more water to gain one pound than animals with medium WI levels ($P = 0.0012$ and $P < 0.0001$, respectively).

Feed to gain for cattle from groups 3, 4, and 5 was not related to the amount of water that the animals consumed ($P > 0.05$). Group 1 and 2 cattle did exhibit differences in

F/G with low WI animals having poorer F/G ratios ($P = 0.0464$ and $P = 0.0126$, respectively) than high WI cattle. Group 2 cattle with low WI also have poorer F/G ratio ($P = 0.0266$) than medium WI cattle. In this study, we noted conflicting relationships between feed efficiency metrics and WI levels depending on whether efficiency was defined as F/G or RFI. Elzo et al. (2009) reported that RFI decreased (cattle became more feed efficient) as the level of Brahman increased, but gain to feed ratio decreased (less efficient). This relationship is consistent with our results, even though the overall level of *Bos indicus* influence was low.

Dry matter intake levels

Results from analyses of DMI levels can be found in Table 4.3. As illustrated in Table 4.3, cattle with low DMI consume less water than cattle with medium or high DMI within all groups. The difference in WI between low and medium DMI levels tended to be smaller (5.94 kg, 4.15 kg, 5.04 kg, 8.71 kg, and 4.36 kg for groups 1, 2, 3, 4, and 5, respectively) than the difference in WI between medium and high DMI levels (7.31 kg, 5.82 kg, 3.74 kg, 9.40 kg, and 6.37 kg for groups 1, 2, 3, 4, and 5, respectively). However, for group 3 there was a smaller increase in WI going from medium to high DMI levels than from low to medium DMI levels. Interestingly, when data was combined across all groups, low DMI animals have reduced WI compared to both medium and high DMI groups ($P < 0.0001$), but the medium and high DMI levels are no longer significantly different ($P < 0.0001$). Winchester and Morris (1956) showed that water requirements for cattle can be reduced by reducing the feed allowance. This concept could be used as a management tool during drought, whereby cattle could be limit fed to reduce the water demand. The type of diet also effects the amount of water consumed by cattle. Rations that contain higher salt

content can increase water consumption by 40 to 60% (Winchester and Morris, 1956). Cattle fed diets with higher levels of protein can have an increase in water consumption of 26% compared to cattle fed low protein diets (Ritzman and Benedict, 1924). In this study, cattle were fed the same ration across all groups, so differences in diet were not a factor in this analysis.

Unsurprisingly, differences were observed in DMI between high, medium, and low DMI levels ($P < 0.0001$) as shown in Table 4.3. The difference in DMI between low and medium DMI levels tended to be larger (1.67 kg, 1.85 kg, 1.96 kg, 1.16 kg, and 1.22 kg for groups 1, 2, 3, 4, and 5, respectively) than the difference in DMI between medium and high DMI levels (1.60 kg, 1.67 kg, 1.72 kg, 0.99 kg, and 1.43 kg for groups 1, 2, 3, 4, and 5, respectively), except for group 5. With feed cost being the largest variable cost in beef production (Arthur et al., 2001), reducing feed intake would be advantageous, provided productivity was not reduced.

Similar to WI, DMI level does have an effect on ADG, except for group 4 between medium and high DMI levels ($P = 0.3029$). Animals that had lower DMI gained less than animals that had medium or high DMI, likely because DMI is the main driver of ADG (Koch et al., 1963). Cattle with reduced daily FI have reduced daily feed cost but could spend more days on feed to reach their desired end point, resulting in increased total feed cost over the feeding period. While this is true for steers, reducing feed intake in cows could potentially reduce feed cost for cow calf producers, because at least 60 to 65% of feed cost is associated with maintenance energy (Arthur et al., 2001).

The only significant difference in RWI between the DMI levels was observed in group 5 between medium and high groups ($P=0.0173$). The amount of feed cattle consumed

did not appear to be related to RWI. However, RFI is different between DMI levels, with low DMI cattle being more feed efficient than high DMI cattle ($P < 0.0001$). Herd et al. (2004) reported that one source of variation in RFI is attributed to variation in feed intake. Variation in maintenance requirements for ruminants is associated with variation in FI (Herd et al., 2004). The amount of energy expended to digest feed increases as FI increases, partly due to changes in digestive organ size (Herd et al., 2004). Heat increment of feeding (HIF) is the increase per unit of weight in energy expended by the tissues during digestion (Herd et al., 2004). Differences in RFI are associated with variation in intake, thus animals that eat less but have equivalent performance could be expected to have less energy expended as HIF (Herd et al., 2004).

There were no differences in W/G between the DMI levels ($P > 0.05$) except for group 2 and across all groups, indicating that level of feed intake tends to not be associated with W/G ratio. Differences in W/G ratio were observed between low and medium ($P = 0.011$ and $P = 0.0188$ for group 2 and all data combined, respectively) and low and high ($P = 0.0009$ and $P = 0.0157$, for group 2 and all data combined, respectively) DMI levels, with low DMI cattle having the highest W/G ratio and high DMI cattle having the lowest W/G ratio. Low DMI cattle in group 2 and all cattle combined had poorer W/G ratio. Gain is a component of W/G ratio, and even though gain has a curvilinear relationship with DMI (Magee, 1962), animals with low DMI would be expected to have lower gains and potentially increased W/G ratio. However, cattle with lower DMI also tend to have lower WI, thus this result may be affected by an interaction between DMI, WI, and ADG that appears to be most relevant for the groups managed using slick bunk feed calling. The first 3 groups had a slick bunk feed protocol where some of the animals could have had slight

restrictions in DMI which could have affected the gain potential of these animals. The other two groups had access to *ad libitum* feed, thus feed availability should not have been a limiting factor in ADG for these animals. Many cattle in a feed lot are managed with a slick bunk protocol to improve performance by minimizing digestive problems from overconsumption of feed (Schwatzkopf-Genswein et al., 2003), and these results suggest that bunk management may have a small (largely numeric) effect on the W/G ratio between low, medium, and high DMI animals.

Feed to gain ratio for cattle from groups 1, 3, and 5 was not affected by the amount of feed that the animals consumed. No differences were observed between low, medium, and high DMI levels ($P > 0.05$). Group 2 cattle did have differences in F/G, with medium DMI animals being less feed efficient than the high DMI group ($P = 0.0108$). Low DMI cattle have higher F/G than medium or high DMI cattle within group 4 and when all groups are combined.

Phenotypic correlations

Pearson and Spearman correlations between all traits are presented in Table 4.4. Water intake has a positive, moderate Pearson correlation with DMI (0.366), which is higher than the Spearman correlation between WI and DMI (0.389). The phenotypic correlation between FI and WI in mice (0.65; Bachmanov et al., 2002) is higher than in the current study. Cattle and mice have different physiology due to the fact that cattle are ruminants and mice are monogastrics. There is also a drastic difference in body size, which leads to differences in maintenance requirements (Demment and Van Soest 1985). The large positive correlation between FI and WI in mice may be due to their mutual dependency on body size, but it might involve another mechanism that is linked to FI and

WI (Bachmanov et al., 2002). Regardless of the cause, the direction of the relationship is the same in beef cattle, although smaller in magnitude. Figure 4.3 panel A shows the linear relationship between WI and DMI ($R^2 = 0.141$). For every 1 kg increase in DMI, WI increases by an average of 2.705 kg. However, much of the variation in WI is independent of DMI (Fig. 4.3, Panel A).

Water intake has a low, positive Pearson correlation with RFI (0.258) and F/G ratio (0.276), although the Spearman correlations are higher for both RFI (0.266) and F/G ratio (0.383). Higher Spearman correlations indicate that there is less reranking among animals for feed efficiency traits when there are changes in WI. Animals with low WI tend to also have low RFI (Fig. 4.3, panel B; $R^2 = 0.102$), but substantial variation also exists. Figure 4.3, panel C illustrates the weak linear relationship between WI and F/G ratio ($R^2 = 0.073$). The most efficient animals (high F/G ratio) have a wide range of WI. While the linear relationship between WI and DMI is low to moderate, relationships between WI and RFI and F/G are much weaker.

Water intake has a strong, positive Pearson correlation with water efficiency measures (0.602, RWI and 0.698, W/G). The Spearman correlation between WI and RWI is lower than the corresponding Pearson correlation (0.451 vs 0.602); however, the Spearman correlation between WI and W/G is slightly higher (0.711 vs 0.698), suggesting that there is slightly more reranking of animals for RWI than W/G ratio at similar WI levels. Cattle with higher WI are less water efficient, as illustrated by the moderate linear relationships depicted in Fig 4.3, panels D and E. No previous phenotypic correlation estimates between WI and water efficiency measures have been reported, but these traits

exhibit the same strong phenotypic correlations that are found between DMI and feed efficiency measures (Archer et al., 2002; Bouquet et al., 2010).

Low, negative Pearson and Spearman correlations exist between WI and ADG (-0.094 and -0.109, respectively). As depicted in Fig. 4.3, panel F, the amount of water consumed by animals has little relationship with ADG. The relationship between WI and ADG is substantially different from the relationship between DMI and ADG, which have a strong, positive correlation (Arthur et al., 2001; Nkrumah et al., 2004).

Dry matter intake has strong, positive Pearson and Spearman correlations with ADG (0.530 and 0.501, respectively) and RFI (0.595 and 0.583, respectively). Cattle that have higher DMI will have greater ADG, but will also be less efficient at utilizing feed, as illustrated by higher RFI values. Similar phenotypic correlations between DMI and ADG have previously been reported by Arthur et al. (2001), Basarab et al. (2003), and Nkrumah et al. (2004). Nkrumah et al. (2004) and Arthur et al. (2001) reported a higher phenotypic correlation of 0.770 and 0.720 between DMI and RFI, thus selecting animals for reduced feed intake would make them more feed efficient (lower RFI) animals.

Phenotypic correlations between DMI and F/G ratio were not different from zero (Pearson $P = 0.710$ and Spearman $P=0.161$). Positive, moderate phenotypic correlations between DMI and F/G ratio have been reported by Koots et al. (1994), Liu et al. (2000), Arthur et al. (2001), and Nkrumah et al. (2004). Cattle that consume less will also generally require less feed per pound of gain. Dry matter intake had a weak, negative Pearson (-0.088) and Spearman (-0.084) correlation with W/G ratio but was uncorrelated to RWI (Pearson $P = 0.999$ and Spearman $P = 0.520$). No correlations between DMI and water efficiency measures currently exist within the scientific literature.

High, negative Pearson and Spearman correlations were observed between ADG and W/G (-0.694 and -0.734, respectively) as well as between ADG and F/G (-0.779 and -0.802, respectively). No previous estimates of phenotypic correlations between ADG and W/G have been reported in the literature. However, Berry and Crowley (2013) reviewed 39 scientific papers and reported that phenotypic correlations between ADG and F/G in the scientific literature ranged from -0.910 and 0.650, with the average being -0.520. Strong correlations exist between ratio traits and their component traits (Berry and Crowley, 2013). Average daily gain is not phenotypically correlated with RFI (Pearson, $P = 0.988$ and Spearman, $P = 0.958$). Pearson correlations between ADG and RWI were not different from zero ($P = 0.223$), but did exhibit a weak, positive Spearman correlation (0.127, $P = 0.002$). Residual feed intake and RWI are phenotypically independent of their regressors when calculated using least squares regression (Berry and Crowley, 2013). However, RFI and RWI are not necessarily genetically independent of their regressors (Kennedy et al., 1993 and Berry and Crowley, 2013). Average daily gain would not be expected to be phenotypically correlated with RFI but could be correlated with RWI, as it was not included in its calculation. Arthur et al. (2001) and Mao et al. (2013) reported phenotypic correlations that were not different from zero for RFI and ADG, which is consistent with the results from this study.

Water efficiency measures have weak linear relationships with each other and to feed efficiency traits, with the exception of F/G and W/G, as illustrated in Fig. 4.4. A strong linear relationship between W/G and F/G could be attributed to gain driving this relationship. Water efficiency measures are positively correlated with each other (Pearson 0.383 and Spearman 0.221). Cattle that are considered water efficient as defined by low

RWI are also considered water efficient as classified by W/G. Feed efficiency traits (F/G and RFI) have low, positive Pearson (0.295) and Spearman (0.383) correlations, and their relationship is illustrated in Fig. 4.4, panel B. Phenotypic correlations between RFI and F/G were reviewed by Berry and Crowley (2013) and ranged from -0.620 to 0.760 (average of 0.390). Similar to the water efficiency measures, cattle that have low RFI also have a low F/G ratio. The estimates from the current study fall within this wide range. Residual water intake and RFI are uncorrelated (Pearson $P = 0.438$ and Spearman $P = 0.684$), as illustrated in Fig. 4.4, panel C. Similar to the relationship between RWI and RFI, RWI and F/G are uncorrelated as defined by the Pearson correlation ($P = 0.341$), but the Spearman correlation is significantly different from zero (-0.102 ; $P = 0.014$).

Genetic parameters

Variance components and heritability estimates for each trait are presented in Table 4.5. Water intake, RWI, and W/G had moderate heritability estimates of 0.39, 0.37, and 0.39, respectively. There are currently no other estimates of heritability for WI, RWI, or W/G in livestock. However, heritabilities for WI have been reported in mice. Bachmanov et al. (2002) utilized 28 different strands of mice, collecting individual WI over a 4-day period, to generate a heritability estimate of 0.69. Ramirez and Fuller (1976) utilized heterogeneous mice, fully inbred mice and partially inbred mice that had individual water intakes collected over 38 days. Heritability was estimated to be 0.44 (Ramirez and Fuller, 1976). Both heritability estimates in mice are higher than our heritability estimate for WI in beef cattle. Beef cattle are much larger in size and are ruminants, whereas mice are monogastric. Differences in how these species metabolize water could be why higher heritabilities were observed in mice. Ahlberg et al. (2018) established that WI in cattle

requires 35 to 42 d of data for accurate measurement of WI phenotypes. Although ruminants are undoubtedly quite different from monogastrics, Bachmanov et al. (2002) only collected data over 4-days, and the short test duration could have affected the heritability estimate. Differences could also be attributed to using inbred line in mice. There could also be differences due to effects of seasonal variation in weather, since mice are housed in a controlled environment and cattle tend to be exposed to different weather effects. The fact that WI is a moderately heritable trait means that the amount of water consumed by beef cattle can be changed through selection. Selecting for water efficiency while accounting for important output traits would be ideal. However, using ratio traits (such as RWI or W/G) for genetic selection presents challenges when trying to predict the changes in component traits for future generations (Arthur et al., 2001). Using the component traits of RFI or RWI to form a selection index to select for improved feed or water efficiency would be a more useful option.

Average daily gain has a moderate heritability, which indicates that ADG would respond well to selection if cattle are selected for increase gain. According to a review by Berry and Crowley (2013), ADG heritability estimates ranges from 0.06 to 0.65. Brown et al. (1988), Archer et al. (1997), Herd and Bishop (2000), Schenkel et al. (2004), and Akanno et al. (2018), reported similar heritability estimates for ADG (0.36, 0.41, 0.38, 0.35, 0.37 respectively).

Dry matter intake and RFI had high heritability estimates of 0.67 and 0.65, respectively. Berry and Crowley (2013) reported heritability estimates for DMI that range from 0.06 to 0.70 from 38 different studies. The heritability estimates for RFI in this study were on the upper end of this range. Koch et al. (1963) reported similar heritability

estimates for DMI using Angus, Hereford, and Shorthorn cattle. Archer et al. (1997) utilized a population of Angus, Hereford, Polled Hereford, and Shorthorn animals and reported a similar heritability to the current study (0.62). Breed composition in Archer et al. (1997) was similar to the current study, as British breeds (Angus, Hereford, Shorthorn, and Red Angus) comprised over 60% of the breed germplasm in the current study (and never less than 50% of each group; Fig. 2). Feed to gain had lower heritability than the other feed intake and efficiency traits (0.16). However, it is within the range of heritability estimates (0.07 to 0.46) reported by Berry and Crowley (2013). Similar heritability estimates were reported by Brown et al. (1988), Korver et al. (1991), Gengler et al. (1995), Herd and Bishop (2000), Hoque et al. (2006), Okanishi et al. (2008), and Elzo et al. (2010). Because breeds were grouped into biological types rather than specific breeds, heritability estimates could be slightly inflated due to incomplete partitioning of some individual breed effects.

Genetic correlations for each trait are reported in Table 4.6. Water intake has positive genetic correlations with all traits, although of different magnitudes. Average daily gain has a very low genetic correlation with WI (0.05 ± 0.62), and with the large standard error, WI and ADG are not different from a correlation of zero. Dry matter intake and RFI have a moderate genetic correlation with WI (0.340 ± 0.290 and 0.330 ± 0.260 , respectively), while RWI, W/G, and F/G have a high genetic correlation with WI (0.880 ± 0.350 , 0.990 ± 0.100 , and 0.900 ± 1.630 , respectively). Although the standard deviations are high in some instances, the current study indicates that there will be minimal effect on ADG if selection emphasis is placed on WI. However, genetic correlations are difficult to estimate with high precision using approximately 500 animals. Cow/calf producers could

select for lower WI in the cowherd without hindering ADG in calves that would be sold. Whether producers are selling calves at weaning or retaining ownership through the finishing phase, calves with high growth potential are desirable in terminal marketplaces. Cattle sold at weaning or after backgrounding are priced on weight, thus heavier calves often generate more revenue.

Selecting animals for lower WI could also result in animals that are more feed efficient due to the positive, high genetic correlations with RFI and F/G (0.880 and 0.990, respectively). Although WI and F/G have a high genetic correlation, this estimate also has a large standard deviation which would be considered not different from zero. Direct selection for decreased WI should also improve feed efficiency. The high genetic correlation between WI and W/G and F/G could be contributed to the fact that water make up a high percentage of body mass. Due to the strong, positive correlation with WI and water efficiency measures, selection to improve water efficiency would also decrease WI. During times when water is limited, having cattle that are efficient at utilizing water would be beneficial. If a priority is placed on WI or W/G along with relevant output traits related to productivity, producers could select cattle that maintain productivity when water resources are limited.

Dry matter intake had weak, negative genetic correlations between RWI (-0.100) and W/G (-0.130) and a weak, positive correlation with F/G (0.080). The current study has a similar genetic correlation between DMI and F/G as reported by Mao et al. (-0.020; 2013). Lower estimates of heritability were reported by Arthur et al. (2001), Renard and Krauss (2002), and Herring and Bertrand (2002; 0.310, 0.570, and 0.550, respectively). Selecting for decreased F/G ratio may reduce the amount of feed required for growth but could also

lead to increases in mature BW, which raises the cost of maintenance in breeding programs (Arthur et al., 2001). Similar to F/G, selecting to decrease W/G could decrease the amount of water needed for growth but could have the same effect on mature BW and maintenance cost as selecting for reduced F/G ratio. Dry matter intake has a strong, positive correlation with ADG (0.680) and RFI (0.680). Previous studies (Arthur et al., 2001 and Mujibi et al., 2010) reported similar genetic correlations between DMI and RFI (0.690, and 0.680, respectively). A review by Berry and Crowley (2013) reported genetic correlations ranging from -0.340 to 0.850 with the average correlation being 0.720, which is similar to DMI and RFI in the current study. Incorporating measures of growth and metabolic body size help capture the variation among animals in energy utilization for growth and maintenance (Nkrumah et al., 2004). Thus, selecting animals for improved RFI (lower RFI) could result in having both animals that are efficient in the feedlot and in the breeding herd (Nkrumah et al., 2004). Strong, positive genetic correlations between ADG and DMI were also reported by Liu et al., (2000), Arthur et al., (2001), and Mujibi et al., (2010; 0.450, 0.540, and 0.530, respectively).

Average daily gain had a negative genetic correlation between feed (RFI, -0.031 and F/G, -0.630) and water (RWI, -0.170 and W/G, -0.570) efficiency traits. The strong genetic correlations between ADG and F/G have raised concerns about its value to improve efficiency in the overall production system as it can lead to direct increases in mature BW and maintenance costs (Barlow, 1984; Archer et al., 1999). The weak negative genetic correlation between ADG and RFI was similar to Herd and Bishop (2000) and Arthur et al. (2001). However, Jensen et al. (1992) reported a genetic correlation between ADG and RFI of 0.320. Due to the nature of RFI calculation, the phenotypic correlation between

ADG and RFI is expected to be zero. This does not mean that ADG and RFI are genetically independent of their regressors (Kennedy et al., 1993 and Berry and Crowley, 2013). Due to the extremely low correlation between RFI and ADG in this study, selecting to improve RFI should not inhibit production of efficient steers in the feedlot or mature cows that efficiently utilize feed for maintenance (Arthur et al., 2001). Because minimal correlations exist between RFI and gain, multi-trait selection can be practiced without unfavorable correlated responses (Moore et al., 2009). A selection index could also be developed including gain and DMI to overcome the unfavorable correlation between the two traits.

Selecting to improve water efficiency by selecting cattle that have lower RWI would result in a slight decrease in growth. One potential solution would be to include ADG in the calculation of RWI, which should make them phenotypically independent, and possibly reduce the genetic correlation between the traits. Both W/G and RFI (0.370) and F/G and RWI (0.420) have moderate, positive genetic correlations. Cattle selected for improved F/G ratio would result in cattle that are more water efficient (reduced RWI). The same relationship holds true when cattle are selected for decreased RFI. Water efficiency measures are highly genetically correlated (RWI and W/G; 0.890) and feed efficiency measures are also highly genetically correlated (RFI and F/G; 0.880). Nkrumah et al., (2004) observed a similar relationship between RFI and F/G ratio, noting that cattle with high RFI also have high F/G ratio. Residual feed intake can contain a large amount of statistical error as well as true differences in feed efficiency (Berry and Crowley, 2013). This same problem can be true for F/G, which can lead to the large variation reported in the genetic relationship between RFI and F/G (Berry and Crowley, 2013). As RWI increases, W/G also increases. Cattle that are selected for improved water efficiency using

RWI will also have improved (lower) W/G ratios. Interestingly, RWI and RFI exhibit a strong, negative genetic correlation (-0.570). Feed costs comprise a high percentage of input cost in cattle production. (Herd et al. 2004), resulting the desire to select animals that are more feed efficient. Due to the antagonistic relationship between RFI and RWI, selecting for both RWI and RFI would be somewhat challenging. Even though water does not tend to be an expensive resource in and of itself, it is not always abundant and can have economic impact through reduction in stocking density or culling of cattle. One possible avenue to solve this dilemma is to include WI, DMI, and ADG in a selection index with other economically relevant traits so that selection pressure is applied to all traits simultaneously and aggregate merit becomes the selection criteria.

CONCLUSION

Water is an essential and economically important nutrient. As water availability changes in regions experiencing drought or the effects of climate change, cattle may need to be not only feed efficient but also water efficient. Water intake, RWI, W/G and ADG are moderately heritable, DMI and RFI are highly heritable, and F/G is lowly heritable. Water intake has a weak genetic correlation with ADG, moderate genetic correlations with DMI and RFI, and strong genetic correlations with RWI, W/G, and F/G. Water efficiency measures are highly genetically correlated and feed efficiency measures are also highly genetically correlated. Favorable genetic correlations exist between RWI and WI, W/G and F/G, but antagonisms exist between RWI and RFI, and DMI. Genetic antagonisms, particularly between feed and water efficiency, can be solved by including WI in a selection index with DMI, ADG, and other economically important traits. Further work should be

done to elucidate the genetic relationships between WI and other economically important traits for both terminal and maternal systems.

References

- Ahlberg, C. M., K. Allwardt, A. Broocks, K. Bruno, A. Taylor, L. McPhillips, C. R. Krehbiel, M. Calvo-Lorenzo, C. J. Richards, S.E. Place, U. DeSilva, D. L. VanOverbeke, R. G. Mateescu, L. A. Kuehn, R. Weaber, J. Bormann, and M. M. Rolf. 2018. Test duration for water intake, average daily gain, and dry matter intake in beef cattle. *J. Anim. Sci.* under review
- Akanno, E. C., M. K. Abo-Ismael, L. Chen, J. J. Crowley, Z. Wang, C. Li, J. A. Basarab, M. D. MacNeil, and G. S. Plastow. Modeling heterotic effects in beef cattle using genome-wide SNP-marker genotypes. *J. Anim. Sci.* 96:830-845. doi:10.1093/jas/skx002
- Allwardt, K., C. Ahlberg, A. Broocks, K. Bruno, A. Taylor, S. Place, C. Richards, C. Krehbiel, M. Calvo-Lorenzo, U. DeSilva, D. VanOverbeke, R. Mateescu, C. Goad, and M. M. Rolf. 2017. Validation of an automated system for monitoring and restricting water intake in group-house beef systems. *J. Anim. Sci.* doi:10/2725/Jas2017.1593
- Aguilar, I., I. Misztal, A. Legarra, and S. Tsuruta. 2011. Efficient computation of the genomic relationship matrix and other matrices used in single-step evaluation. *J. Anim. Breed. Genet.* 128:422-428. doi:10.1111/j.1439-0388.2012.00991.x
- Aguilar, I., I. Misztal, D. L. Johnson, A. Legarra, S. Tsuruta, and T. H. Lawlor. 2010. Hot topic: A unified approach to utilize phenotypic, full pedigree, and genomic information for genetic evaluation in Holstein final score. *J. Dairy. Sci.* doi:10.3168/jds.2009-2730

- 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. *J. Anim. Sci.* 75:2024-2032. doi:10.2527/1997.7582024x
- Archer, J. A., A. Reverter, R. M. Herd, D. J. Johnson, and P. F. Arthur. 2002. Genetic variability in feed intake and efficiency of mature beef cows and relationships with postweaning measurements. In *Proc. 7th World Congr. Genet. Appl. Livest. Prod.* Montpellier, France.
- 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. *Aust. J. Agric. Res.* 44:361-369
- 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. *J. Anim. Sci.* 79:2805-2811. doi:10.2527/2001.79112805x
- Bachmanov, A. A., D. R. Reed, G. K. Beauchamp, and M. G. Todoff. 2002. Food intake, water intake, and drinking spout side preference of 28 mouse strains. *Behavior. Genet.* 32:435-443. doi:10.1023/A:1020884312053
- Barlow, R. 1984. Selection for growth and size in ruminants: Is it time for a moratorium? In *Proc. 2nd World Cong. Sheep, Beef Cattle Breed.* Pretoria, South Africa. P421-432
- 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 you growing cattle. *Can. J. Anim. Sci.* 83:189-204. doi:10.4141/A02-065

- Berry, D. P. and J. J. Crowley. 2013. Cell Biology Symposium: Genetics of feed efficiency in dairy and beef cattle. *J. Anim. Sci.* 91:1594-1613. doi:10.2527/jas2012-5862
- Bouquet, A. M. N. Fouilloux, G. Renand, and F. Phocas, 2010. Genetic parameters for growth, muscularity, feed efficiency, and carcass traits of young beef bulls. *Livest. Sci.* 129:38-48. doi:10.1016/j.livsci.2009.12.010
- Blackwell, R. L., J. H. Knox, C.E. Shelby, and R. T. Clark. 1962. Genetic analysis of economic characteristics of young Hereford cattle. *J. Anim. Sci.* 21:101-107. doi:10.2527/jas1962.211101x
- Brew, M. N., R. O. Myer, M. J. Hersom, J. N. Carter, M. A. Elzo, G. R. Hansen, and D. G. Riley. 2011. Water intake and factors affecting water intake of growing beef cattle. *Livest. Sci.* 140:297-300. doi: 10.1016/j.livsci.2011.03.030
- Brown, A. H., Jr, A. B. Johnson, J. J. Chewning, and C. J. Brown. 1988. Relationships among absolute growth rate, relative growth rate and feed conversion during postweaning feedlot performance test. *J. Anim. Sci.* 66:2524-2529. doi:10.2527/jas1988.66102524x
- Chiang, C. W. K., Z. K. Z. Gajdos, J. M. Korn, F. G. Kuruvilla, J. L. Butler, R. Hackett, C. Guiducci, T. T. Nguyen, R. Wilks, T. Forrester, C. A. Haiman, K. D. Henderson, L. Le Marchand, B. E. Henderson, M. R. Palmert, C. A. McKenzie, H. N. Lyon, R. S. Cooper, X. Zhu, and J. N. Hirschhorn. 2010. Rapid assessment of genetic ancestry in populations of unknown origin by genome-wide genotyping of pooled samples. *PLoS Genet.* 6:e1000866. doi:10.1371/journal.pgen.1000866
- Christensen, O. F., and M. S. Lund. 2010. Genomic prediction when some animals are not genotyped. *Genet. Sel. Evol.* 42:2. doi:10.1186/1297-9686-42-2

- Demment, M. W., and R. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*. 125:641-672. doi:10.1086/284369
- Elzo, M. A., D. D. Johnson, G. C. Lamb, T. D. Maddock, R. O. Myer, D. G. Riley, G. R. Hanson, J. G. Wasdin, and J. D. Driver. 2010. Heritabilities and genetic correlations between postweaning feed intake, growth, and ultrasound traits in a multibreed Angus-Brahman cattle population in the subtropics. In. *Proc. 9th World Congr. Genet. Appl. Livest. Prod.* Leipzig, Germany. P203-207
- Gengler, N., C. Seutin, F. Boonen, and L. D. Van Vleck. 1995. Estimation of genetic parameters for growth, feed consumption, and conformation traits for double-muscled Belgian blue bulls performance-tested in Belgium. *J. Anim. Sci.* 73:3269-3273. doi:10.2527/1995.73113269x
- Jensen, J., I. L. Mau, B. B. Anderson, and P. Madsen. 1992. Phenotypic and genetic relationships between residual energy intake and growth, feed intake and carcass traits of young bulls. *J. Anim. Sci.* 70:386-395. doi:10.2527/1992.702386x
- 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. *Livest. Prod. Sci.* 63:111-119. doi:10.1016/S0301-6226(99)00122-0
- Herd, R. M., V. H. Oddy and E. C. Richardson. 2004. Biological basis for variation in residual feed intake in beef cattle. *Aust. J. Exp. Agric.* 44:423-430. doi:10.1071/EA02220

- Herring, W. O., and J. K. Bertrand. 2002. Multi-trait prediction of feed conversion in feed lot cattle. Proc. Beef Improvement Federation. 34th Annual Research symposium and Annual Meeting. University of Nebraska, Omaha, NE. P89-97
- 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. *Livest. Sci.* 99:111-118. doi:10.1016/j.livprodsci.2005.06.004
- Kennedy, B. W., J. H. J. van der Werf, and T. H. E. Meuwissen. 1993. Genetic and statistical properties of residual feed intake. *J. Anim. Sci.* 71:3239-3250. doi:10.2527/1993.71123239x
- Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. *J. Anim. Sci.* 22:486-494. doi:10.2527/jas1963.222486x
- Korver, S, E. A. M. van Eekelen, H. Vos, G. J. Nieuwhof, and J. A. M. van Arendonk. 1991. Genetic parameters for feed intake and feed efficiency on growing dairy heifers. *Livest. Prod. Sci.* 29:49-59. doi:10.1016/0301-6226(91)90119-B
- Kraly, F. S., 1983. Histamine plays a part in induction of drinking by food intake. *Nature.* 302:65-66. doi:10.1016/0301-6226(91)90119-B
- Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef traits. 2. Phenotypic and genetic correlations. *Anim. Breed.* 62:825-853
- Kuehn, L. A., J. W. Keele, G. L. Bennett, T. G. McDanel, T. P. L. Smith, W. M. Snelling, T. S. Sonstegard, and R. M. Thallman. 2011. Predicting breed composition using breed frequencies of 50,000 markers from the US Meat Animal Research Center 2,000 Bull Project. *J. Anim. Sci.* 89:1742-1750. doi:10.2527/jas.2010-3530

- Langemeier, M., T. Schroeder, and J. Mintert. 1992. Determinants of cattle finishing profitability. *Southern J. Agric. Econ.* 24:41-47. doi:10.1017/S0081305200018367
- Liu, M. F., L. A. Goonewardene, D. G. C. Bailey, J. A. Basarab, R. A. Kemp, P. F. Arthur, E. K. Okine, and M. Makarechian. 2000. A study on the variation of feed efficiency in station tested beef bulls. *Can. J. Anim. Sci.* 80:435-441. doi:10.4141/A99-030
- Magee, W. T. 1962. Relationship between daily feed consumption and feed efficiency. *J. Anim. Sci.* 21:880-882. doi:10.2527/jas1962.214880x
- Mao, F., L. Chen, M. Vinsky, E. Okine, Z. Wang, J. Basarab, D. H. Crews Jr., and C. Li. 2013. Phenotypic and genetic relationships of feed efficiency with growth performance, ultrasound, and carcass merit traits in Angus and Charolais Steers. *J. Anim. Sci.* 91:2067-2076. doi:10.2527/jas2012-5470
- Mark, D. R., T. C. Schroeder, and R. Jones. 2000. Identifying economic risk in cattle feeding. *J. Agribus.* 18:331-344.
- Meyer, K., and D. Houle. 2013. Sampling based approximation of confidence intervals for functions of genetic covariance matrices. *Proc. Assoc. Advmt. Anim. Breed. Genet.* 20: 523–526. Available at: <http://www.aaabg.org/aaabghome/AAABG20papers/meyer20523.pdf>
- Misztal, I., S. Tsuruta, D. A. L. Lourenco, I. Aguilar, A. Lagarra, and Z. Vitezica. 2014. Manual for BLUPF90family of programs. http://nce.ads.uga.edu/wiki/lib/exe/fetch.php?media=blupf90_all1.pdf. (Accessed 4 January 2018.)

- Moore, S. S., F. D. Mujibi, and E. L. Sherman. 2009. Molecular basis for residual feed intake in beef cattle. *J. Anim. Sci.* 87(E. Suppl.):E41-47. doi:10.2527/jas.2008-1418. doi:10.2527/jas.2008-1418
- 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. *J. Anim. Sci.* 88:3789-3799. doi:10.2527/jas.2009-2407
- Nardone, A., B. Ronchi, N Lacetera, M.S. Ranieri, and U. Bernabucci. 2010. Effects of climate changes on animal production and sustainability of livestock systems. *Livest. Prod.* 130:57-69. doi:10.106/j.livprodsci.2010.02.011
- 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. 2004. Genetic and phenotypic relationships of feeding behavior and temperament with performance, feed efficiency, ultrasound, and carcass merit of beef cattle. *J. Anim. Sci.* 85:2382-2390. doi:10.2527/jas.2006-657
- Okanishi, T, S. Masayuki, K. Tomohiro, O. Kenji, and F. Mukai. 2008. Genetic analysis of residual feed intake and other performance test traits of Japanese Black cattle from revised protocol. *Anim. Sci. J.* 79:291-296. doi:10.1111/j.1740-0929.2008.00529.x
- Ramirez, I. and J. L. Fuller. 1976. Genetic influence on water and sweetened water consumption in mice. *Physiology & Behavior.* 16:163-168. doi:10.1016/0031-9384(76)90300-0
- Renard, G. and D. Krauss. 2002. Genetic relationship between fattening and slaughter traits in purebred Charolais young bulls. In. Proc. 7th World Congr. Genet. Appl. Livest. Prod. Montpellier, France. Commination No. 10-08.

- Ritzman, E. G., and F. G. Benedict. 1924. The effect of varying feed levels on the physiological economy of steers. *New Hamp. Agr. Exp. Sta. Tech. Bul. Mo.* 26.
- Rosegrant, M. W., X. Cai, and S. A. Cline. 2002. Global water outlook to 2020, Averting an impending crisis, A 2020 vision for food, agriculture, and the environment initiative. International Food Policy Research Institute/International Water Management Institute, Washington, D. C. U.S.A/Colombo, Sri Lanka
- Schenkel, F. S., S. P. Miller, and J. W. Wilton. 2004. Genetic parameters and breed difference for feed efficiency, growth and body composition traits of young beef bulls. *Can. J. Anim. Sci.* 84:177-185. doi:10.4141/A03-085
- Schwarzkopf-Genswein, K. S., K. A. Beauchemin, D. J. Gibb, D. H. Crews, Jr, D. D. Hickman, M. Streeter, and T. A. McAllister. 2003. Effect of bunk management on feeding behavior, ruminal acidosis and performance of feedlot cattle: A review. *J. Anim. Sci.* 81(E. Suppl. 2):E149-E158. doi:10.2527/2003.8114_suppl_2E149x
- Thornton, P. K., J. van de Steeg, A. Notenbaert, and M. Herrero. 2009. The impact of climate change on livestock and livestock systems in developing countries: A review of what we know and what we need to know. *Agric. Syst.* 101:113-127. doi:10.1016/j.agsy.2009.05.002
- VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. *J. Dairy. Sci.* 91:4414-4423. doi:10.3168/jds.2007-0980
- World Economic Forum. 2017. The Global Risks Report 2017. World Economic Forum. 12:1-78.

Table 4.1 Summary statistics for water intake (WI), Dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain ratio (W/G) and feed to gain ratio (F/G) for each group

Variable	Group	N	Mean	Minimum	Maximum	Std Dev
WI, kg/d	1	117	40.50	21.20	65.80	8.01
	2	116	28.23	15.60	44.70	5.63
	3	117	36.37	24.10	61.40	6.75
	4	105	49.46	32.00	101.40	13.07
	5	123	34.92	25.50	50.90	4.84
DMI, kg/d	1	117	10.12	6.36	13.69	1.39
	2	116	10.23	6.04	14.07	1.62
	3	117	10.24	7.16	14.76	1.52
	4	105	10.53	7.76	12.74	0.92
	5	123	11.67	8.96	16.17	1.23
ADG, kg/d	1	117	1.39	0.62	2.24	0.29
	2	116	1.74	0.41	2.45	0.34
	3	117	1.46	0.53	2.32	0.31
	4	105	1.27	0.42	1.81	0.29
	5	123	1.84	1.10	2.55	0.29
RWI, kg/d	1	117	0.00	-13.49	18.85	6.42
	2	116	0.00	-7.38	17.56	3.91
	3	117	0.00	-10.39	23.75	5.38
	4	105	0.00	-20.87	46.16	10.93
	5	123	0.00	-5.49	9.08	2.64
RFI, kg/d	1	117	-0.08	-2.69	2.60	0.95
	2	116	-0.71	-3.00	1.47	0.88
	3	117	-0.21	-3.40	1.93	1.11
	4	105	-0.09	-1.72	1.52	0.64
	5	123	0.45	-3.02	2.93	0.76
WG, kg/d	1	117	29.83	18.33	55.99	6.30
	2	116	16.86	9.82	51.50	5.10
	3	117	25.78	15.54	54.84	6.51
	4	105	41.16	20.80	105.16	14.37
	5	123	19.31	13.32	28.29	2.99
FG, kg/d	1	117	10.11	6.08	18.93	1.85
	2	116	8.26	4.66	20.11	1.95
	3	117	9.93	6.61	24.69	2.34
	4	105	12.02	7.64	31.62	3.38
	5	123	9.26	6.54	15.28	1.44

Table 4.2 LSMEANS for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain (W/G), and feed to gain (F/G) for each group at low, medium, and high water intake levels^a

Trait	Group 1	Group 2	Group 3	Group 4	Group 5	ALL
WI, kg/d						
Low	34.86 ^b	23.39 ^b	29.44 ^b	39.81 ^b	31.23 ^b	32.79 ^b
Medium	45.22 ^c	28.83 ^c	36.67 ^c	50.31 ^c	36.68 ^c	39.77 ^c
High	54.62 ^d	36.10 ^d	45.85 ^d	68.86 ^d	43.64 ^d	50.91 ^d
DMI, kg/d						
Low	9.64 ^b	9.31 ^b	9.42 ^b	10.20 ^b	11.00 ^b	10.01 ^b
Medium	10.48 ^c	10.44 ^c	10.51 ^c	10.65 ^c	11.96 ^c	10.90 ^c
High	11.57 ^d	11.42 ^d	10.94 ^c	11.10 ^d	13.22 ^d	11.68 ^d
ADG, kg/d						
Low	1.29 ^b	1.51 ^b	1.31 ^b	1.23 ^b	1.70 ^b	1.41 ^b
Medium	1.47 ^c	1.80 ^c	1.49 ^c	1.27 ^b	1.92 ^c	1.61 ^c
High	1.68 ^d	2.00 ^d	1.64 ^d	1.35 ^b	2.14 ^d	1.77 ^d
RWI, kg/d						
Low	-3.99 ^b	-2.55 ^b	-4.91 ^b	-6.72 ^b	-1.50 ^b	-3.98 ^b
Medium	3.46 ^c	0.06 ^c	-0.29 ^c	-0.03 ^c	0.82 ^c	0.85 ^c
High	9.14 ^d	5.00 ^d	7.61 ^d	15.08 ^d	3.74 ^d	8.69 ^d
RFI, kg/d						
Low	-0.19 ^b	-0.22 ^b	-0.38 ^b	-0.25 ^b	-0.40 ^b	-0.28 ^b
Medium	0.17 ^{bc}	-0.00 ^b	0.18 ^c	0.07 ^c	0.13 ^c	0.13 ^c
High	0.61 ^c	0.49 ^c	0.16 ^{bc}	0.44 ^d	1.02 ^d	0.52 ^d
W/G, kg/d						
Low	28.10 ^b	17.12 ^b	24.12 ^b	36.16 ^b	18.76 ^b	25.57 ^b
Medium	31.75 ^{bcd}	16.37 ^b	25.47 ^{bc}	40.94 ^b	19.30 ^b	26.74 ^b
High	32.88 ^d	17.86 ^b	28.55 ^c	52.76 ^c	20.53 ^b	31.23 ^c
F/G, kg/d						
Low	7.74 ^b	6.59 ^b	7.60 ^b	9.09 ^b	6.61 ^b	7.57 ^b
Medium	7.28 ^{bc}	5.91 ^c	7.24 ^b	8.71 ^b	6.29 ^b	7.06 ^{cd}
High	6.94 ^c	5.60 ^{cd}	6.73 ^b	8.28 ^b	6.13 ^b	6.72 ^d

^aIndividuals divided into low, medium, and high water intake levels based on k-mean clustering of individual average daily water intake, Group 1: low n=66, medium n=38, high n=13, Group 2: low n=44, medium n=48 high n=23, Group 3: low n=36 medium n=56, high n=26, Group 4: low n=49, medium n=34, high n=22, Group 5: low n=56, medium n=54, high n=12

^{bcd}Differences in superscripts within each column and variable indicate significant differences between groups (P<0.05)

Table 4.3 LSMEANS for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain (W/G), and feed to gain (F/G) for each group at low, medium, and high DMI levels^a

Trait	Group 1	Group 2	Group 3	Group 4	Group 5	All
WI, kg/d						
Low	35.27 ^b	24.24 ^b	30.85 ^b	40.89 ^b	32.13 ^b	34.08 ^b
Medium	40.96 ^c	27.50 ^c	36.56 ^c	51.00 ^c	35.39 ^c	38.84 ^d
High	47.60 ^d	31.65 ^d	40.76 ^d	58.02 ^d	41.95 ^d	43.82 ^d
DMI, kg/d						
Low	8.71 ^b	8.15 ^b	8.31 ^b	9.52 ^b	10.78 ^b	9.29 ^b
Medium	10.38 ^c	10.02 ^c	10.28 ^c	10.69 ^c	11.99 ^c	10.77 ^c
High	11.98 ^d	11.69 ^d	12.00 ^d	11.68 ^d	13.44 ^d	12.34 ^d
ADG, kg/d						
Low	1.16 ^b	1.35 ^b	1.22 ^b	1.07 ^b	1.71 ^b	1.32 ^b
Medium	1.44 ^c	1.66 ^c	1.49 ^c	1.34 ^{cd}	1.87 ^c	1.58 ^c
High	1.66 ^d	2.04 ^d	1.66 ^d	1.41 ^d	2.19 ^d	1.83 ^d
RWI, kg/d						
Low	-0.39 ^b	1.06 ^b	-0.99 ^b	0.11 ^b	0.10 ^b	0.05 ^b
Medium	-0.42 ^b	-0.22 ^b	0.04 ^b	0.41 ^b	-0.57 ^{bc}	-0.37 ^b
High	0.72 ^b	-0.11 ^b	0.32 ^b	-1.81 ^b	1.35 ^{bd}	0.00 ^b
RFI, kg/d						
Low	-0.72 ^b	-0.86 ^b	-1.15 ^b	-0.66 ^b	-0.63 ^b	-0.71 ^b
Medium	0.10 ^c	-0.06 ^c	-0.03 ^c	0.04 ^c	0.27 ^c	0.08 ^c
High	1.09 ^d	0.63 ^d	1.12 ^d	0.87 ^d	1.12 ^d	0.96 ^d
W/G, kg/d						
Low	31.27 ^b	20.15 ^b	26.37 ^b	44.00 ^b	19.16 ^b	28.70 ^b
Medium	29.04 ^b	16.96 ^c	25.55 ^b	39.18 ^b	19.23 ^b	26.22 ^c
High	28.87 ^b	15.04 ^c	25.20 ^b	41.22 ^b	19.11 ^b	25.47 ^c
F/G, kg/d						
Low	7.73 ^b	6.73 ^b	9.72 ^b	10.15 ^b	6.44 ^b	7.62 ^b
Medium	7.39 ^b	6.18 ^{bc}	9.89 ^b	8.17 ^c	6.55 ^b	7.10 ^c
High	7.37 ^b	5.64 ^{bd}	10.18 ^b	8.29 ^c	6.08 ^b	6.94 ^c

^aIndividuals divided into low, medium and high dry matter intake levels based on k-mean clustering of individual average daily dry matter intake, Group 1: low n=41, medium n=52, high n=12, Group 2: low n=24, medium n=50 high n=24, Group 3: low n=31 medium n=54, high n=33, Group 4: low n=32, medium n=52, high n=21, Group 5: low n=45, medium n=57, high n=20

^{bcd}Differences in superscripts within each column and variable indicates significant differences between groups (P<0.05)

Table 4.4 Pearson (below the diagonal) and Spearman (above the diagonal) phenotypic correlations for water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI) water to gain (W/G) and feed to gain (F/G)^a

	WI	DMI	ADG	RWI	RFI	W/G	F/G
WI		0.389***	-0.109*	0.451***	0.266***	0.711***	0.383***
DMI	0.366***		0.501***	0.027	0.583***	-0.084*	0.058
ADG	-0.094*	0.530***		0.127**	0.002	-0.734***	-0.892***
RWI	0.602***	-0.000	0.051		-0.017	0.221***	-0.102*
RFI	0.258***	0.595***	0.001	-0.032		0.168***	0.383***
W/G	0.698***	-0.088*	-0.694***	0.383***	0.149**		0.811***
F/G	0.276***	-0.012	-0.779***	-0.04	0.295***	0.808***	

^aUnits for all traits are in kg/d

*Correlations are significantly different from zero at * P<0.05, **P< 0.01, ***P < 0.0001

Table 4.5 Variance components and heritability estimates for average daily water intake (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain (W/G), and feed to gain (F/G)

Trait	Genetic Var ^a	Residual Var ^a	Phenotype Var ^b	Heritability ^b
WI, kg/d	23.32 (8.76)	36.75 (8.07)	60.07 (3.75)	0.39 (0.14)
DMI, kg/d	0.94 (0.26)	0.46 (0.20)	1.40 (0.09)	0.67 (0.16)
ADG, kg/d	0.04 (0.01)	0.06 (0.01)	0.10 (0.01)	0.37 (0.15)
RWI, kg/d	14.83 (6.21)	25.67 (5.73)	40.50 (2.53)	0.37 (0.15)
RFI, kg/d	0.49 (0.14)	0.26 (0.12)	0.75 (0.05)	0.65 (0.17)
W/G, kg/d	22.95 (8.26)	36.38 (7.60)	59.33 (3.68)	0.39 (0.13)
F/G, kg/d	0.42 (0.34)	2.11 (0.33)	2.53 (0.15)	0.16 (0.14)

^astandard errors, reported in parenthesis, were generated by AIREML

^bstandard deviations, reported in parenthesis, because phenotypic variance and heritability were calculated from genetic and residual var.

Table 4.2 Genetic correlations^a for water intake, (WI), dry matter intake (DMI), average daily gain (ADG), residual water intake (RWI), residual feed intake (RFI), water to gain (W/G) and feed to gain (F/G)

	WI	DMI	ADG	RWI	RFI	W/G	F/G
WI		0.34 (0.29)	0.05 (0.62)	0.88 (0.35)	0.33 (0.26)	0.99 (0.10)	0.90 (1.63)
DMI			0.68 (0.20)	-0.10 (0.31)	0.68 (0.14)	-0.13 (0.27)	0.08 (0.70)
ADG				-0.17 (0.58)	-0.031 (0.32)	-0.57 (0.33)	-0.63 (0.99)
RWI					-0.57 (0.31)	0.89 (0.43)	0.42 (1.11)
RFI						0.37 (0.25)	0.88 (0.66)
W/G							0.68 (0.86)
F/G							

^astandard deviations are reported in parenthesis

Figure 4.1 Mean breed composition estimated for each group and across all groups for 16 different breeds

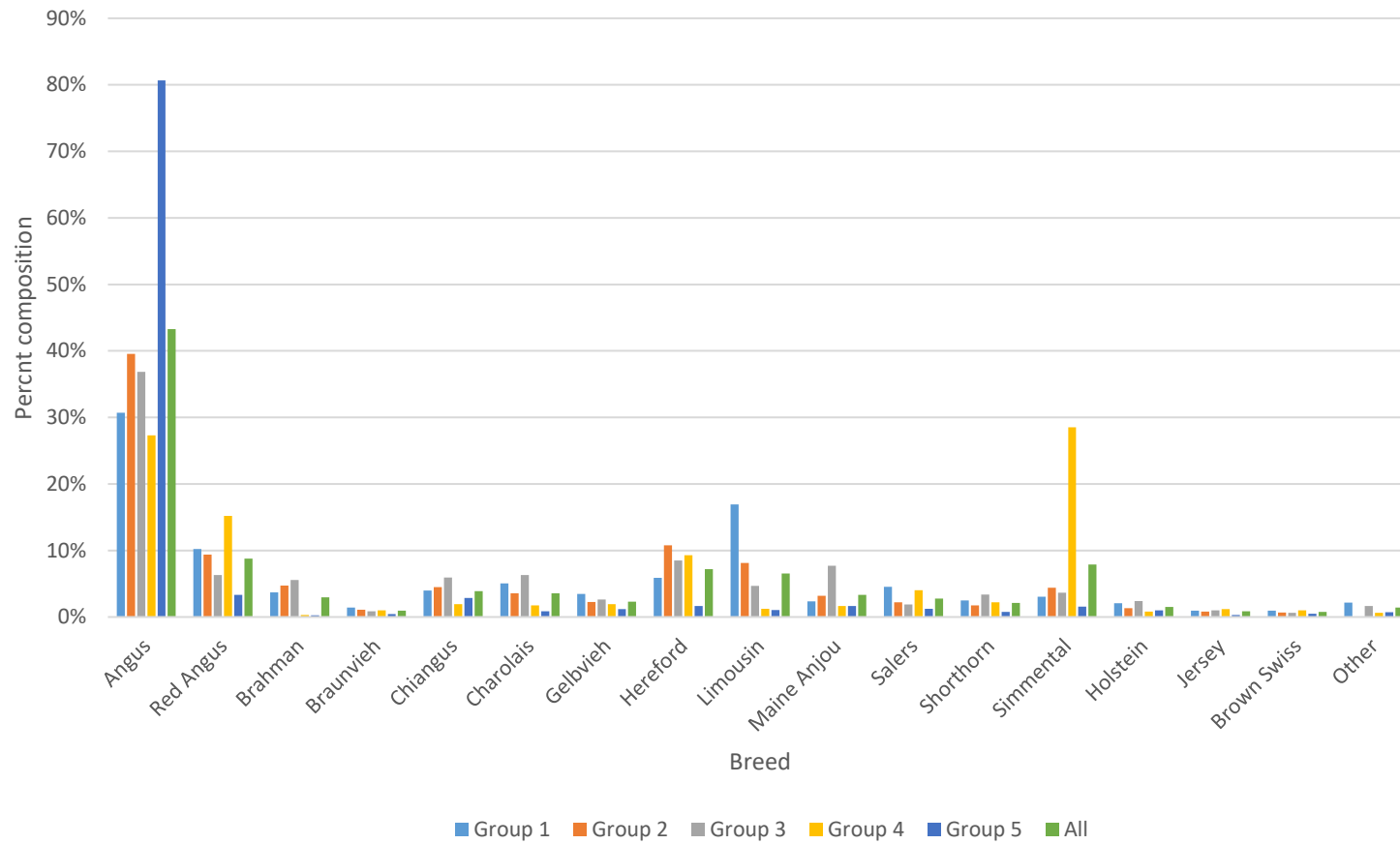


Figure 4.2 Mean breed composition when individual breeds were combined into their biological grouping within each group and across groups.

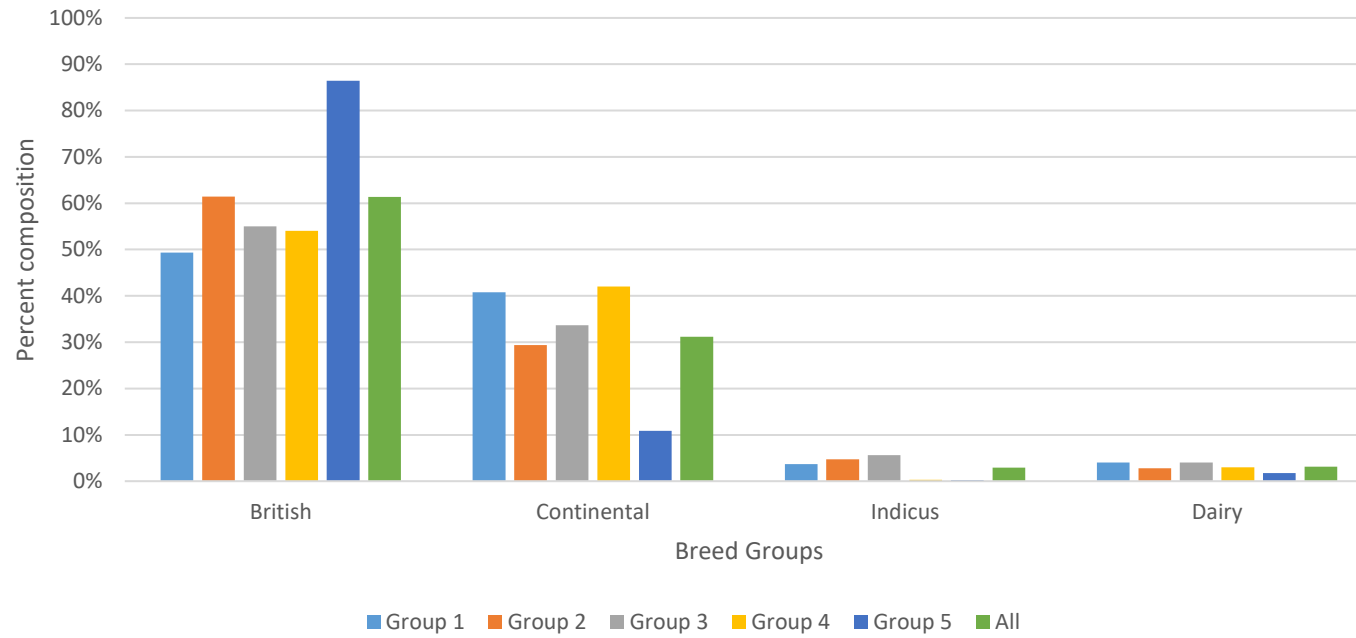


Figure 4.3 Plots depicting relationships between water intake and various feed and water efficiency traits. Panel A: Dry matter intake (DMI) and water intake (WI), Panel B- Residual feed intake (RFI) and water intake (WI), Panel C- Feed to gain (F/G) and water intake (WI), Panel D- Water to gain (W/G) and water intake (WI), Panel E- Residual water intake (RWI) and water intake (WI), Panel F- Average daily gain (ADG) and water intake (WI)

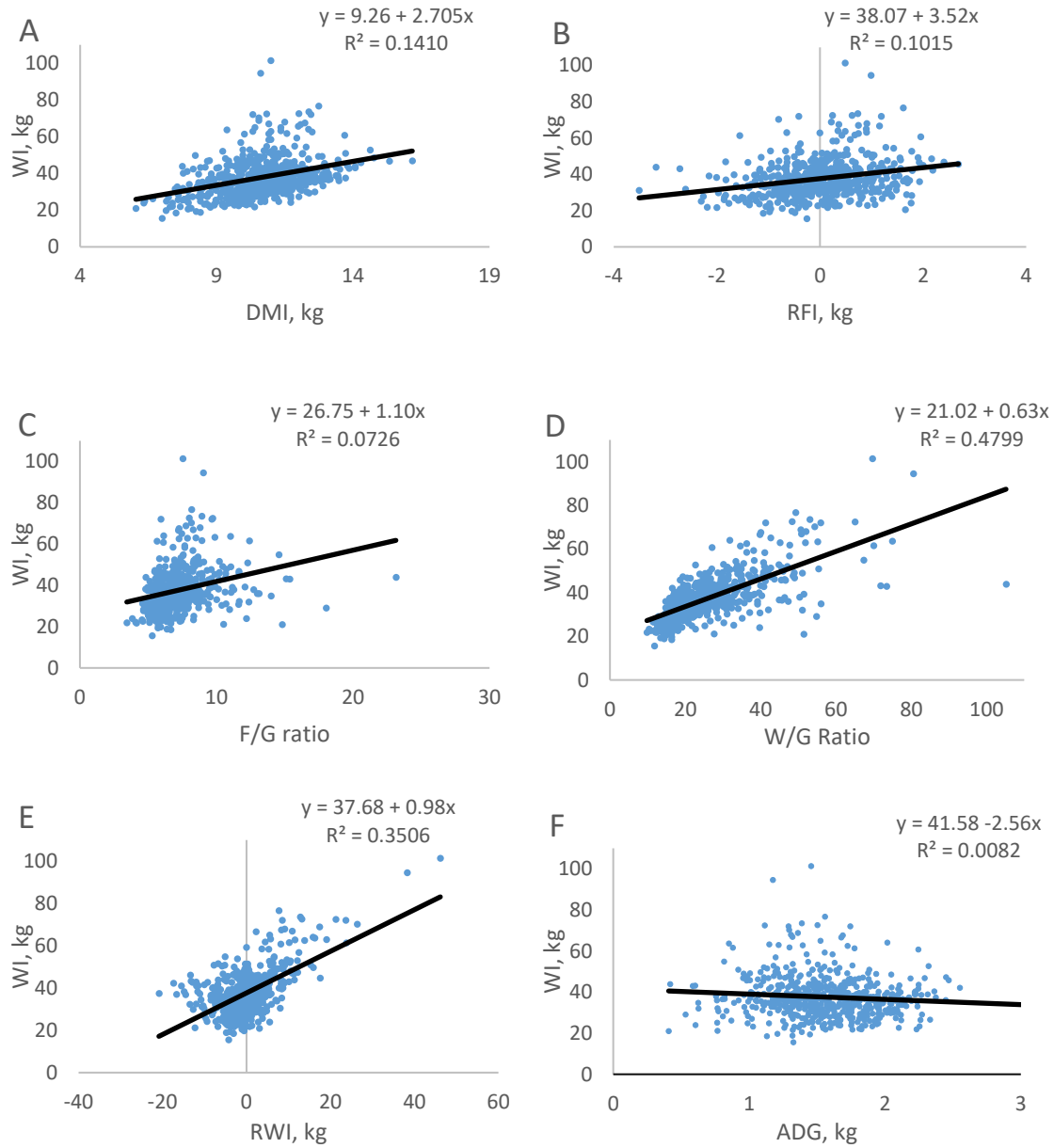
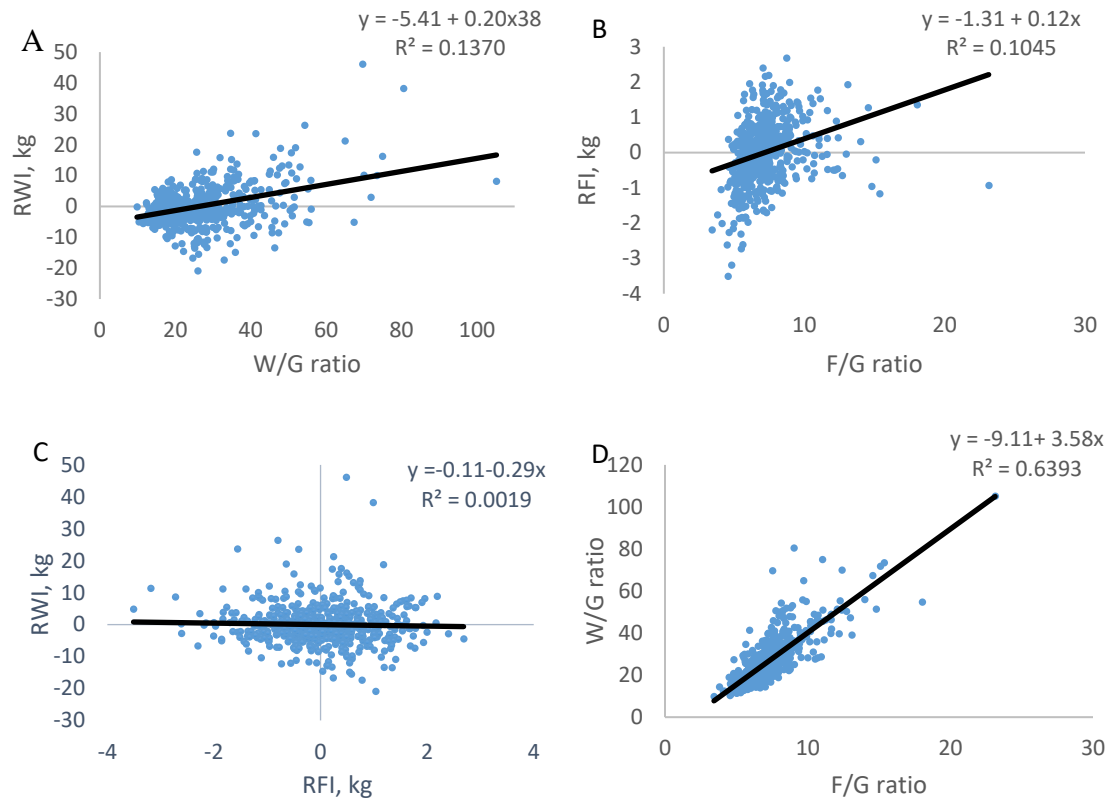


Figure 4.4 Plots depicting relationships between various feed and water efficiency traits. Panel A - individual water to gain (W/G) plot against individual residual water intake (RWI), Panel B - individual residual feed intake (RFI) plot against individual feed to gain ratio (F/G), Panel C - individual residual feed intake (RFI) plot against individual residual water intake (RWI), Panel D - individual feed to gain ratio (F/G) plot against individual water to gain ratio (W/G)



**Chapter 5 - Phenotypic and Genetic Relationship between Water Intake and
Carcass Traits in Beef Cattle**

ABSTRACT

Genetic correlations between water intake and carcass performance are unexplored in the scientific literature. The objective of this study was to determine the phenotypic and genetic relationships between water intake and carcass performance. Individual daily water intake (WI) records were collected on 579 crossbred steers over 140 d, which included both a 70 d *ad libitum* and 70 d restricted WI trial. Steers were subsequently finished, and carcass data was collected at harvest. K-means clustering was utilized to assign WI levels of low, medium, and high to individual animals within each group. Cattle that had low WI levels had lighter final body weights (FBW) and hot carcass weights (HCW) than cattle with high WI ($P < 0.05$). Between WI levels there were no significant differences for marbling (MARB), longissimus muscle area (REA), back fat thickness (BFAT), and yield grade (YG) for most groups. Phenotypic (Pearson) correlations were positive between WI and carcass traits (0.71, HCW; 0.223, BFAT; 0.177, MARB; 0.223, YG; 0.180, FBW) except between WI and REA (-0.025). Spearman rank correlations between phenotypes were similar to Pearson correlations. Bi-variate linear models were utilized to fit all pair wise combination of traits to estimate variance components, heritabilities, and genetic correlations using AIREML. Heritabilities were derived by averaging the heritability estimates for each bi-variate analysis for the trait of interest. Heritability estimates for WI, HCW, REA, BFAT, MARB, YG and FBW were 0.42, 0.31, 0.27, 0.71, 0.26, 0.53, and 0.58 respectively. Positive genetic correlations of 0.38, 0.08, 0.36, 0.17, 0.29, and 0.29 were observed between WI and HCW, REA, BFAT, MARB, YG, and FBW, respectively. Due to the genetic correlations between WI and carcass traits, selecting for decreased WI would have a negative impact on most carcass traits, except for BFAT and YG. These

genetic antagonisms would necessitate selecting for WI in the context of a selection index to prevent undesirable changes in carcass quality.

Key words: Water Intake, Beef Cattle, Carcass traits, genetic correlation, heritability

INTRODUCTION

The availability of fresh water has become a global concern in recent years (World Economic Forum, 2017) thus, quantifying water use in livestock production has become more of a priority. Understanding the relationship between water intake (WI) and carcass traits is critical if selection for decreased WI is implemented. Currently, the relationship between WI and carcass performance is unknown. Water intake is a difficult trait to accurately measure on individual animals because it requires either housing animals in individual pens or measuring individual intakes with an automated system that allows group housing. Housing animals in individual pens is problematic because it does not mimic conditions that are utilized in normal production settings (Friend et al., 1977). Differences in the amount of water consumed between individual vs group housed cattle has not been reported, however there was no significant difference between the amount of feed consumed by individual animals if they were housed individually vs group housed pigs (De Haer and de Vries, 1993).

Heritability estimates and genetic correlations for carcass traits have been previously been reported, but there are no such estimates of the relationship between carcass performance and WI. Determining the relationships between carcass traits and WI is important to understanding how selecting for lower WI in the cow/calf sector might affect their offspring's performance at harvest. Therefore, it is critical to have knowledge of the

relationship between WI and carcass performance. The objective of this study is to evaluate the relationship between WI and carcass performance.

MATERIALS AND METHODS

Study Design

Crossbred steers (n=578) were fed in 5 feeding groups and daily water intake (WI) was collected using an Insentec system (Hokofarm Group, The Netherlands) at the Willard Sparks feedlot located at Oklahoma State University. Intakes were collected over a 3 year period from May 2014 to March 2017. The Insentec system consists of 1 water bunk and 6 feed bunks per pen, and bunks were beneath a shade structure. Additional information on the facility structure and layout can be found in Ahlberg et al. (2018). Within each group, steers were blocked by weight (low and high) and randomly assigned to 1 of 4 pens, each containing approximately 30 steers per pen. To ensure data were high quality, filtering procedures were applied as outlined in Allwardt et al. (2017). Cattle had access to *ad libitum* water but on days that *ad libitum* WI was not achieved (such as weigh dates, equipment malfunction, etc.), data were treated as missing. Two different feed protocols were administered: a slick bunk protocol was utilized for group 1-3 steers and *ad libitum* feed was distributed to group 4 and 5. Water intakes were collected over a 70-day baseline period following a 21-day acclimation period to be in accordance with test length guidelines established by Ahlberg et al. (2018a). After the 21-day acclimation period, cattle were given Compudose (Elanco Animal Health, Greenfield, IN), an implant containing estradiol 17 β (E₂ β). Body weights (BWTS) were collected at the beginning (SWT) of the baseline period and within 24 hours of being harvested (FBW). During the 140 day trial period BWTS were recorded every two weeks. Before finishing, cattle were also enrolled

in a 70-day water restriction trial, which followed the collection of baseline WI. All groups were fed a growing diet throughout the 140-d test period that consisted of 15% cracked corn, 51.36% wet corn sweet bran, 28.44% prairie hay, and 5.20% supplement and mean gross energy of composited samples was ~4,524.6 cal/g on a dry matter basis. Dry matter for the groups ranged from 70.04% to 74.02% for the growing ration. During the baseline period, two blood samples were collected during the feeding period via jugular venipuncture in BD vacutainer blood collection tubes of size 10.0 ml and contained 1.5 mL of ACD as an anticoagulant. Whole blood was centrifuged to obtain white blood cells. DNA was extracted from white blood cells for each individual animal using a phenol:chloroform:isoamyl alcohol extraction and ethanol precipitation. Five hundred nanograms of DNA from each individual animal was sent to GeneSeek (Lincoln, NE) for genotyping on the GeneSeek Genomic Profiler High-Density (GGP HD150K). Genotypes were used to estimate breed composition in each individual animal and to create a genomic relationship matrix for estimate of variance components.

Cattle from groups 1, 2, 3, and 5 were removed from the Insentec facility, blocked by weight, placed into finishing pens, and managed as a group (no individual intake data was collected). Group 4 cattle were finished in the Insentec facility and remained in the same pens that they were originally assigned at the start of the study, which were blocked by starting weight. Cattle were transitioned from the growing ration to the finishing ration over 28 d. During the finishing phase, all groups were fed a diet that consists of 57.5% cracked corn, 30% wet corn sweet bran, 7.0% prairie hay and 5.5% supplement. The number of days in the finishing period varied between and within each group (Table 5.1). These cattle were producer-owned, so the wide variation seen in length of finish, time of

harvest, and plant location was due to the producers' response to changing market conditions. All groups received two additional implants of Component TE-S with Tylan (Elanco Animal Health, Greenfield, IN), an implant containing estradiol 17 β (E₂ β), during the finishing phase, except for group 2, which received three. All animal procedures were approved by the Institutional Animal Care and Use Committee at Oklahoma State University (protocol AG13-18) in accordance with Federation of Animal Science Societies (FASS, 2010) guidelines.

Carcass data

Within 24 hours of being sent to the plant, final body weights (FBW) were taken. A detailed description of number of animals and the corresponding harvest plant are presented in Table 5.1. At harvest, hot carcass weight (HCW) was recorded for each steer. Carcasses were chilled for 24-h before being evaluated for marbling (MARB), rib eye area (REA), back fat thickness measured at the 12th rib (BFAT), and yield grade (YG). Yield grade measurements in our dataset were not rounded down to the nearest integer value like they are generally reported to better represent true variation in YG. To improve consistency of carcass data across plants, Marbling score REA, and BFAT were all collected using the camera system installed at each plant, except for animals harvested at the Food and Agriculture Products Center (FAPC). Carcass data for cattle harvested at FAPC were collected by trained meat science personnel, as no camera grading system was available at this location. For cattle in groups 1-3 sent to Tyson Fresh Meats in Amarillo, TX, marbling score had values between 100 and 1000 units (100=devoid and 1000=abundant). Marbling scores from other plants were reported as traces (TR), slight (SL), small (SM), modest (MT), moderate (MD), slightly abundant (SA), and moderately abundant (MA) with degree

of marbling within each class ranging from 0 to 90 with increments of 10 (i.e. SM60, MA70, or MD40). Marbling scores for animals that were not recorded as numeric values were converted to numeric scores as reported by Nephawe (2004) so that all measures were on an identical scale. Marbling scores were not recorded for group 2 steers sent to Creekstone on July 2, 2015, and group 3 steers sent to Creekstone on February 11, 2016. Summary statistics are presented in Table 5.2 for all traits.

Statistical analysis

For each group, animals were assigned to either high, medium or low WI groups using K-means clustering with $k=3$. This methodology was chosen to more objectively establish intake groups and avoid arbitrarily ranking animals and assigning the top, middle, and bottom third of the data into each category. Breed composition of the steers was unknown, so breed composition was estimated using a regression method developed by Chiang et al. (2010) and Kuehn et al. (2011), based on each animal's genotypes. Detailed description of breed composition on these steers can be found in Ahlberg et al. (2018b). Summary statistics of phenotypic data for each group and level within group as well as phenotypic (Pearson and Spearman) correlations between WI and carcass traits were calculated using SAS 9.4.

To determine if WI levels had an effect on carcass performance, pairwise comparisons between all WI levels were analyzed (within group) using proc GLM in SAS 9.4 (SAS Institute Inc., Cary, NC, USA) using the following model:

$$\text{Trait}_{ij} = \text{Intake level}_i + \text{DOF}_j + \text{British}_j + \text{Continental}_j + \text{Bos indicus}_j + \text{Dairy}_j + e_{ij}$$

where,

Trait_{ij} is the trait of interest (HCW, REA, BFAT, MARB, and YG) for the ith WI intake level for the jth individual,

Intake level_i is the ith intake level (low, medium, or high for WI),

DOF is the number of days in the finishing phase for animal j fitted as a covariate,

British is the percent of British breeds for animal j fitted as a covariate,

Continental is the percent of continental breed ancestry for animal j fitted as a covariate,

Bos indicus is the percent of *Bos indicus* ancestry for animal j fitted as a covariate,

Dairy is the percent of dairy breed ancestry for animal j fitted as a covariate,

e_{ij} is the random residual.

For analysis of data across all groups, feed management (slick vs adlib) was added to the previous model as an additional fixed effect.

To determine if carcass traits were different between groups, pairwise comparisons between groups were analyzed in SAS 9.4 (SAS Institute Inc., Cary, NC, USA) using the following model:

$$\text{Trait}_{ijk} = \text{Intake level}_i + \text{Group}_j + \text{DOF}_k + \text{British}_k + \text{Continental}_k + \text{Bos indicus}_k \\ + \text{Dairy} + e_{ijk}$$

where,

Trait_{ij} is the trait of interest (HCW, REA, BFAT, MARB, and YG) for the ith WI intake level for the jth group and the kth individual,

Intake level_i is the ith intake level (low, medium, or high for WI),

Group_j is the jth feeding group,

DOF is the number of days in the finishing phase for animal k fitted as a covariate,

British is the percent of British breeds for animal k fitted as a covariate,

Continental is the percent of continental breeds for animal k fitted as a covariate,

Bos indicus is the percent of *Bos indicus* for animal k fitted as a covariate,

Dairy is the percent of dairy breeds for animal k fitted as a covariate,

e_{ij} is the random residual.

Genetic (co)variance parameters were estimated using single-step genomic best linear unbiased prediction (ssGBLUP) with the average information restricted maximum likelihood (AIREML) algorithm implemented within the BLUPF90 software package (Misztal et al., 2014). Pedigree information was not available so the numerator relationship matrix is replaced with genomic relationship matrix in ssGBUP. The genomic relationship matrix was calculated as $G=ZZ'/k$ based on methods presented in VanRaden (2008), where Z is a matrix of SNP markers centered based on allele frequency estimated from genotyped animals, and k is $2*\sum(p*(1-p))$. Traits were fitted as bivariate mixed linear animal models for each pairwise combination of traits to estimate variance components, heritabilities, and genetic correlations using the following model:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 b_1 \\ X_2 b_2 \end{bmatrix} + \begin{bmatrix} Z_1 u_1 \\ Z_2 u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_i is a vector of observations for trait 1 and trait 2, X_i is an incidence matrix relating observations to fixed effects, b_i is a vector of fixed effects for trait 1 and 2, Z_i is an incidence matrix relating observations to additive direct genetic effect for trait 1 and 2, u_i is a vector of additive direct genetic effect for trait 1 and 2, and e_i is a vector of random residuals for trait 1 and 2. Fixed effects for WI were group and feed management (slick or adlib), and covariates included start weight, percent British, percent continental, percent *Bos indicus*, and percent dairy ancestry. Days to finish was included as an additional covariate for carcass traits. The calculation of heritability and standard deviation are derived from the

average of the 6 bivariate analysis for each trait. An unstructured (co)variance structure was fitted for residual (co)variance. An unstructured genetic (co)variance were fitted as follows:

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} G\sigma_{u1}^2 & G\sigma_{u1,u2} \\ G\sigma_{u2,u1} & G\sigma_{u2}^2 \end{bmatrix}$$

where G is the genomic relationship matrix. Standard deviations were calculated for heritability and genetic correlations by repeated sampling of parameter estimates from the asymptotic multivariate normal distribution, based on methodology presented by Meyer and Houle (2013).

RESULTS AND DISCUSSION

Water intake levels

As shown in Table 5.3, group 4 cattle had the numerically lightest HCW, but it was not significantly different from group 5 ($P < 0.0001$, $P = 0.0035$, $P = 0.0003$, and $P = 0.4321$, for groups 1, 2, 3, and 5, respectively). The lighter HCW observed in group 4 and 5 cattle could be attributed to having the least DOF (35 and 45 d, respectively). Fewer days spent in the finishing phase can lead to lighter HCW, as reported by Zinn et al. (1970), Hicks et al. (1987), May et al. (1992), and Van Koevinger et al. (1995). Group 1 cattle had the highest HCW ($P < 0.0001$), followed by Group 3 ($P < 0.02$). Group 1 and 3 cattle had the most days on feed at 114 days and 110 days, respectively. Hot carcass weight results for low, medium, and high WI groups are presented in Table 5.4. For all groups, animals that were in the high WI group had heavier HCW than cattle with low WI (29.64 kg, $P = 0.0118$; 30.04 kg, $P = 0.0002$; 21.73 kg, $P = 0.0205$; 26.65 kg, $P = 0.0019$; 32.22 kg, $P = 0.0104$; and 37.91kg $P < 0.0001$; for group 1, 2, 3, 4, 5, and across all groups, respectively). For all groups except 1, 2 and 5, cattle with medium WI had heavier HCW than low WI

intake cattle (13.83 kg, $P = 0.0433$; 14.57 kg, $P = 0.0360$; and 22.99 kg $P < 0.0001$; for group 3, 4, and across all groups, respectively). Animals that consume less water tend to have lighter HCW. Because cattle are generally sold by the pound, cattle that have lighter HCW would potentially decrease profit potential for cattle sold on the rail.

There were no differences observed in REA, regardless of the WI level for any group or across all groups ($P > 0.05$). Despite the lack of significance noted for various WI levels, there are significant differences in REA between groups (Table 5.3). Group 4 animals had the smallest REA by a substantial margin (77.12 cm²) and group 1 cattle had the largest REA (104.16 cm²). Cattle from groups 2 and 5 had similar REA (92.89 cm² vs 90.08 cm²; $P = 0.1834$). Differences observed across groups could be attributed to differences in the amount of time that each of these groups spent on feed during the finishing phase. Van Koevering et al. (1995) showed that the number of days spent on feed did not alter REA size; however, Hicks et al. (1987), Williams et al. (1992), and May et al. (1992) reported that REA increased with increasing time on feed.

Group 5 cattle had the least BFAT (1.13 cm) and group 3 animals had the most BFAT (1.68 cm), as presented in Table 5.3. Similar BFAT was observed between groups 1 and 4 (1.40 cm vs 1.50 cm; $P = 0.6204$), 1 and 5 (1.40 cm vs 1.13 cm; $P = 0.1454$), 2 and 5 (1.17 cm vs 1.13 cm; $P = 0.7792$), and 3 and 4 (1.68 cm vs 1.50 cm; $P = 0.4851$). Based on these results, groups fed during the summer (groups 1, 3, and 4) did have differences in BFAT and groups fed during the winter (groups 2 and 5) had similar BFAT, despite large differences in breed composition (Ahlberg et al., 2018b). Previous studies (Hicks et al., 1987; Miller et al., 1987; May et al., 1992; Van Koevering et al., 1995) have reported that as the number of days on feed increases, BFAT will also increase; however, this study does

not seem to support this result. This could be attributed to cattle in different groups having different start weights. Groups 4 and 5 were the heaviest entering the trial period, thus they did not require as many days on feed to reach a desired end weight. Back fat results for low, medium, and high WI intake groups are presented in Table 5.4. No differences in BFAT were detected between low, medium, and high WI levels for any groups except for group 2. Group 2 low WI steers had less BFAT than medium (1.01 cm vs 1.23 cm; $P=0.0107$) or high (1.01 cm vs 1.29 cm; $P=0.0076$) WI levels, but cattle in the medium and high groups were not significantly different (1.23 cm vs 1.29 cm; $P=0.4995$). Cattle that consumed low or medium WI had less BFAT than high intake animals when all groups were combined (1.29 cm vs 1.49 cm, $P=0.0010$; and 1.35 cm vs 1.49 cm, $P=0.0211$, respectively). There were no differences in BFAT between low and medium intake groups when data was analyzed across all groups (1.29 cm vs 1.35 cm; $P=0.1630$).

Differences in marbling score between groups are presented in Table 5.3. Group 2 cattle had the numerically lowest MARB (427.51) and group 4 had the numerically highest MARB (550.48). Marbling scores between group 1 and 2 (437.68 vs 427.51 cm; $P=0.6289$) and between group 4 and 5 (550.48 vs 536.42; $P=0.3920$) were similar. Marbling score and the percent of animals that grade choice or higher generally increases with increased days on feed (Dolezal et al., 1982; Miller et al 1987; May et al., 1992). In the current study however, the cattle that were on feed the fewest days (group 4) had the highest marbling scores. This may be a result of the breed background of the steers, which all came from difference sources and genetic backgrounds (Ahlberg et al., 2018b). Gregory et al. (1994) reported that British breeds have higher MARB than continental cattle when killed at the same DOF. Group 4 steers had the highest marbling and group 5 steers had the second

highest marbling and contained the highest average percentage of British 86.5% (Ahlberg et al, 2018b). Group 2 cattle had the second highest average percentage of British ancestry (61.4%), but these steers also had the highest average percentage of *Bos indicus* ancestry (4.7%). Groups 4 and 5 had an average percentage of *Bos indicus* of 0.3% (Ahlberg et al., 2018b). Crouse et al. (1989) reported that *Bos indicus* influenced cattle had less MARB than *Bos taurus* cattle. Marbling results for low, medium, and high WI intake groups are presented in Table 5.4. No differences in MARB were detected between low, medium, and high WI levels except for group 4 and across all groups. Cattle from group 4 that consumed less water had lower MARB scores than cattle that had high WI (67.31, $P = 0.0115$; 65.32, $P = 0.0146$; for low vs high and medium vs high, respectively). For the analysis including data across all groups, medium WI animals had the least MARB and high intake animals had the most MARB (483.11 vs 500.63; $P = 0.0273$). The amount of marbling present in individual carcasses determines quality grade, and value-based marketing systems pay premiums for quality grades of Choice or better (Feuz, 1999). Cattle with a marbling score higher than 500 would have a USDA quality grade of choice or better. For groups 1-3, average marbling scores for each WI level did not exceed 500 (USDA quality grade of select). Group 4 and 5 had mean MARB above 500 for all WI levels which is an average quality grade of choice. Water consumption does not seem to have large phenotypic effects on marbling and would not impact cattle marketed on a value-based grid that pays premiums based on quality grades.

Group 1 animals had the lowest average YG (2.73) and group 4 had the highest mean YG (3.98), as presented in Table 5.3. Group 4 YG was significantly higher than all other groups (2.98 vs 2.72, $P < 0.0001$; 2.89, $P < 0.0001$; 3.09, $P < 0.0001$; 2.95, $P < 0.0001$;

for group 4 vs 1, 2, 3, and 5, respectively). Differences in YG were also observed between group 1 and group 3 (2.73 vs 3.09; $P=0.0010$). The breed composition of each animal and their genetic makeup could influence differences observed in YG. Cattle that have more British breed ancestry have higher YG than their continental counterparts (Wheeler et al., 2005). Cattle in all groups had varying percentages of British (49.3%, 61.4%, 55.0%, 54.0%, and 86.5%, for group 1, 2, 3, 4, and 5, respectively) and continental (40.1%, 29.4%, 33.6%, 42.0%, and 10.8%, for group 1, 2, 3, 4, and 5, respectively) germplasm (Ahlberg et al., 2018b). Water intake levels did not have an effect on YG for group 1, 4 and 5, as shown in Table 5.4. Low WI cattle from group 2 had lower YG compared to medium (2.69 vs 3.13; $P = 0.0046$) and high (2.69 vs 3.17, $P = 0.0119$) WI cattle. Group 3 cattle with high WI had higher YG than medium (3.63 vs 3.27; $P = 0.0400$) and low (3.63 vs 3.17 $P = 0.0243$) WI animals. Across all groups, low WI animals had lower YG than medium (2.98 vs 3.30; $P = 0.0433$) and high (2.98 vs 3.30; $P = 0.0004$) animals and medium intake animals had lower YG than high (3.11 vs 3.30; $P = 0.0399$) WI animals.

Weather cattle are marketed on a value-based grid or not, they are sold based on live weight, thus having heavier cattle will often generate greater revenue at sale time. Final body weights were different among the different groups ($P < 0.05$) with group 1 being the heaviest (729.57kg) and group 5 being the lightest (618.95 kg; Table 5.3). The ranking of groups with the heaviest to lightest FBW mirrors the number of days spent on feed during the finishing phase. The level of water consumed by cattle did impact their FBW as shown in Table 5.4. Low WI animals were the lightest and high WI animals were the heaviest within all groups and across all groups. For groups 4 and 5 as well as across all groups, low WI animals were lighter than medium intake animals. Medium WI cattle from

groups 1 and 5 as well as across all groups had lighter FBW than high intake animals. Low WI cattle within all groups as well as across all groups had lighter FBW than high intake animals. Cattle with high WI have heavier FBW, thus would be expected to generate more income if sold by the pound than low WI cattle.

Phenotypic correlations

Pearson and Spearman correlations are presented in Table 5.5. Water intake has a weak, positive Pearson correlation with HCW (0.171), BFAT (0.223), MARB (0.177), YG (0.223), and FBW (0.180). The Spearman correlations are similar to the Pearson correlations (0.202, 0.247, 0.136, 0.207, and 0.225 for HCW, BFAT, MARB, YG, and FBW, respectively). Water intake and REA are uncorrelated (Pearson $P = 0.5724$ and Spearman $P = 0.6590$). Figure 5.1 illustrates the weak linear relationships that exist between WI and HCW ($R^2 = 0.032$), REA ($R^2 = 0.0003$), BFAT ($R^2 = 0.0507$), MARB ($R^2 = 0.0295$), YG ($R^2 = 0.05$), and FBW ($R^2 = 0.032$). Although there are multiple phenotypic correlations between WI and carcass traits that are significantly different from zero, the values are small, indicating that the amount of water cattle consume has minimal relationship to carcass performance.

The phenotypic correlations between some of the carcass traits are much higher, as shown in Table 5.5. Hot carcass weight has a high, positive Pearson correlation with FBW (0.753), moderate correlation with REA (0.491), and weak correlation with BFAT (0.176) and YG (0.133). Spearman correlations were lower than the corresponding Pearson correlations between HCW and REA (0.451) as well as between HCW and FBW (0.744), but were higher between HCW and BFAT (0.17) as well as between HCW and YG (0.159). Hot carcass weight and FBW would be expected to have a high positive correlation because

HCW is a function of FBW ($FBW \times \text{dressing percentage} = HCW$). However, out of the four component traits for YG, HCW has the lowest weighting in the prediction equation (Lamb et al., 1990). Similar phenotypic correlations between HCW and REA were reported by Cundiff et al. (0.46; 1964) and larger correlations of 0.579, and 0.53 were reported by Lamb et al. (1990) and Devitt and Wilton (2001), respectively. Spearman correlations indicate the amount of reranking between individuals. Correlations between HCW and BFAT were observed to be 0.176 and 0.179 (Pearson and Spearman, respectively), which is stronger than the Pearson correlations of 0.095, -0.007, and -0.004 reported by Lamb et al. (1990), Cundiff et al. (1964), and Devitt and Wilton (2001), respectively. In the current study, a slightly stronger relationship is observed between HCW and BFAT, thus as carcass weights increase, they are depositing more fat. Small negative Pearson and Spearman correlations were observed between HCW and MARB (-0.076; $P = 0.1164$ and -0.101; $P = 0.0354$, respectively). Both Lamb et al. (1990) and Devitt and Wilton (2001) reported positive phenotypic correlations between HCW and MARB (0.190 and 0.15, respectively), which is in contrast to our results. Final body weight has moderate, positive Pearson and Spearman correlations with REA (0.358 and 0.348, respectively) and weak negative Pearson and Spearman correlations with MARB (-0.167 and -0.180, respectively). As cattle reach heavier FBW they will tend to have a larger REA and less MARB. Marbling is measured as the amount of intramuscular fat present at the in the *longissimus* muscle area; thus, as REA increases the amount of intramuscular fat in relation to REA tends to decrease. Pearson and Spearman correlations were not significantly different from zero for BFAT and FBW (0.090; $P = 0.0598$ and 0.079; $P = 0.0992$) and YG and HCW (0.085; $P = 0.0631$ and 0.076; $P = 0.0942$). Due to the weak positive phenotypic correlation between

HCW and BFAT, a similar relationship would be expected between FBW and BFAT, considering HCW is a function of FBW.

USDA Yield grade is comprised of four components traits including BFAT, REA, percent kidney-pelvic-heart fat (%KPH), and HCW (Lamb et al., 1990). BFAT, %KPH, and HCW increase YG (less favorable) and REA decreases YG (more favorable). High, negative Pearson and Spearman correlations were reported between YG and REA (-0.638 and -0.593) and strong, positive Pearson and Spearman correlations were reported between YG and BFAT (0.822 and 0.819). Lamb et al. (1990) reported a phenotypic correlation between BFAT and YG of 0.276, which is substantially lower than the value observed in the current study. Rib eye are would be expected to have a high, negative correlation with YG because it is one of four traits that are used by USDA to estimate cutability (Koch et al., 1982). The strong phenotypic correlations between BFAT and YG as well as REA and YG would indicate that BFAT and REA would be good predictors of YG.

Back fat has a positive Pearson and Spearman correlation with MARB (0.367 and 0.383) and negative Pearson and Spearman correlation with REA (-0.229 and -0.216). Lamb et al. (1990) reported a weak phenotypic correlation of 0.095 between REA and BFAT, which is lower in magnitude and has different directionality from the current study. The current study would suggest that fatter cattle have smaller REA, whereas Lamb et al. (1990) demonstrated that as cattle become fatter, they also have a larger REA. Lamb et al. (1990) reported similar phenotypic correlations between MARB and BFAT (0.250). Marbling has a positive Pearson and Spearman correlation with YG (0.230 and 0.219). There is an antagonistic relationship between MARB and YG; thus, as cattle have more marbling they are also going to have higher YG. Marbling has a moderate positive Pearson

and Spearman correlation with REA (0.397 and 0.493). Devitt and Wilton (2001) reported that REA and MARB are uncorrelated (0.04), whereas Lamb et al. (2001) reported a weak, positive correlation between REA and MARB (0.19) which is lower than the current study.

Genetic Parameters

Heritability estimates are presented in the diagonal elements of Table 5.6 for all traits. Water intake had a heritability of 0.42 (SE), which is similar to the estimate of 0.39 ± 0.17 in Ahlberg et al. (2018b). It should be noted that these two estimates are not independent and was generated using the same animals, but with bivariate analyses including different traits. The only other estimates of WI heritability have been in mice. Bachmanov et al. (2002) utilized 28 different strains of mice (12 individuals from each strain), which were housed individually in plastic cages. Water intakes were measured daily for 4 days and heritability was calculated by taking the sums of squares among strains divided by sums of square total to obtain a heritability estimate of 0.69 (Bachmanov et al., 2002). Ramirez and Fuller (1976) utilized daily WI measured over 10 days on heterogeneous mice, fully inbred mice, and partially inbred mice that were housed in individual cages to obtain a heritability estimate of 0.44. The moderate heritability estimate for WI demonstrates that selection on WI would be effective.

Hot carcass weight had a low to moderate heritability estimate of 0.31 ± 0.15 , which is similar to estimates found by Koots et al. (1994), Marshall (1994), Shanks (1999), Shanks et al., (2001), Wheeler et al. (2010). However, larger estimates of 0.57, 0.61, 0.48 and 0.51 reported by Smith et al. (2007), Nogi et al. (2011), Kause et al. (2015) and Su et al. (2017). The moderate heritability indicates that HCW would respond to selection. Koch et al. (1982) estimated heritability in carcass weight using crossbred cattle that had similar

breed backgrounds to the steers utilized in the current study. In their study, 14 out of the 16 breeds that were utilized to estimate breed composition were included in the analysis and they reported a higher heritability estimate than the current study (0.43). In the current study, crossbred animals with ancestry from a variety of breeds were utilized, whereas Koch et al. (1982) utilized crossbred calves produced by mating purebred sires of each particular breed mated to Angus or Hereford cows. Gregory et al. (1995) reported heritability estimates of carcass weight for both purebred (0.20) and crossbred cattle (0.34).

Rib eye area had a heritability estimate of 0.27 ± 0.16 , which indicates that REA is moderately heritable. Similar heritability estimates for REA have been reported by Koch et al. (1978), Lamb et al. (1990), Morris et al. (1990), Shanks et al. (2001), Smith et al. (2007), Wheeler et al. (2010), Nogi et al. (2011), and Su et al. (2017), although both higher and lower estimates have been reported in various studies reviewed by Utrera and Van Vleck (2004). Reynolds et al. (1991) reported the lowest heritability estimate of 0.01 and Pariacote et al. (1998) had the highest estimate at 0.97. The minimal estimate reported by Reynolds et al. (1991) was in Hereford bulls and a son-sire regression analysis was used to obtain the heritability estimate. The near perfect heritability estimate reported in Pariacote et al. (1998) was obtained using a restricted maximum likelihood (REML) analysis of Shorthorn steers. Koch et al. (1982) reported a heritability estimate of 0.56 in crossbred steers using a mixed model equation. Rib eye area heritability estimates of 0.17 (purebred animals) and 0.35 (crossbred animals) were reported by Gregory et al. (1995), which were based on a sire model.

The heritability estimate obtained for BFAT (0.71 ± 0.21) was higher than previous estimates that ranged from 0.30 to 0.57 (Utrera and Van Vleck (2004) but was lower than

the highest reported heritability estimate in the literature (0.94; Dunn et al., 1970). Su et al. (2017) reported heritability estimates for BFAT in Simmental (0.25) and Hereford (0.41). The heritability estimate for BFAT in the current study is higher than most other studies; however, it is associated with a large standard deviation. The high estimate reported by Dunn et al. (1970) was reported in crossbred steers that were composed of three different breeds: Angus, Hereford and Shorthorn. Gregory et al. (1995) reported much lower heritability estimates of 0.20 in purebred animals and 0.39 in crossbred animals. Koch et al. (1982) reported a moderate heritability estimate of 0.41. A heritability estimate of 0.84 was reported by Wheeler et al. (2001) for *Bos indicus* cross animals, which is higher than the current study.

Marbling had a low heritability estimate of 0.26 and had a large standard deviation (0.16). Higher heritability estimates were reported by Smith et al. (2007), Wheeler et al. (2010), McAllister et al. (2011), Miar et al. (2014) and Su et al. (2017). Lee et al. (2000) showed that the choice of covariate (back fat thickness, slaughter age, or slaughter weight) used can have an effect on the heritability estimates for marbling. Low heritability estimates reported by Lee et al. (2000) could be attributed to the small number of records. Previous literature estimates for MARB adjusted to a constant age range from 0.08 (Lee et al., 2000) to 0.88 (Pariacote et al., 1998) with the average being 0.45 (Utrera and Van Vleck 2004). Gregory et al. (1995) reported a higher heritability estimates for crossbred animals (0.55) than purebred animals (0.45); however, both estimates were higher than the current study. A moderate heritability estimate of 0.40 for MARB was reported by Koch et al. (1982).

Yield grade was estimated to have high heritability at 0.53 ± 0.16 . Unlike the other carcass traits that have been extensively studied, there are fewer estimates of YG presented in the literature, possibly because it is a linear function of several other carcass metrics. Heritability estimates for YG in the literature include 0.24, 0.76, 0.54, 0.85 and 0.46, as reported by Lamb et al. (1990), Wheeler et al. (1996), Pariacote et al. (1998), Wheeler et al. (2001), and Smith et al. (2007), respectively. The current study's estimate is similar to Pariacote et al. (1998), but higher than Lamb et al. (1990) and lower than Wheeler et al. (1996) and Wheeler et al. (2001).

Final body weight had a high heritability of 0.58 ± 0.17 . Similar to YG, few previous studies have estimated heritability for final body weight. Lower heritability estimates were reported for purebred cattle (0.26) and crossbred cattle (0.37) by Gregory et al (1995). Lamb et al. (1990) reported moderate heritability estimates of 0.41 in Hereford-sired progeny.

Genetic correlations are presented in the off-diagonal elements of Table 5.6. Water intake has positive, low to moderate genetic correlations with HCW (0.38), BFAT (0.36), YG (0.29), and FBW (0.29). Water intake is lowly correlated with REA (0.08) and MARB (0.17). Selecting to decrease water consumption in cattle will result in decreased HCW, BFAT, YG, FBW, REA, and MARB, although decreases in REA and MARB would be smaller in relative magnitude. Decreased YG would be beneficial for producers as lower YG and less BFAT is more desirable. However, genetic antagonisms exist with WI and HCW, FBW, and MARB. Selection indices can be formed to minimize the effect of these antagonisms (VanRaden, 2004), but the correlations would slow progress in breeding objectives. The key to the selection index being successful is to make sure the right

economic weights are assigned to each trait (VanRaden, 2004). When selecting for more than one trait, the use of a selection index is more efficient than selecting for one trait at a time (Hazel, 1943). Therefore, designing a selection index where each trait receives attention proportional to its net economic value given a specific breeding objective (Hazel, 1943) would be beneficial.

Hot carcass weight has a moderate genetic correlation with REA (0.45), which is intermediate to other estimates documented in the literature (0.66, Cundiff et al., 1964; 0.678, Lamb et al., 1990; 0.42, Devitt and Wilton 2001; 0.51, Su et al., 2017). Rib eye area is expected to have a strong positive correlation with HCW because REA is an indicator of carcass muscling, which is a factor in total carcass weight (Devitt and Wilton, 2001). A moderate, positive genetic correlation was observed between HCW and BFAT (0.42) which is higher than all other literature estimates (0.15, Devitt and Wilton, 2001; 0.283, Lamb et al., 1990; 0.15, Cundiff et al., 1964; -0.06, Wilson et al., 1993; -0.05, Moser et al., 1997; 0.08, Su et al., 2014). Our data would suggest that selecting for increased HCW would also increase carcass fatness, which may be a result of differences in days on feed in our study, as animals were not fed to a constant endpoint. The negative genetic correlations reported by Wilson et al. (1993) and Moser et al. (1997) would suggest that selection to increase HCW would decrease the amount of fat on the animals. However, the correlations noted in these analyses are small, so minimal changes in BFAT would be expected. Hot carcass weight had a moderate genetic correlation with MARB (0.46), which was slightly lower than the 0.56 reported by Lamb et al. (1990). However, Devitt and Wilton (2001) reported a negative genetic correlation of -0.32 between HCW and MARB. Differences between the current study and previous literature estimates could be due to the

end point measurements adjustments. Differences also could be attributed to genetic type and admixture within the population. Crossbred animals estimates can be influenced by breed effects. Crossbred animals composed of a breed known for producing heavier HCW mated to a breed known for added marbling could result in cattle that have the genetic potential for heavier carcasses and more marbling. Yield grade had a moderate, positive genetic correlation with HCW (0.36) and FBW is completely correlated with HCW (1.0). Selecting to increase HCW would also result in increased YG, as HCW is a component of the USDA YG calculation. The perfect genetic correlation between HCW and FBW was unsurprising, as HCW is a percentage of FBW for each animal.

Hot carcass weight had moderate to high genetic correlations with the other carcass traits, most of which are favorable (REA, MARB and FBW). Whether cattle are marketed on a value-based grid or by weight, the total value of the carcass is based on a price per pound. However, there is a limit to the size of carcasses that are desirable or can be handled by packing plants. A balance between all carcass traits must be achieved to produce carcasses that are both profitable for beef producers and desired by consumers.

Rib eye area was positively correlated with FBW (0.86). Similar to the relationship between HCW and REA, REA would be expected to have a high, positive correlation with FBW because REA is an indicator of muscling, and the amount of muscle an animal has is strongly associated with their total weight (Devitt and Wilton, 2001). Final body weight has a positive and moderate genetic correlation with BFAT (0.27) and YG (0.32) and a strong positive genetic correlation with MARB (0.58). Cattle with heavier FBW would most likely spend more days on feed and have more time to deposit fat (Zinn et al., 1970).

Yield grade had a negative genetic correlation with REA (-0.44), but was positively correlated with BFAT (0.85). Genetic correlations between REA and YG from Koch et al. (0.53; 1982) are different from the relationship noted in this study and also contradict the negative relationship between REA and YG that would be expected based on the YG prediction equation. Back fat has a high, positive genetic correlation with YG in this study (0.85). Koch et al. (1982) reported a strong negative genetic correlation between BFAT and percent retail product (-0.74), which is contradictory to the results obtained in this population. Percent retail product and YG are both measures of cutability in beef cattle (Abraham et al., 1980). Lamb et al. (1990) also reported a positive genetic correlation, but it was a much weaker relationship (0.184). Back fat thickness is another trait that is used to calculate USDA YG, so it would be expected to have a high correlation with YG because in the calculation as BFAT has an unfavorable, positive impact on YG. Due to the high genetic correlation between BFAT and YG, it would be expected that BFAT would be a useful predictor of YG (Koch et al., 1982).

REA had a negative genetic correlation with BFAT (-0.38) and MARB (-0.13). Heavier muscled cattle that are faster growing have less total body fat (Devitt and Wilton, 2001), which is consistent with our results. Su et al. (2017) also reported a negative genetic correlation between REA and BFAT (-0.23). However, a positive genetic correlation was reported between REA and BFAT by Lamb et al. (0.128; 1990). Lamb et al. (1990) also reported a high, positive genetic correlation with MARB (0.57), whereas Devitt and Wilton (2001) reported a moderate, negative correlation (-0.37) between REA and MARB and Su et al. (2017) reported a low negative correlation (-0.27). Our results indicated that a minimal unfavorable relationship exists between REA and MARB, which is most similar to the

results for Devitt and Wilton (2001). As REA increases, the amount of marbling also has to increase at the same or greater rate to maintain or improve the marbling score, compared to animals with smaller REA and the same volume of intramuscular fat (Shiranita et al., 2000). Because cattle with higher quality grades (higher MARB) are more desirable for consumers (Feuz, 1999), cattle are selected for higher MARB.

A moderate, negative genetic correlation was observed between BFAT and MARB (-0.29), as well as between MARB and YG (-0.27). Selecting animals for increased MARB would result in leaner animals with lower (more desirable) YG. Lamb et al. (1990) and Su et al. (2017) reported positive genetic correlations that was similar in magnitude between MARB and YG (0.32 and 0.22, respectively). Lamb et al. (2001) and Koch et al. (1982) reported positive genetic correlations between BFAT and MARB that were of similar magnitude (0.227 and 0.24, respectively), whereas Dunn et al. (1970) reported a genetic correlation of 1 between BFAT and MARB. Back fat is a measure of subcutaneous fat and MARB is a measure of intramuscular fat. As both traits are related to fat deposition, a positive undesirable genetic correlation between BFAT and MARB would be expected. Growing cattle first deposit intermuscular (seam fat) and subcutaneous fat and then start to deposit intramuscular fat (Hood, 1982). In the current study, cattle may still deposit more intermuscular and subcutaneous fat than intramuscular fat depending on where cattle were in their growth curve.

Positive genetic correlations exist between all traits except between REA and BFAT, MARB, and YG and between MARB and YG. The strength of genetic correlations vary depending on the traits and antagonisms exist between WI and YG, MARB and YG and HCW and YG. These antagonists can be overcome by using selection indices. Multi-

trait selection can be practiced by producers to simultaneously improve multiple carcass traits and WI.

CONCLUSION

It is important to produce a desirable beef product for consumers, but we must do so while efficiently using natural resources. The linear relationships between WI and carcass traits were minimal with R^2 values ranging from 0.0003 (WI and REA) to 0.0507 (WI and BFAT). Low, positive Pearson and Spearman correlations were observed between WI and HCW, BFAT, MARB, YG, and FBW. Pearson and Spearman correlations between WI and REA were not significantly different from zero.

Hot carcass weight, REA, and MARB were estimated to be moderately heritable traits (0.31, 0.27, and 0.26, respectively). Water intake was moderately heritable (0.42) and BFAT, YG, and FBW were highly heritable with estimates of 0.71, 0.53, and 0.58 respectively. Heritability for carcass traits ranged from 0.26 (MARB) to 0.71 (BFAT) and were within the ranges of previous literature estimates.

Genetic antagonisms exist between HCW and YG, REA and BFAT, REA and MARB, BFAT and MARB, and BFAT and YG (genetic correlations of 0.36, -0.38, -0.13, -0.29, 0.85, respectively). All other genetic correlations between carcass traits were favorable. Because of the noted antagonisms, using an economic index to practice multi-trait selection and make improvements in carcass performance is ideal and has already been effectively implemented in the beef industry.

Water intake genetic correlations with carcass traits included in this analysis were low and positive (HCW 0.38, REA 0.08, BFAT 0.36, MARB 0.17, YG 0.29, and FBW 0.29). Due to the low genetic correlations between WI and carcass traits, impact should be

minimal and easy to address. There are genetic antagonisms present between WI and most of the carcass traits, except for WI and YG and WI and BFAT. Due to these antagonisms, selection for WI should incorporate a selection index to avoid antagonisms with carcass quality and yield.

REFERENCES

- Abraham, H. C., C. E. Murphey, H. R. Cross, G. C. Smith, and W. J. Franks, Jr. 1980. Factors Affecting Beef Carcass Cutability: an Evaluation of the USDA Yield Grades for Beef. *J. Anim. Sci.* doi:10.2527/jas1980.505841x
- Ahlberg, C. M., K. Allwardt, A. Broocks, K. Bruno, A. Taylor, L. McPhillips, C. R. Krehbiel, M. Calvo-Lorenzo, C. J. Richards, S. E. Place, U. DeSilva, D. L. VanOverbeke, R. G. Mateescu, L. A. Kuehn, R. Weaber, J. Bormann, and M. M. Rolf. 2018a. Test duration for water intake, average daily gain, and dry matter intake in beef cattle. *J. Anim. Sci.* under review
- Ahlberg, C. M., K. Allwardt, A. Broocks, K. Bruno, A. Taylor, L. McPhillips, C.R. Krehbiel, M. Calvo-Lorenzo, C.J. Richards, S.E. Place, U. DeSilva, D.L. VanOverbeke, R.G. Mateescu, L. A. Kuehn, R. Weaber, J. Bormann, and M.M. Rolf. 2018b. Characterization of water intake and water efficiency in beef cattle. *J. Anim. Sci.*
- Allwardt, K., C. Ahlberg, A. Broocks, K. Bruno, A. Taylor, S. Place, C. Krehbiel, C. Richards, M. Calvo-Lorenzo, U. DeSilva, D. VanOverbeke, R. Mateescu, C. Goad, and M. Rolf. 2017. Technical note: Validation of an automated system for monitoring animal intake in group-housed beef steers. *J. Anim. Sci.* 95:4213-4219. doi: 10.2527/jas.2017.1593
- Aguilar, I., I. Misztal, A. Legarra, and S. Tsuruta. 2011. Efficient computation of the genomic relationship matrix and other matrices used in single-step evaluation. *J. Anim. Breed. Genet.* 128:422-428. doi:10.1111/j.1439-0388.2012.00991.x

- Bachmanov, A. A., D. R. Reed, G. K. Beauchamp, and M. G. Todoff. 2002. Food intake, water intake, and drinking spout side preference of 28 mouse strains. *Behav. Genet.* 32:435-443. doi:10.1023/A:1020884312053
- Chiang, C. W. K., Z. K. Z. Gajdos, J. M. Korn, F. G. Kuruvilla, J. L. Butler, R. Hackett, C. Guiducci, T. T. Nguyen, R. Wilks, T. Forrester, C. A. Haiman, K. D. Henderson, L. Le Marchand, B. E. Henderson, M. R. Palmert, C. A. McKenzie, H. N. Lyon, R. S. Cooper, X. Zhu, and J. N. Hirschhorn. 2010. Rapid assessment of genetic ancestry in populations of unknown origin by genome-wide genotyping of pooled samples. *PLoS Genet.* 6:e1000866. doi:10.1371/journal.pgen.1000866
- Crouse, J. D., L. V. Cundiff, R. M. Koch, M. Koohmaraie, and S. C. Seideman. 1989. Comparisons of *Bos indicus* and *Bos taurus* inheritance for carcass beef characteristics and meet palatability 1, 2, 3 . *J. Anim. Sci.* 67:2661-2668. doi:10.2527/jas1989.67102661
- Cundiff, L. V., D. Chambers, D. F. Stephens, and R. L. Willham. 1964. Genetic analysis of some growth and carcass traits in beef cattle. *J. Anim. Sci.* 23:1133-1138. doi:10.2527/jas1964.2341133x
- De Haer, L. C. M. De Haer, and A. G. de Vries. 1993. Feed intake patterns and feed digestibility in growing pigs housed individually or in groups. *Livest. Prod. Sci.* 33:277-292. doi:10.1016/0301-6226(93)90008-6
- Divitt, C. J. B., and J. W. Wilton. 2001. Genetic correlation estimates between ultrasound measurements on yearling bulls and carcass measurements on finished steers. *J. Anim. Sci.* doi:10.2527/2001.79112790x

- Dolezal, H. G., G. C. Smith, J. W. Savell, and Z. L. Carpenter. 1982. Effect of time-on feed on palatability of rib steaks from steers and heifers. *J. Food. Sci.* 47:368-373. doi:10.1111/j.1365-2621.1982.tb10083.x
- Dunn, R. J., W. T. Magee, K. E. Gregory, L. V. Cundiff, and R. M. Koch. 1970. Genetic parameters in straightbred and crossbred beef cattle. *J. Anim. Sci.* 31:656–663. doi:10.2527/jas1970.314656x
- Feuz, D. 1999. Market signals in value-based pricing premiums and discounts. *J. Agric. Resource Exon.* 24:327-341. Retrieved from <http://www.jstor.org/stable/40987026>
- Friend, T. H., C. E. Polen, and M. L. McGilliard. 1977. Free stall and feed bunk requirements relative to behavior, production and individual feed intake in dairy cows. *J. Dairy. Sci.* 60:108-116. doi:10.3168/jds.S0022-0302(77)83835-6
- Gregory, K. E., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and M. Koohmaraie. 1994. Breed effects, retained heterosis, and estimates of genetic and phenotypic parameters for carcass and meat traits of beef cattle. *J. Anim. Sci.* 72:1174–1183. doi:10.2527/1994.7251174x
- Hazel, L. N. 1943. The genetic basis for constructing selection indexes. *Genetics.* 28:476-490
- Hicks, R. B., F. N. Owens, D. R. Gill, J. J. Martin, H. G. Dolezal, F. K. Ray, V. S. Hays, and C. A. Strasia. 1987. The effect of slaughter date on carcass gain and carcass characteristics of feedlot steers. *Oklahoma Agric. Exp. Sta. Res. Rep.* MP-119:351
- Hood, R. L. 1982. Relationship among growth, adipose cell size, and lipid metabolism in ruminant adipose tissue. *Federation Proceedings*, 41, 2555–2561.

- Kause, A., L. Mikkola, I. Strandén, and K. Sirkko. 2015. Genetic parameters for carcass weight, conformation and fat in five beef cattle breeds. *Animal* 9:35–42.
doi:10.1017/S1751731114001992
- Koch, R. M. 1978. Selection in beef cattle III. Correlated response of carcass traits to selection for weaning weight, yearling weight and muscling score in cattle. *J. Anim. Sci.* 47:142–150. doi:10.2527/jas1978.471142x
- Koch, R. M. L. V. Cundiff, and K. E. Gregory. 1982. Heritabilities and genetic, environmental and phenotypic correlations of carcass traits in a population of diverse biological types and their implications in selection programs. *J. Anim. Sci.* 55:1319–1329. doi:10.2527/jas1982.5561319x
- Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994. Analyses of published genetic parameter estimates for beef traits. 2. Phenotypic and genetic correlations. *Anim. Breed.* 62:825-853
- Kuehn, L. A., J. W. Keele, G. L. Bennett, T. G. McDanel, T. P. L. Smith, W. M. Snelling, T. S. Sonstegard, and R. M. Thallman. 2011. Predicting breed composition using breed frequencies of 50,000 markers from the US Meat Animal Research Center 2,000 Bull Project. *J. Anim. Sci.* 89:1742-1750. doi:10.2527/jas.2010-3530
- Lamb, M. A., O. W. Robison, and M. W. Tess. 1990. Genetic parameters for carcass traits in Hereford bulls. *J. Anim. Sci.* 68:64–69. doi:10.1093/ansci/68.1.64
- Lee, J. W., S. B. Choi, J. S. Kim, J. F. Keown, and L.D. Van Vleck. 2000. Parameter estimates for genetic effects on carcass traits of Korean native cattle. *J. Anim. Sci.* 78: 1181-1190

- May, S., H. G. Dolezal, D. R. Gill, F. K. Ray, and D. S. Buchanan. 1992. Effect of days feed, carcass grade traits, and subcutaneous fat removal on postmortem muscle characteristics and beef palatability. *J. Anim. Sci.* 70:444-453. doi:10.2527/1992.702444x
- Marshall, D. M. 1994. Breed differences and genetic parameters for body composition traits in beef cattle. *J. Anim. Sci.* 72:2745-2755. doi:10.2527/1994.72102745x
- McAllister, C., S. Speidel, D. Crews, and R. Enns. 2011. Genetic parameters for intramuscular fat percentage, marbling score, scrotal circumference, and heifer pregnancy in Red Angus cattle. *J. Anim. Sci.* 89:2068–2072. doi:10.2527/jas.2010-3538
- Meyer, K., and D. Houle. 2013. Sampling based approximation of confidence intervals for functions of genetic covariance matrices. *Proc. Assoc. Advmt. Anim. Breed. Genet.* 20: 523–526. Available at: <http://www.aaabg.org/aaabghome/AAABG20papers/meyer20523.pdf>
- Miar, Y., G. Plastow, H. Bruce, S. Moore, O. Durunna, J. Nkrumah, and Z. Wang. 2014. Estimation of genetic and phenotypic parameters for ultrasound and carcass merit traits in crossbred beef cattle. *Can. J. Anim. Sci.* 94:273–280. doi:10.4141/cjas2013-115
- Miller, R. K., H. R. Cross, J. D. Crouse, and J. D. Tatum. 1987. The influence of diet and time on feed on carcass traits and quality. *Meat Sci.* 19:303-313. doi:10.1016/0309-1740(87)90077-5
- Misztal, I., S. Tsuruta, D. A. L. Lourenco, I. Aguilar, A. Lagarra, and Z. Vitezica. 2014. Manual for BLUPF90family of programs.

http://nce.ads.uga.edu/wiki/lib/exe/fetch.php?media=blupf90_all1.pdf. (Accessed 4 January 2018.)

- Morris, C. A., R. Baker, A. Carter, and S. Hickey. 1990. Evaluation of eleven cattle breeds for crossbred beef production: Carcass data from males slaughtered at two ages. *Anim. Prod.* 50:79-92. doi:10.1017/S0003356100004487
- Moser, D. W., J. K. Bertrand, I. Misztal, L. A. Kriese, and L. L. Benyshek. 1998. Genetic parameter estimates for carcass and yearling ultrasound measurements in Brangus cattle. *J. Anim. Sci* 76:2542–2548. doi:10.2527/1998.76102542x
- Nephawe, K. A., L. V. Cundiff, M. E. Dikeman, J. D. Crouse, L. D. Van Vleck. 2004. Genetic relationships between sex-specific traits in beef cattle: Mature weight, weight adjusted for body condition score, height and body condition score of cows, and carcass traits of their steer relatives. *J. Anim. Sci.* 82:647–653. doi:10.1093/ansci/82.3.647
- Nogi, T., T. Honda, F. Mukai, T. Okagaki, and K. Oyama. 2011. Heritabilities and genetic correlations of fatty acid compositions in longissimus muscle lipid with carcass traits in Japanese Black cattle. *J. Anim. Sci.* 89:615-621. doi:10.2527/jas2009-2300
- Pariacote, F., L. D. Van Vleck, R. E. Hunsley. 1998. Genetic and phenotypic parameters for carcass traits of American Shorthorn beef cattle. *J. Anim. Sci.* 76:2584–2588. doi:10.2527/1998.76102584x
- Ramirez, I. and J. L. Fuller. 1976. Genetic influence on water and sweetened water consumption in mice. *Physiol. Behav.* 16:163-168. doi:10.1016/0031-9384(76)90300-0

- Reynolds, W. L., J. J. Urick, D. A. Veseth, D. D. Kress, T. C. Nelsen, and R. E. Short. 1991. Genetic parameters by son-sire covariances for growth and carcass traits of Hereford bulls in a nonselected herd. *J. Anim. Sci.* 69:1000–1007. doi:10.2527/1991.6931000x
- Shanks, B. C. 1999. The effect of slaughter end-points on carcass trait parameter estimates and subsequent EPD. In Proc. 31st. Beef Improvement Federation Res. Symp. and Annu. Mtg., Roanoke, VA. Pp 226-245
- Shanks, B. C., M. W. Tess, D. D. Kress, and B. E. Cunningham. 2001. Genetic evaluation of carcass traits in Simmental-sired cattle at different slaughter end points. *J. Anim. Sci.* 79:595–604. doi:10.2527/2001.793595x
- Shiranita, K., K. Hayashi, A. Otsubo, T. Miyajima, and R. Takiyama. 2000. Grading meat quality by image processing. *Pattern. Recognition.* 33:97-104. doi: 10.1016/S0031-3203(99)00035-7
- Smith, T., J. D. Domingue, J. C. Paschal, D. E. Franke, T. D. Bidner, and G. Whipple. 2007. Genetic parameters for growth and carcass traits of Brahman steers. *J. Anim. Sci.* 85:1377-1384
- Su, H., B. Golden, L. Hyde, S. Sanders, and D. Garrick. 2017. Genetic parameters for carcass and ultrasound traits in Hereford and admixed Simmental beef cattle: Accuracy of evaluating carcass traits. *J. Anim. Sci.* 95:4718-4727. doi:10.2527/jas2017.1865
- Utrera, A. R., and L. D. Van Vleck. 2004. Heritability estimates for carcass traits of cattle: a review. *Genet. Molec. Resear.* 3:380-394

- Van Koeving, M. T. D. R. Gill, F. N. Owens, H. G Dolezal, and C. A. Strasia. 1995. Effect of time on feed on performance of feedlot steers, carcass characteristics, and tenderness, and composition of longissimus muscles. *J. Anim. Sci.* 73:21-28. doi: 10.2527/1995.73121x
- VanRaden, P. M. 2004. Invited Review: Selection on net merit to improve lifetime profit. *J. Dairy. Sci.* doi:10.3168/jds.S0022-0302(04)73447-5
- VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. *J. Dairy. Sci.* 91:4414-4423. doi:10.3168/jds.2007-0980
- Wheeler, T. L., L. V. Cundiff, R. M. Koch, J. D. Crouse. 1996. Characterization of biological types of cattle (Cycle IV): carcass traits and longissimus palatability. *J. Anim. Sci.* 74:1023–1035. doi.10.2527/1996.7451023x
- Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2001. Characterization of biological types of cattle (Cycle V): Carcass traits and longissimus palatability. *J. Anim. Sci.* 79:1209–1222. doi.10.2527/2001.7951209x
- Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2005. Characterization of biological types of cattle (Cycle VIII): Carcass, yield, and longissimus palatability. *J. Anim. Sci.* 83:196-207. doi: 10.2527/2005.831196x
- Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2010. Characterization of biological types of cattle (Cycle VII): Carcass, yield, and longissimus palatability. *J. Anim. Sci.* 88:3070-3083. doi: 10.2527/jas.2009-2497

- Wilson, D. E., R. L. Willham, S. L. Northcutt, G. H. Rouse. 1993. Genetic parameters for carcass traits estimated from Angus field records. *J. Anim. Sci.* 71:2365–2370. doi:10.2527/1993.7192365x
- Wilson, L. L., J. M. Stout, J. H. Ziegler, M. J. Simpson, H. Varela-Alvarez, M. C. Rugh, and J. L. Watkins. 1971. Heritability of live and carcass characters in a crossbred beef herd. *J. Hered.* 62:123-125.
- Zinn, D. W., R. M. Durham, and H. B. Hedrick. 1970. Feedlot and carcass grade characteristics of steers and heifers as influenced by days on feed. *J. Anim. Sci.* 31:302-306. doi:10.2527/jas1970.312302x

Table 5.1 Harvest location, number of head (n), and days on finishing ration (DOF) for each group.

Group	Plant	n	DOF^a	Location
1	FAPC ^b	5	85	Stillwater, OK
	Creekstone Farms	48	106	Arkansas City, KS
	Tyson Fresh Meats	8	106	Amarillo, TX,
	FAPC ^b	6	115	Stillwater, OK
	Tyson Fresh Meats	42	127	Amarillo, TX,
	FAPC ^b	3	130	Stillwater, OK
	Average		114	
2	Tyson Fresh Meats	28	70	Garden City, KS
	Tyson Fresh Meats	26	91	Amarillo, TX,
	Creekstone Farms	57	93	Arkansas City, KS
	Average		87	
3	Creekstone Farms	45	79	Arkansas City, KS
	Tyson Fresh Meats	27	130	Amarillo, TX,
	Creekstone Farms	32	133	Arkansas City, KS
	Average		110	
4	Cargill Meat Solutions	105	37	Dodge City, KS
5	Creekstone Farms	123	45	Arkansas City, KS

^aThe number of days after the water intake trial period that cattle were fed a finishing diet (including acclimation diets)

^bFood and Agricultural Products Center

Table 5.2 Summary statistics for hot carcass weight (HCW), rib eye area (REA), back fat (BFAT), marbling (MARB), yield grade (YG), and final body weight (FBW) for each group.

Group	Trait	N	Mean	STD	Min	Max
1	HCW, kg	111	431.90	38.86	306.82	504.45
	BFAT, cm	108	1.22	0.50	0.21	2.67
	REA, cm ²	108	97.67	12.61	63.51	140.10
	YG, units	108	2.79	0.90	0.65	5.13
	Marb, units	108	408.52	77.57	300.00	650.00
	Final BW, kg	107	686.45	52.19	538.64	769.19
2	HCW, kg	111	404.53	31.26	288.64	479.59
	BFAT, cm	108	1.17	0.41	0.43	2.46
	REA, cm ²	108	90.77	9.40	69.68	114.18
	YG, units	108	2.99	0.78	1.18	4.86
	Marb, units	53	426.42	91.42	290.00	860.00
	Final BW, kg	85	681.95	52.02	543.18	781.82
3	HCW, kg	104	416.61	28.34	321.36	480.36
	BFAT, cm	58	1.52	0.51	0.30	2.84
	REA, cm ²	103	91.64	9.00	67.28	121.03
	YG, units	103	3.29	0.68	1.11	5.24
	Marb, units	72	450.88	99.23	216.00	692.00
	Final BW, kg	101	681.71	50.80	515.91	797.73
4	HCW, kg	105	387.37	31.89	301.36	455.00
	BFAT, cm	104	1.43	0.48	0.30	2.54
	REA, cm ²	104	85.48	8.77	62.58	108.39
	YG, units	104	3.40	0.73	1.72	5.39
	Marb, units	104	547.32	96.34	372.00	813.00
	Final BW, kg	105	641.49	51.01	500.00	770.45
5	HCW, kg	119	390.85	37.94	307.27	489.73
	BFAT, cm	110	1.32	0.40	0.56	2.24
	REA, cm ²	110	93.27	8.84	73.03	115.68
	YG, units	110	2.91	0.63	1.00	4.31
	Marb, units	110	566.3	99.27	394.00	819.00
	Final BW, kg	122	646.29	53.75	502.27	790.91

Table 5.3 LSMEANS for hot carcass weight (HCW), rib eye area (REA), back fat (BFAT), marbling (MARB), yield grade (YG), and final body weight (FBW) for each group

Trait	Group 1	Group 2	Group 3	Group 4	Group 5
HCW, kg	446.50 ^a	408.70 ^b	422.38 ^c	386.76 ^d	391.21 ^{de}
REA, cm ²	104.16 ^a	92.89 ^b	96.81 ^c	77.12 ^d	90.08 ^{be}
BFAT, cm	1.40 ^a	1.17 ^b	1.68 ^c	1.50 ^{abd}	1.13 ^{abe}
MARB, units	437.68 ^a	427.51 ^{ab}	474.94 ^c	550.48 ^d	536.42 ^{de}
YG, units	2.73 ^a	2.89 ^{ab}	3.09 ^{bc}	3.98 ^d	2.95 ^{abce}
FBW, kg	729.57 ^a	693.83 ^b	710.85 ^c	618.95 ^d	636.97 ^e

^{abcde}Differences in superscripts within each column indicate significant differences between groups (P<0.05)

Table 5.4 LSMEANS for hot carcass weight (HCW), rib eye area (REA), back fat (BFAT), marbling (MARB), yield grade (YG), and final body weight (FBW) for each group at low, medium, and high water intake levels

Trait	Group 1		Group 2		Group 3		Group 4		Group 5		Group 6	
	N ^a	Mean	N ^a	Mean	N ^a	Mean	N ^a	Mean	N ^a	Mean	N ^a	All
HCW												
Low	64	424.70 ^b	43	391.22 ^b	32	406.10 ^b	49	377.25 ^b	55	383.04 ^b	243	396.65 ^b
Medium	34	439.67 ^{bc}	46	408.67 ^c	51	419.93 ^{cd}	34	391.82 ^{cd}	52	395.04 ^{bc}	217	410.75 ^c
High	11	454.34 ^{cd}	22	421.27 ^c	21	427.83 ^d	22	403.90 ^d	12	415.26 ^c	88	425.93 ^d
REA												
Low	62	96.69 ^b	40	90.85 ^b	31	91.18 ^b	49	83.86 ^b	50	93.35 ^b	232	91.22 ^b
Medium	33	98.26 ^b	46	89.8 ^b	51	92.18 ^b	33	86.32 ^b	49	94.52 ^b	212	92.19 ^b
High	13	101.17 ^b	22	92.79 ^b	21	90.76 ^b	22	87.76 ^b	11	93.56 ^b	89	93.22 ^b
BFAT												
Low	62	1.15 ^b	40	1.01 ^b	26	1.52 ^b	49	1.39 ^b	50	1.32 ^b	227	1.29 ^b
Medium	33	1.28 ^b	46	1.23 ^c	25	1.48 ^b	33	1.46 ^b	49	1.27 ^b	186	1.35 ^b
High	13	1.40 ^b	22	1.29 ^c	7	1.91 ^b	22	1.46 ^b	11	1.44 ^b	75	1.49 ^c
MARB												
Low	62	412.4 ^b	14	397.27 ^b	20	476.30 ^b	49	520.36 ^b	50	582.93 ^b	195	483.11 ^b
Medium	33	409.56 ^b	25	421.15 ^b	34	427.89 ^b	33	562.17 ^{bc}	49	551.3 ^b	174	472.47 ^{bc}
High	13	393.76 ^b	14	456.92 ^b	18	464.08 ^b	22	586.23 ^c	11	591.29 ^b	78	500.63 ^{bd}
YG												
Low	64	2.74 ^b	41	2.69 ^b	31	3.17 ^b	49	3.37 ^b	50	2.87 ^b	235	2.98 ^b
Medium	33	2.92 ^b	46	3.13 ^c	51	3.27 ^b	33	3.44 ^b	49	2.82 ^b	212	3.11 ^c
High	13	3.04 ^b	22	3.17 ^c	21	3.63 ^c	22	3.46 ^b	11	3.17 ^b	89	3.30 ^d
FBW												
Low	64	678.23 ^b	33	667.88 ^b	32	663.85 ^b	49	624.68 ^b	56	621.81 ^b	234	651.36 ^b
Medium	32	688.34 ^b	33	684.14 ^{bc}	50	683.76 ^{bc}	34	649.56 ^c	54	656.84 ^c	203	673.14 ^c
High	11	736.24 ^c	19	700.77 ^{cd}	19	707.56 ^{cd}	22	668.87 ^c	12	717.22 ^d	83	709.60 ^d

^aIndividuals divided into low, medium and high water intake levels based on k-mean clustering of individual average daily water intake with k=3

^{bcd}Differences in superscripts within each column indicate significant differences between groups ($P < 0.05$)

Table 5.5 Pearson (above the diagonal) and Spearman (below the diagonal) phenotypic correlations between water intake (WI) and carcass traits^a. P-values indicate whether the correlation was significantly different from zero

	WI	HCW	REA	BFAT	MARB	YG	FBW
WI		0.171***	-0.025	0.223***	0.177**	0.223***	0.180***
HCW	0.202***		0.491	0.176	-0.076	0.133	0.753***
REA	0.020	0.451***		-0.229	-0.041	-0.638	0.358***
BFAT	0.247***	0.179***	-0.216***		0.367	0.822	0.090
MARB	0.136**	-0.101**	-0.033	0.383***		0.230	-0.167**
YG	0.207***	0.159**	-0.593***	0.819***	0.219***		0.085
FBW	0.225***	0.744***	0.348***	0.079	-0.180**	0.076	

^a Hot carcass weight, kg (HCW), rib eye area, cm² (REA), back fat, cm (BFAT), marbling (MARB), yield grade (YG), and final body weight, kg (FBW)

*Correlations are significantly different from zero at * P<0.05, **P< 0.01, ***P < 0.0001

Table 5.6 Heritability estimates^a (on the diagonal) and genetic correlations^a (above the diagonal) for water intake and carcass traits^b

	WI	HCW	REA	BFAT	MARB	YG	FBW
WI	0.42 (0.17)	0.38 (0.49)	0.08 (0.07)	0.36 (0.36)	0.17 (0.97)	0.29 (0.40)	0.29 (0.41)
HCW		0.31 (0.15)	0.45 (1.07)	0.42 (0.52)	0.46 (1.02)	0.36 (0.57)	1.00 (0.06)
REA			0.27 (0.16)	-0.38 (0.04)	-0.13 (0.47)	-0.44 (0.77)	0.86 (1.16)
BFAT				0.71 (0.21)	-0.29 (0.45)	0.85 (0.31)	0.27 (0.29)
MARB					0.26 (0.16)	-0.27 (0.25)	0.58 (0.70)
YG						0.53 (0.16)	0.32 (0.34)
FBW							0.58 (0.17)

^aStandard deviations are reported in parenthesis

^b Hot carcass weight, kg (HCW), rib eye area, cm² (REA), back fat, cm (BFAT), marbling (MARB), yield grade (YG), and final body weight, kg (FBW)

Figure 5.1. Regression analyses of carcass traits on water intake (WI). Panel A: hot carcass weight (HCW), Panel B: longissimus muscle area (REA), Panel C: back fat (BFAT), Panel D: marbling score (MARB), Panel E: yield grade (YG), and Panel F: final body weight (FBW)

