

The Relationship between Residual Feed Intake, Dry Matter Intake, and Reproductive Performance in Holstein Dairy Cows

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ABSTRACT

Feed represents a large portion of input costs for dairy operations. Decreasing the feed consumed, measured here as dry matter intake (DMI), would therefore be advantageous to producers. However, this decrease could result in cows that do not supply the necessary energy to maintain high production, growth, and reproduction. Measures of feed efficiency try to capture important energy expenditures to ensure that cows consume less while maintaining production. Feed efficiency in this study is measured in residual feed intake (RFI), which is calculated as the difference between DMI and expected DMI based on production and growth measures. However, the RFI model does not capture the energy stores required for reproduction; therefore, selection for RFI may lead to reduced reproductive performance. In this thesis, I explored the phenotypic and genetic relationships between RFI, DMI, and reproductive performance as measured by number of services (NS), days open (DO), and days to first calving (DFC). First, ANOVA tests and phenotypic correlations determined the phenotypic relationship between the traits. Then, heritability and genetic correlations were used to estimate the genetic parameters. Phenotypically, results indicated mixed relationships between traits. Heritability estimates were low for reproductive traits and moderate for DMI and RFI. There was no unfavorable genetic relationship between DMI or RFI with any of the reproductive traits. Therefore, neither selection for DMI nor RFI will unfavorably impact reproduction.

GENERAL ABSTRACT

Dairy cows consume significant resources in the form of feed. Decreasing the feed consumed, measured here as dry matter intake (DMI), would therefore be advantageous to producers and consumers. However, this decrease could result in cows that do not supply the necessary energy to maintain high production, growth, and reproduction. Measures of feed efficiency try to capture important energy expenditures to ensure that cows consume less while maintaining production. Feed efficiency in this study is measured in residual feed intake (RFI), which is calculated as the difference between DMI and expected DMI based on production and growth measures. However, the RFI model does not capture the energy stores required for reproduction; therefore, selection for RFI may lead to reduced reproductive performance. In this thesis, I explored the phenotypic and genetic relationships between RFI, DMI, and reproductive performance as measured by number of services, days open, and days to first calving. First, ANOVA tests and phenotypic correlations determined the phenotypic relationship between the traits. Then, heritability and genetic correlations were used to estimate the genetic relationship between traits. Heritability estimates were low for reproductive traits and moderate for DMI and RFI. There was no unfavorable genetic relationship between DMI or RFI with any of the reproductive traits. Therefore, neither selection for DMI nor RFI will unfavorably impact reproduction.

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LIST OF ABBREVIATIONS

RFI	Residual Feed Intake
DMI	Dry Matter Intake
NS	Number of Services
DO	Days Open
DFC	Days to First Calving
SNP	Single-Nucleotide Polymorphisms
GWAS	Genome-Wide Association Studies
MLMM	Multi-Locus Mixed Model
ASE	Allele Substitution Effect

Chapter 1

Introduction

The average dairy cow consumes roughly \$1,700 in feed per year (Laughton, 2015). This is 39% of average milk sales per cow, meaning that current feed consumption significantly decreases profit for dairy producers (Laughton, 2015). Therefore, having animals who consume less while maintaining production would decrease one of the major input requirements for producers; thereby, increasing profit. A conceptually simple trait to represent feed consumption is dry matter intake (DMI), a measure of how much feed an animal consumes. However, decreased feed intake can unfavorably affect milk yield and growth (Veerkamp, 1998). Compared to feed intake, the measure of feed efficiency is designed to avoid this unfavorable relationship, instead identifying animals who are able to consume less feed, but maintain high growth and production.

There are several different methods that may be used to quantify feed efficiency, but fundamentally, feed efficiency is calculated as the ratio of growth/production to feed intake. In this thesis, feed efficiency will be measured in residual feed intake (RFI) which is defined as the difference between DMI and expected DMI (VandeHaar et al., 2012). Expected DMI is calculated using a function of body weight, change in body weight, milk energy output, and parity (Potts et al., 2015). This means that growth, milk production, and maintenance are all accounted for in the RFI model; therefore, these measures should not be indirectly affected by selection for RFI. This independence would suggest that RFI reveals variation in basic metabolic processes within cows. However, there is another area that requires energy in cows that is important to producers: reproduction. Energy taken for more efficient metabolism may be reducing the energy stores available for high reproductive performance. This research focuses on determining the interrelationships between RFI and DMI with reproductive performance, as measured by number of services required to become bred (NS), days open between calves (DO), and days to first calving (DFC).

The overall objective of this study is to determine whether selection for RFI or DMI will unfavorably impact reproductive performance. This is done by examining the relationship between both RFI and DMI with reproductive performance. This thesis is divided into three

parts, all of which reveal different facets of these relationships: phenotypic and genetic. Secondary objectives were to determine the phenotypic and genetic relationship among RFI, DMI, and reproductive measures and estimate heritability for all 5 traits.

The phenotypic data was examined using ANOVA tests and Pearson correlations which are presented in chapters 3. Analysis of variance tests compare the means of groups to determine whether they are significantly different from each other. Therefore, the first step in running ANOVA tests on the data to break the continuous variables RFI and DMI into low, medium, and high groups. There were multiple types of clustering methods used for this type of grouping in the literature, so within this study a variety of methods were explored and compared. Once cows were divided by RFI and DMI, ANOVA tests determined whether groups differed significantly in terms of NS, DO, or DFC. This was used to determine whether cows with the more desirable low DMI or RFI had unfavorable reproductive performance relative to cows in the medium and high groups. Phenotypic correlations provided an additional method for determining how the measured performance in RFI or DMI relates to the measured performance in NS, DO, and DFC.

Chapter 4 includes genetic correlations between traits and heritability estimates for all traits. Comparative to phenotypic correlations, genetic correlations add in the use of pedigree information to the measured phenotype information, to determine whether genetic selection for RFI or DMI will indirectly affect any reproductive traits. These effects are important, since the primary focus of this study is determining the suitability of RFI and DMI in breeding programs. Heritability estimates similarly use pedigree information, in addition to phenotypic data, to determine the amount of variation in a trait that is due to additive genetic effects. Genetic progress is less likely to be made in traits with low heritability estimates, because they are more a product of environment effects, not of underlying genes.

Combined, the components discussed in these chapters reveal the phenotypic, genetic, and genomic relationship between RFI, DMI and reproductive performance in Holstein dairy cows.

Chapter 2

Literature Review

Feed Efficiency

Feed costs are the largest variable operating input for dairy producers accounting for roughly 60% on typical operations (Ho et al., 2013). Variable costs are dependent on output (e.g., feed and labor), as opposed to fixed costs that are constant expenses for the producer (e.g., facilities). Feed efficiency is one of many factors that impact an operation's feed costs. Feed efficiency is broadly defined as feed consumption relative to growth and production (Van Arendonk et al., 1991). Relative to contemporaries, dairy cows that produce more milk while consuming less feed are considered "feed efficient".

Traditionally, this trait may be measured using the ratio of gain to feed, in beef cattle, or to milk, in dairy cattle (Connor and Hill, 2012). However, in general directly selecting for a ratio between 2 traits leads to unpredictable results because selection pressure is not distributed proportionally between the component traits (Gunsett, 1984). Selection using a linear model allows selection pressure to be predetermined. Further complicating feed efficiency in dairy cattle is the lactation cycle that dairy cows go through. In early lactation, cows are unable to consume enough feed to account for the energy being expended in milk production and so rely on energy stores within the body. However, gross feed efficiency is correlated with higher weight loss and lower body condition score during lactation which may negatively impact metabolic balance and fertility (Vallimont et al., 2011).

An alternative to this method of measuring for feed efficiency is to estimate feed requirements based on bodyweight and production (Visscher et al., 1994). By selecting for animals with decreased body weight to production ratios, gross efficiency increases. However, predicted feed efficiency from bodyweight and production does not phenotypically correlate perfectly (0.84) with true feed efficiency (Gibson, 1986). This suggests that there is additional variation that could be selected for if close to true measurements of feed efficiency were possible. To better measure the true efficiency of milk production, energy expenditures besides milk production must be considered. Residual feed intake (RFI) developed by Koche et al.

(1963) seeks to capture the remaining variation in energy usage and provide a more accurate measure of true feed efficiency.

Residual feed intake

Residual feed intake is the difference between actual and predicted dry matter intake (Sainz and Paulino, 2004; Herd, 2008). Animals with lower RFI values are more efficient as they are able to achieve the same levels of production with feed comparative to high RFI animals. Residual feed intake was first proposed as an alternative to measuring true feed efficiency by Koch et al. (1963). Feed intake was divided into 2 portions: expected intake for a given level of production and the residual. This residual portion (i.e., RFI) allows producers to identify animals that deviate from their expected levels of feed intake. As shown in Table 2.1 RFI heritability estimates range from 0.07 – 0.54 (Koch et al., 1963). This suggests that genetic improvement can be made on this trait. Genetic selection to reduce RFI has been shown to result in progeny that consume less while maintaining growth performance (Herd et al., 1997).

However, traditionally genetic selection strategies have focused almost exclusively on production traits to the exclusion of traits which can reduce the cost of inputs like feed, despite profitability being a function of the two (Sainz and Paulino, 2004). Historically, genetic selection has focused on increasing milk production and milk components (Walsh et al., 2011). However, RFI has had a recent resurgence of interest because of its suitability for marker-assisted selection and because technology such as Calan Gates and GrowSafe has made measuring feed intake easier and less costly. In order to use marker-assisted selection, phenotypic and genomic data is first collected on a reference population to generate prediction equations. This allows for the estimation of phenotypic performance based on the genomes of animals outside the reference population (Gonzalez-Recio et al., 2014). Animals can then be selected for low RFI without the prohibitively high costs of obtaining phenotypic measurements. Instead, producers will be able to genotype their calves and make selection decisions without collecting individual feed intake, growth, and performance measures.

Calculating RFI

Daily feed intake is calculated from the amount of feed offered and the amount refused. In beef cattle, expected feed intake is obtained from a linear regression model of dry matter intake and mid-test bodyweight and average daily gain (Sainz and Paulino, 2004). Calculations

for RFI differ between dairy animals and other livestock species because of the inclusion of milk production as a significant energy drain for the cows (VandeHaar et al., 2012). In dairy cows, RFI is calculated using growth and milk energy traits. Compared to traditional feed efficiency measures, RFI takes into account the level of production, parity, and body weight (VandeHaar et al., 2012). This trait also has repeatability between diets that differed in levels of starch (Potts et al., 2015) and across different stages of lactation (Connor et al., 2013). This suggests that differences in RFI may be the result of differences in true feed efficiency.

Physiological reasons for differences in RFI

Residual feed intake is a complex trait that is a culmination of many factors. In beef cattle, factors have been shown to include differences in digestion, body composition, animal metabolism, activity, and thermoregulation (Herd and Arthur, 2009). With increased intake, there is an increase in visceral organ size of the animal, which leads to increased energy expense and, therefore, decreased animal efficiency (Herd and Arthur, 2009). Both dairy and beef cattle with lower RFI also tend to consume fewer meals at a slower pace (Herd and Arthur, 2009; Connor et al., 2013). In mice, less efficient (high RFI) females and males released more body heat and were generally more active in their enclosures (Mousel et al., 2001). Beef cattle showed similar levels of increased activity with more steps being taken by animals with high RFI than animals with low (Herd and Arthur, 2009). This suggests that feeding behavior is a key contributor to RFI status. Digestion also plays a role in animal efficiency because as intake increases feed digestion subsequently decreases (Herd et al., 2004). Beef cattle with lower RFI have increased feed digestibility (Richardson and Herd, 2004). Less energy is also lost with methane in low RFI cows (Nkrumah et al., 2006). Low RFI beef cattle were found to have decreased whole body fat and increased lean tissue (Richardson and Herd, 2004). Maintenance energy requirements per unit of bodyweight is strongly phenotypically correlated with RFI (Herd and Bishop, 2000). Therefore, much of the energy conserved is due to decreased maintenance costs. The goal of using RFI in breeding programs is to select for these decreased energy losses. This allows for cows who maintain production while consuming less feed, which is measured here in dry matter intake.

Residual feed intake and dry matter intake

Dry matter intake is a measure of the amount of feed an animal consumes that is used to estimate RFI. As expected, there is a strong phenotypic ($r_p = 0.61 \pm 0.04$) and genetic correlation ($r_g = 0.85 \pm 0.08$) between RFI and DMI (Zamani et al., 2008; Lancaster et al., 2009). This suggests that selection against DMI will decrease RFI; additionally, DMI could serve as an indirect indicator for RFI. However, some studies suggest that decreased DMI may be genetically correlated with lower milk yield: Svendsen et al. (1994), Van Arendonk et al. (1991), and Persaud et al. (1991) estimated this genetic correlation at $r_g = 0.46$, 0.65 , and 0.60 respectively. Moore et al. (1992) and Lee et al. (1992) both found higher genetic correlations ($r_g = 0.84$ and 0.95), but in these studies, and in many commercial herds, cows were fed according to milk yield which may lead to artificially high correlations (Veerkamp, 1998). This suggests that selection for lower DMI may result in decreased milk yield. Unlike DMI, RFI accounts for milk yield within its model, so it does not phenotypically correlate with production (VandeHaar et al., 2012). Finally, DMI is expensive and labor intensive to measure, like RFI, but new technologies such as Calan Gate and GrowSafe allow for easier and cheaper direct measurements of feed intake (Pryce et al., 2015).

Genetic Parameters

Genetic parameters such as heritability estimates and genetic correlations are used to assess the genetic variation and genetic relationships between traits. Economically relevant phenotypes that demonstrate variation and favorable relationships between other economically relevant traits provide opportunities for genetic improvement. By definition, heritability is the proportion of total variation between individuals in a given population due to genetics. Traits with low heritability are difficult to make genetic progress on, as they are primarily influenced by environment. Heritability is calculated using trait data and pedigree information by comparing the phenotypes of animals with varying degrees of relatedness in order to estimate the environmental and genetic variance within the trait.

Genetic correlations estimate additive genetic effects shared between two traits. Phenotypic data and pedigree information is used to calculate genetic relationships between traits. Increased or stronger genetic correlations between traits suggest that traits are controlled by similar genes; therefore, genetic selection for one trait would indirectly impact the other trait.

Genetic selection for residual feed intake

In dairy cows, heritability estimates for RFI vary (Table 2.1) but are generally moderate. This suggests that RFI could be used in breeding programs to increase the feed efficiency of dairy herds (Connor, 2015). Selection for RFI has been shown to decrease the amount of feed required for growth in both cattle and swine (Arthur et al., 2005; Cai et al., 2008); however, the impact on production in dairy cattle is unknown. Three major challenges with using RFI to improve feed efficiency in commercial dairy cattle includes: 1) lack of knowledge about genetic correlations between RFI and other economically important traits, 2) impracticality of evaluating RFI on commercial dairies, and 3) low availability of RFI data due to high costs associated with collecting individual feed intake (VandeHaar et al., 2012; Connor, 2015).

For RFI to be used as an alternative measure for feed efficiency, it must not have an unfavorable genetic relationship with other economically important traits (VandeHaar et al., 2012). Selection for lower RFI has been estimated to reduce feed costs by 10-15% (Nkrumah et al., 2006). However, costs saved could be offset by any detrimental relationship identified between RFI and other economically important traits. Therefore, it is imperative that genetic relationships between health traits be elucidated.

Because RFI is difficult and expensive to measure, moderately heritable, and economically relevant, it serves as an ideal trait for genomic selection and(or) marker-assisted selection. To do this, genomic and biological markers must be identified. With genomic technology becoming cheaper and more common, identifying genomic markers associated with RFI could make selection for this trait feasible for producers (Pryce et al., 2014).

Currently, measurement of daily intake is limited to academic and government institutions and a subset of bull stud companies. Because determining feed intake requires time, labor, and specialized equipment, limited RFI data is available to incorporate it into a large-scale genetic evaluation (Van Arendonk et al., 1991; Veerkamp et al., 1995; Veerkamp, 1998).

Energy and production

Feed consumed by cows is converted into energy for production as shown in Figure 2.1. Energy for production, including reproduction, is only available after several losses reduce the amount available. Lower DMI leads to animals who do not consume as much feed, but this may result in a loss of energy for growth, milk, and reproduction. Residual feed intake takes into

account both milk and growth within its model, but not reproduction. This could mean that energy for more efficient metabolism is being taken from reproduction which would be detrimental to the fertility of cows.

Reproduction

Dairy production systems have become more intensive overtime to meet market demands (Pryce et al., 2004). Milk cooperatives reward producers for high milk production and milk components which has led to genetic selection based heavily on production. Though primarily impacted by management and environment, there is a moderate positive genetic correlation ($r_g = 0.48$ to 0.49) between production and calving interval and days to first calving in dairy cows (Pritchard et al., 2012). Additionally, there is a moderate negative genetic correlation ($r_g = -0.23$) between daughter pregnancy rate and milk production (CDCB, 2014). Selection for milk production has unfavorably contributed to the overall decline in dairy cow fertility over the past 50 yrs. Failure to be bred is the 3rd contributing factor for culling, which impacts a dairy herd's overall economic efficiency (Stott et al., 1999; González-Recio et al., 2004; Cabrera, 2014). When cows and heifers have a difficult time conceiving, they cost producers more for semen, labor, and animal maintenance (Stott et al., 1999; González-Recio et al., 2004). Because the dairy industry is faced with infertility challenges, it is important to determine the genetic interactions with new traits prior to incorporating them into a large-scale evaluation. Reproductive performance is difficult to measure because it is heavily impacted by management decisions (Gröhn and Rajala-Schultz, 2000). Days open, days to first calving, and number of services are indicators of reproductive performance in production herds (Gröhn and Rajala-Schultz, 2000). Days open is calculated as the time between calving and the next conception. Days to first calving is defined as the days before a first-calf heifer calves for the first time. Number of services is determined by the number of insemination attempts made before a cow conceives. Performing favorably in these reproductive traits requires sufficient energy being utilized for fertility which may be affected by changes in feed efficiency or feed intake (De Vries and Veerkamp, 2000).

Residual feed intake and reproductive performance

Sows

Yorkshire pigs were bred for low RFI and then compared to a control line of non-selected pigs for feed efficiency (Gilbert et al., 2010; Young et al., 2010). Sows in the low-RFI line were lighter and leaner ($P \leq 0.002$) at farrowing and ate less during lactation. However, feed efficient sows also farrowed more ($P < 0.001$) piglets that grew faster during lactation and the piglets weighed more at birth, had greater pre-weaning growth rates, and weighed more at weaning (Gilbert et al., 2010; Young et al., 2010). Growth of the piglets came at the expense of body resources of the sows, as low RFI sows lost more ($P < 0.001$) body condition than control sows. Piglets' growth accounted for some loss of body condition, but approximately 60% of the difference between the lines in their daily feed intake during lactation was accounted for by RFI at the time (Gilbert et al., 2010).

Beef cattle

Similar to Gilbert et al. (2015), (Arthur et al., 2005) selected cows for low RFI, which were compared to controls after an average of 1.5 generations. The lines differed in estimated breeding value for RFI by 0.8 kg/day. Cows lost subcutaneous fat during the period when they were nursing calves, and gained fat after weaning. No significant selection line differences in weight were observed. However, the cows either maintained or lost weight during the calf nursing period, and gained weight after weaning. There were no differences in pregnancy, calving, weaning rates, milk yield or calf weaning weight between lines. The study indicated that after 1.5 generations of divergent selection for RFI there were no significant line differences for maternal productivity traits.

In beef bulls, breeding soundness exam traits did not differ between high RFI bulls and low RFI bulls, but the proportion of bulls that failed to meet the 60% minimum sperm motility requirement tended ($P = 0.07$) to be greater (10.2% vs. 4.4%, respectively) in the low RFI group than in the high RFI group (Wang et al., 2012). In a subpopulation of 115 bulls, individual progressive sperm motility was greater ($P = 0.02$) in high RFI than low RFI bulls (Wang et al., 2012).

Dry matter intake and reproduction

Dry matter intake and reproductive performance have been shown to have a neutral to unfavorable relationship. Cows with lower DMI tended to have longer intervals to first ovulation and had a longer negative energy balance (Lucy et al., 1992). Greyface Dartmoor ewes on restricted diets resulted in decreased ($P < 0.01$) ovulation rates (1.81 vs. 2.09; Rhind et al., 1989).

Ova wastage rates also increased ($P < 0.01$) in restricted diet ewes (0.26 v. 0.14). Westwood et al. (2002) determined that Holstein cows ($n = 82$) fed a low-degradable or high-degradable diet with increased DMI were more likely to become pregnant by 150 d. Increased DMI may be related to increased fertility rates, as animals will have more energy available for reproductive processes. This suggests that selection for decreased DMI, while reducing necessary feed costs, may unfavorably impact reproductive performance. However, this relationship requires further investigation to determine if selection for DMI would detrimentally impact reproductive performance in Holstein cows.

Genetic selection for feed efficiency

Genetic selection is effective as long as the trait being selected is heritable and the accuracy of the genetic predictions for the trait are acceptable (Pryce et al., 2014). Domesticated species, including dairy cows, have been selected for traits advantageous to humans for generations. Methods of evaluation have historically included appearance, lineage, and empirical measurements of desired traits. All of these methods of evaluation are attempts to assess what traits the animal will pass on to the next generation. The statistical advancements over recent decades have allowed producers to more accurately predict the genetic makeup of an animal. Generally desirable traits are quantitative, controlled by a large number of genes which are influenced by environmental factors (Falconer, 1975). To predict how these complex traits would be passed on, statistical tools use phenotypic measurements and pedigree information to obtain the predicted transmitting ability (PTA) for each individual (Falconer, 1975). These tools break down phenotype data into its genetic and environmental components based on the performance on the individual and its relatives. Henderson's Best Linear Unbiased Prediction (BLUP) became the widely adopted method of calculating those EBV (Estimated Breeding Value) (Henderson, 1975). These statistical models of genetic effects led to the greatest increases in genetic merit seen at the time (Lande and Thompson, 1990). However, this was still an estimation of genetic effect and has limitations, such as being unable to distinguish full-sibs (Hayes et al., 2009). Relatively recently, it became possible to use the DNA of cattle to predict the phenotypic traits and breeding values of young animals.

Heritability estimates

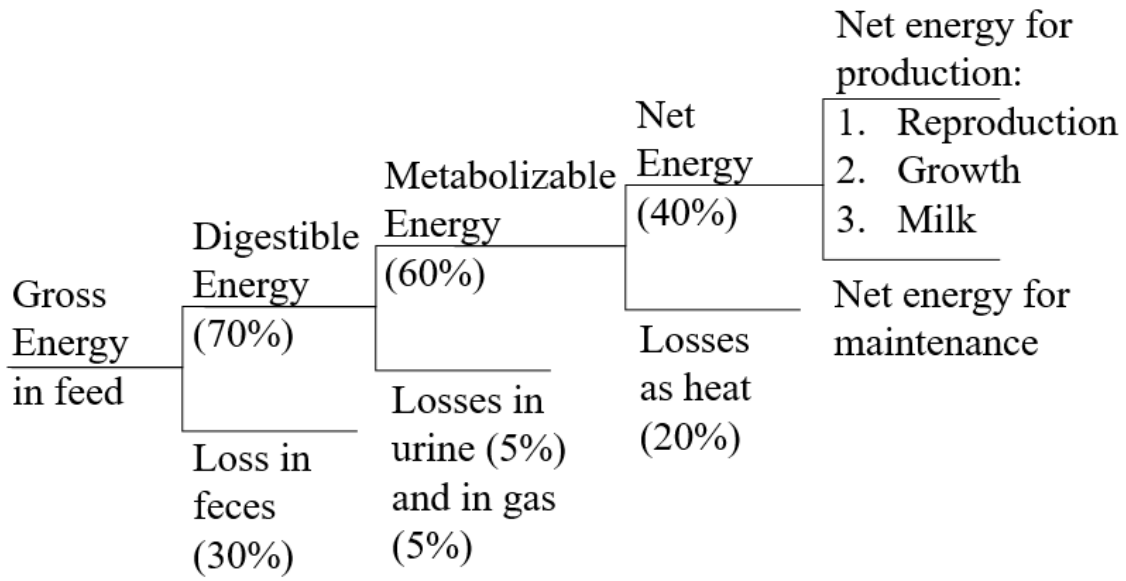
Heritability estimates for RFI range from 0.21 ± 0.15 to 0.36 ± 0.06 (Dechow et al., 2001; Connor et al., 2013) and heritability estimates for DMI range from 0.21 to 0.46 (Veerkamp and Brotherstone, 1997; Berry et al., 2007). Both of these estimates are high enough that genetic selection for these traits could lead to improvement. Accuracy of genetic prediction for DMI was estimated between 0.20 and 0.35 (Mujibi et al., 2011; De Haas et al., 2012). Accuracy for RFI was estimated between 0.40 and 0.43 (Mujibi et al., 2011; Pryce et al., 2012). While these accuracies for DMI and RFI are not too low, RFI and DMI are both expensive and difficult traits to measure, so increasing their accuracy would increase the value proposition for these traits. Expanded research and improved technology, such as incorporation of genomic data, are required to improve accuracy going forward.

FIGURES AND TABLES

Table 2.1: Previously published heritability estimates for RFI and DMI in beef and dairy cattle

Heritability estimate \pm SE	Breed	Citation
RFI		
0.39 \pm 0.03	Post weaning Angus	(Arthur et al., 2001)
0.21 \pm 0.12	Mixed breed beef cattle	(Nkrumah et al., 2007)
0.45 \pm 0.06	Mixed breed beef cattle	(Crowley et al., 2010)
0.22 \pm 0.07	Australian dairy heifers	(Pryce et al., 2012)
0.38 \pm 0.09	New Zealand dairy heifers	(Pryce et al., 2012)
0.47 \pm 0.12	Angus steers	(Durunna et al., 2013)
0.18 \pm 0.02	Holstein cows	(Templeman et al., 2015)
DMI		
0.39 \pm 0.03	Post weaning Angus	(Arthur et al., 2001)
0.54 \pm 0.15	Mixed breed beef cattle	(Nkrumah et al., 2007)
0.07 \pm 0.14	Holstein cows	(Toshniwal et al., 2008)
0.34 \pm 0.07	Dairy cattle	(De Haas et al., 2012)
0.34 \pm 0.11	Holstein cows	(Spurlock et al., 2012)

Figure 2.1: Division of energy from feed within dairy cows



(James G. Linn, 2005)

Chapter 3

Phenotypic relationship between feed efficiency, feed intake, and reproductive performance

ABSTRACT

Breeding in the dairy industry takes place during lactation. This, combined with nadir body energy storage, contributes to decreased conception rates in the dairy industry. As traits such as residual feed intake (RFI) and DMI are being incorporated into selection schemes to reduce feed intake, there is growing concern that reproductive challenges will be further exacerbated. Therefore, to incorporate RFI or DMI into current lifetime production indices, they must not be unfavorably associated with reproduction. We hypothesized that increased feed efficiency and decreased feed intake would be significantly associated with decreased reproductive performance. To test this hypothesis, the objectives of this study were to 1) determine phenotypic relationships between RFI and DMI with reproductive traits, 2) identify the appropriate clustering method to partition cows into RFI and DMI groups, and 3) evaluate the correlations of RFI and DMI groups with reproductive performance. Holstein cows ($n = 1,513$) varying in stage of lactation from Virginia Tech and Iowa State University had production, growth, and reproduction measured. Cows were divided into RFI and DMI groups using five clustering methods (K-Means, Half deviation, One-third, Split-on-zero, and Ten-percent) and compared with reproductive performance using a mixed ANOVA model in R. *Post hoc* analyses were conducted using a Tukey's adjustment for multiple comparisons. Reproductive measures used were number of services (NS), days open (DO), and days to first calving (DFC). The clustering method, half-deviation was determined as the most appropriate model based on theoretical merit and statistical analysis of clusters. Between low, medium, and high RFI groups we observed significant differences for both NS ($P = 0.006$) and DFC ($P = 0.002$). Between DMI groups, we observed significant differences for DO ($P = 0.006$). We also determined that low RFI or low DMI cows had decreased NS and DO, suggesting a marginally beneficial

relationship. However, we observed that low RFI cows had increased DFC. Overall, we determined that selecting for RFI or DMI would have minimal impact on reproductive performance in dairy cows.

INTRODUCTION

A major goal for improving cattle is to decrease feed costs while maintaining or increasing production. Feed is the largest variable cost for dairy operations, accounting for approximately 60% of operating costs (VandeHaar et al., 2012). It is, therefore, advantageous to select for animals that consume less feed, as measured by dry matter intake (DMI), but maintain or increase production as compared to contemporaries. One approach to reduce feed intake without impacting production is through selection for feed efficiency. In this study, feed efficiency is defined as residual feed intake (RFI), which is the difference between the actual DMI and the expected DMI. Two of the components in calculating RFI are production and growth of the individual animal. Therefore, using RFI will not unfavorably affect production, as opposed to DMI which may unfavorably affect production. Although both traits are useful for evaluating dairy cows, neither of these traits take into account reproductive performance, which may also be unfavorably influenced by reduced feed intake.

Reproductive performance, as measured by traits such as number of services, days open, and days to first calving, is also crucial for economic profitability. Number of services is economically important because it is costly to breed cows multiple times – ideally they would become pregnant after the first service. Days open and days to first calving are also important since it is expensive to maintain an animal that is producing reduced milk. The more days open, the more money that is being spent with reduced return for producers; the more days to first calving, the longer until heifer becomes a producing member of the herd.

We hypothesized that increased feed efficiency and decreased feed intake would be significantly associated with decreased reproductive performance. The objectives of this study were to 1) determine phenotypic correlations between RFI and DMI with reproductive traits (i.e., days open, number of services, and days to first calving), 2) identify the appropriate clustering method to allocate cows into RFI and DMI groups (i.e., low, medium, high) and 3) elucidate

relationships between RFI and DMI group clusters with reproductive parameters. We expect that there will be an unfavorable relationship between RFI and DMI with reproduction in dairy cows.

MATERIALS AND METHODS

Data Collection

All animal procedures were conducted in accordance to each participating University's animal care and use committee. Feed, milk, growth and reproductive data were collected on 1,513 lactating Holstein cows at Virginia Tech and Iowa State University. Cows were between 50 and 200 d post-partum. Phenotypic feed and milk data included RFI, DMI (kg), metabolic body weight, change in body weight, net energy in milk, milk (kg), fat percentage, and protein percentage (Yao et al., 2017). Feed intake and milk yield were recorded daily for each cow using electronic measurement systems. Dry matter intake was calculated for individual animals using dry matter percentages of the feed and feed intake measurements (Yao et al., 2017). A linear model was created to estimate feed intake and determine individual RFI (VandeHaar et al., 2016) whereby:

$$DMI_i = \beta_0 + \beta_1 \times MilkE_i + \beta_2 \times MWWT_i + \beta_3 \times \Delta BodyE_i + Parity + Experiment + Cohort(Experiment) + Diet(Cohort \times Experiment) + \varepsilon_i$$

where DMI_i is the dry matter intake of an individual, β_n are the regression coefficients, $MilkE_i$ is the milk energy output for an individual, $MWWT$ is the metabolic body weight, $\Delta BodyE_i$ is the change in body energy for an individual, and ε_i is the residual error for an individual (aka RFI). Cows with $RFI < 0$ are considered low RFI (i.e., feed efficient) and cows with $RFI > 0$ are considered high RFI (i.e., feed inefficient).

Net milk energy was calculated based on the gross energy per kilogram in fat, protein, and lactose according to the equation below (VandeHaar et al., 2016):

$$MilkE(Mcal) = \left(\begin{array}{l} 0.0929 \times fat\% + 0.0563 \times protein\% \\ + 0.0395 \times lactose\% \end{array} \right) \times \text{daily milk yield}(kg)$$

Cows ranged from 1st parity heifers to 7th parity cows with an average parity of 1.56 ± 0.03 . There were also 4 experimental groups for unrelated experiments that cows were in: A (n = 105), B (n = 533), C (n = 382), and NA (n = 493). Each animal belonged to one herd: Iowa State University with two herds (ISU1, n = 502 and ISU2, n = 446) and Virginia Tech with one herd (n = 172).

All reproductive data was gathered during the same lactation as when feed intake was measured for RFI. Three measures of reproductive performance were examined: number of services (NS; n = 1,337), days open (DO; n = 816), and days to first calving (DFC; n = 572). Number of services is the number of times an animal is bred before she becomes pregnant. Days open is the number of days between calving and the next conception. Days to first calving is the days between birth and when a heifer has her first calf.

Statistical Analyses

Descriptive statistics were generated using the *plotrix* and *pastecs* packages in R (R Development Core Team, 2013) as well as native summary statistic functions. The observations, means, minimums, maximums, and standard errors are provided in Table 3.1. All cows with at least one reproductive parameter reported were retained within the dataset.

Cows were grouped according to 5 different clustering methods by both DMI and RFI, to ensure parallel structure of analysis. Analysis of variance tests compared the means of groups within data to determine if they were significantly different from each other. The ANOVA tests required one categorical and one continuous variable to run. Both RFI and DMI are continuous variables, so before ANOVA tests could be used, cows must be divided into groups based on thresholds for these traits. In this section, five methods of clustering animals are introduced and compared: Half-deviation, One-third, Ten-percent, Split-by-Mean, and K-means.

Half-deviation method

The Half-deviation method clustered cows into high, medium, and low groups based on their distance from the mean. Cows that were half a standard deviation above the mean were high, cows that were half a standard deviation below the mean were low, and cows within half a standard deviation of the mean were medium.

The Half-deviation method included all cows within the dataset and divided them into three clusters. Assuming that the underlying data used with this methodology was normally-distributed, the medium cluster included roughly 38% of the animals while both high and low

clusters included 31% each. If the dataset was not normally distributed, these percentages differed; therefore, using this clustering method with non-normal distributions led to diverging results from percentage clustering methods.

One-third method

The One-third method was an intuitive way of dividing animals into high, medium, and low groups. In this method, the top, middle, and bottom third are each used as a cluster. Like the Half-deviation method, the One-third method used all animals within a dataset and divided them into three equally-sized clusters. Unlike the Half-deviation method, the percentage of each cluster remained the same even if the data used was not normally distributed. However, this method did not account for any of the spread within the dataset because it did not use any measures of variation.

Ten-percent method

The Ten-percent method took only the top ten percent, middle ten percent, and bottom ten percent of the animals. This method was similar to the One-third method; there were three clusters divided by percentage within the dataset and the spread is not captured with any measures of variation. Unlike the previous two methods, however, this method did not use all the animals. Instead, the Ten-percent method focused on the extremes of each group. The Ten-percent method was useful for magnifying differences seen in One-third clusters, if the trends are consistent across the dataset.

Split on mean method

The Split-on-Mean method was when a line is drawn at the mean of the data: everything above the line was placed into a high cluster and everything below the line was placed in a low cluster. This method creates two clusters of 50% each, which included the entire dataset. In the case of RFI data, the Split-by-Mean method was approximately the same as splitting on zero, because the mean of residuals should always be close to zero. All animals who consume more feed than expected were above zero, and thus are in the high group. Those who consume less feed than expected were below zero in the low group.

K-means method

K-means was a method of dividing a dataset into k clusters (Hartigan and Wong, 1979). What differentiates K-means from the other methods was that the groups are determined not based on standard deviation or percentage but by the K-means clustering algorithm. This

algorithm functions by iteratively refining cluster means in order to minimize differences within groups and maximize distances between groups (Hartigan and Wong, 1979), as given by the formula:

$$\operatorname{argmin}_S \sum_{i=1}^k \sum_{x \in S_i} \|x - \mu_i\|^2$$

where s is a set of k clusters, and where each cluster is composed of some observations (x). The μ term represents the mean of the cluster, and is used to calculate the distances within a cluster between observations.

The goal of using this method was to find emergent clusters within the data rather than defining arbitrary thresholds. Here, the K-means method groups the entire dataset into three clusters. Like the Half-deviation method, the K-means method accounts for variation within the dataset. In this study, K-means were implemented using R with $k = 3$ via the built-in stats package, so that there would be three clusters (R: A language and environment for statistical computing, 2011).

Methods were compared based on R^2 , their use in the literature, and complexity. Ultimately Half-deviation was selected as the most appropriate. Table 3.2 shows the R^2 which indicated how well RFI and DMI clusters model the RFI and DMI continuous variables. This was performed for every group of cows based on the reproductive records available on them. The K-means and Half-deviation methods were consistently highest with Half-deviation coming in second; however, Half-deviation was less computationally complex method than K-means and has been used more frequently in previous research (Zorzi et al., 2013; Potts et al., 2015).

After clustering, ANOVA analyses were performed in R using the car package and built-in R functions with a Tukey's adjustment to correct for multiple comparisons. Models were selected by using the `anova` function in R to compare nested models. Cohort and sire were both initially included in the model, but neither were significant probably due to the large number of sires ($n = 190$) and similar phenotypes between cohorts. The final model included RFI or DMI group and the reproductive traits. Any animals missing phenotypes were removed and the model contained no covariates; therefore, arithmetic means were reported.

Phenotypic correlations were performed in R using the Hmisc package and its' dependency package boot. A Pearson correlation \pm SE was calculated for each of the 3 reproductive traits with RFI and DMI.

RESULTS & DISCUSSION

Table 3.1 contains descriptive statistics for RFI components and reproductive traits. The means \pm SE for RFI and DMI were 0.00 ± 0.051 and 23.51 ± 0.10 respectively. Sample size was the same across the RFI data. The number of samples available differed between reproductive traits with NS: $n = 1337$, DO: $n = 816$, and DFC: $n = 572$. The reproductive records used were from the same period that RFI was collected; additionally, some records were missing. Therefore, the most complete set of records was available on NS ($n = 1,337$). Days open ($n = 816$) was only available on cows who were at least in their second lactation. DFC had the smallest sample size ($n = 572$) because only first lactation heifers were used.

The average number of services (3.61 ± 0.079) were greater than the herd national average, but within 1 SD (2.9 (1.1)). Treating the national average as a known population mean, there was no significant difference from the national average. Days open was within 1 SD of the national average (148.7 (39.7)). The average of DFC was 728.36 ± 1.61 , did not differ from the national standard (771.3 (63.7); DRMS, 2017).

The phenotypic correlations between RFI and DMI with reproductive traits are shown in Table 3.4 and the results of ANOVA tests are shown in Table 3.5. We observed a difference ($P \leq 0.006$) for the main effect of RFI with NS and DFC (

Table 3.5). Specifically, low RFI cows had 15% less ($P = 0.004$) NS compared to high RFI cows, but medium RFI cows did not differ ($P \geq 0.11$) from high or low RFI. Additionally, DFC increased ($P = 0.002$) by 2% in low RFI cows compared to high RFI cows. Days to first calving also increased ($P = 0.048$) in medium RFI cows compared to high RFI cows. Days open did not significantly differ among RFI cluster groups.

Based on correlation and ANOVA analyses, marginal favorable relationships between RFI and reproductive performance were determined. Our research agrees with literature showing that RFI does not have a detrimental relationship with NS or DO. In previous research, there appears to be a neutral relationship between female fertility and RFI. Specifically, research on sows divergently selected for low and high RFI found no differences in fertility (Gilbert et al., 2010; Young et al., 2010). There was also no difference between pregnancy rates, calving rates, weaning rates, or weaning weight in Angus cows bred for diverging lines of RFI (Arthur et al.,

2005; Donoghue et al., 2011). Finally, there was no difference in pregnancy rate, first-service conception rate, or calving date in heifers sired by low and high RFI, but low RFI sired heifers did have higher calving rates in their second parity (Blair et al., 2013). It is costly to breed cows multiple times and to maintain cows who are not producing as highly; therefore, having lower RFI correlated with lower NS and DO would not be a detrimental relationship. Having cows who require lower NS will require less in semen and labor costs to breed. Having reduced DO results in animals who can be dried off while still producing acceptably high amounts of milk. These findings for DO and NS are more favorable than previous research, but neither our research nor the literature suggest an unfavorable relationship with RFI. Therefore, we suggest that there is no unfavorable relationship between RFI and DO or NS

However, we also suggest that low RFI first-calf heifers may calve later than those with high RFI. In our results this difference was around two weeks because high RFI cows had an average DFC of 719.24 ± 2.53 days while low had an average of 733.98 ± 3.32 . This would create a financial burden to producers because they would have to raise heifers for longer before they begin to produce. Previous literature reflects our findings that DFC in that Angus heifers selected for low RFI calved 1 week later than high RFI cows (Donoghue et al., 2011). Differences in DFC may be due to low RFI reaching puberty later than high RFI heifers because energy in animals with differing RFI may be partitioned more toward growth and away from other functions during this time (Crowley et al., 2011). However, the two difference found here for DFC represents only a 1.95% increase from low RFI cows to high RFI cows. The difference between these means is statistically significant, but the functional difference to producers is small. It is still important, however, to consider all possible reductions in reproductive performance. Both our and previous research suggests that low RFI cows may have increased DFC.

Similar to observed relationships with RFI, NS and DO ($r_p = 0.17 \pm 0.04$; $r_p = 0.22 \pm 0.04$, $P < 0.01$) had a weak, positive phenotypic correlations with DMI. This suggests that cows with lower DMI required fewer services and days to achieve pregnancy. For the ANOVA tests, we no longer saw this relationship with NS as no significant difference was observed between low and high DMI cows. However, we did observed a difference ($P \leq 0.006$) for the main effect of DO for DMI (Table 3.5). After running Tukey's HSD test, there were significant differences between the all three of the groups ($P \leq 0.017$). Specifically, low DMI cows had 17% fewer DO

relative to medium DMI cows and 34% fewer DO relative to high DMI cows. The medium DMI group was also 14% lower than the high DMI group. Neither DO nor DFC differed significantly among DMI clusters. This contrasts previous research that suggested cows who consumed more required fewer services (Lucy et al., 1992). There was no relationship between DFC and DMI. Research in beef cows suggested a negative phenotypic correlation with DMI (Crowley et al., 2011). This could mean that cows with decreased DMI would require more days to reach their first calving. However, our findings did not support this previous research with no unfavorable relationship seen between DMI and DFC.

Overall, literature on the relationship between reproductive performance and RFI and DMI is inconsistent. As reproduction is largely influenced by environmental conditions, it makes sense that previous research elucidating these relationships with RFI and DMI vary (Berry et al., 2014). This variation within the literature and our own results suggests that the relationship between RFI and DMI and reproductive traits is a complex one. There is no obvious and consistent reduction in fertility. Thus each reproductive trait must be examined individually. Further, other measures of fertility, such as daughter pregnancy rate, must also be researched for their own individual relationship with RFI and DMI. Our own research only looked at three reproductive parameters, two of which, NS and DO, are closely linked ($r_p = 0.68$) (Berger et al., 1981; Chang et al., 2006). The number and variety of reproductive parameters examined must be expanded upon in future research to develop a full understanding of how RFI and DMI may affect reproductive performance.

Additionally, reproduction takes little energy relative to other energy expenditures of cows, so reproduction may be affected more by body stores than by feed intake or feed efficiency (Butler, 2003). This means that a study on changes in BCS (body condition score) in animals with low and high RFI may better reflect the relationship between RFI and reproductive performance. Residual feed intake was shown to have a negative phenotypic correlation (-0.70) with BCS in dairy cows (Vallimont et al., 2011) suggesting that low RFI cows tend to have lower BCS. Another study found positive genetic correlations between BCS and fertility (0.29 to 0.42) (Berry et al., 2003) suggesting that lower BCS would unfavorably impact reproduction. Together, this research suggests that lower RFI cows may have lowered reproductive performance. However, both in our research and in previous studies these are not consistently the

result. Further research must be done to determine why the hypothesized detrimental relationship is not consistently seen.

To continue to elucidate the relationships between RFI and DMI with reproduction several approaches should be considered. First, the impact that selecting feed efficiency would have on reproduction could be more directly measured. Specifically, another study could be performed where dairy cattle are bred for diverging lines of RFI, and the groups compared. Such a study would more clearly highlight the long-term results of breeding for feed efficiency, and could potentially reveal other characteristics of high and low RFI dairy cattle. A second potential direction is to consider other measures of fertility beyond DO, DFC, and NS, for example, the daughter pregnancy rate, calving rate, calving ease, etc.

CONCLUSION

Based on our findings, we failed to reject our hypothesis that increased feed efficiency and decreased feed intake would be significantly associated with decreased reproductive performance. We determined that NS and DO had significant, positive phenotypic correlations with RFI and DFC had a negative phenotypic correlation with RFI. Additionally, NS and DO both had positive phenotypic relationship with DMI, but no relationship with DFC. From the ANOVA tests we ran, NS were significantly lower between low and high RFI cows, DO were significantly lower between low and high DMI cows, and DFC was significantly higher between low and high RFI cows. Based on these findings, we suggest that low RFI cows may require fewer services to become pregnant; however, low RFI heifers may be delayed in producing their first calf.

Overall, there were similar phenotypic relationships between RFI and DMI with reproductive performance. To confirm the phenotypic relationships and to understand the underlying mechanisms associated with these traits, genetic analyses must be conducted.

TABLES

Table 3.1: Descriptive statistics of reproductive and RFI traits in Holstein cows at Virginia Tech and Iowa State University (n = 1,513).

Trait	n	Mean \pm SE	Min	Max
<i>Feed efficiency and components</i>				
RFI ¹ (kg)	1513	0.00 \pm 0.05	-6.35	6.29
DMI ² (kg)	1513	23.51 \pm 0.10	15.18	36.48
Milk Production (kg)	1513	40.82 \pm 0.24	13.72	61.84
Fat Percentage (%)	1513	3.73 \pm 0.02	2.34	5.49
MilkE ³ (Mcal)	1513	28.72 \pm 0.18	9.06	49.09
MWWT ⁴ (kg ^{0.75})	1513	119.40 \pm 0.29	95.33	144.80
Δ BodyE ⁵ (kg)	1513	0.38 \pm 0.01	-0.4494	1.67
Parity	1513	2.06 \pm 0.04	1.00	8.00
<i>Reproductive traits</i>				
NS ⁶ (services)	1337	3.61 \pm 0.079	1	13
DO ⁷ (days)	816	121.50 \pm 2.85	18	292
DFC ⁸ (days)	572	728.36 \pm 1.61	631	842

¹Residual Feed Intake

²Dry Matter Intake

³Net Energy of Lactation

⁴Metabolic BW

⁵Delta Bodyweight

⁶Number of Services

⁷Days Open

⁸Days to First Calving

Table 3.2: R² value for each clustering of cows by feed for each ANOVA model

Clustering Method	DMI ¹			RFI ²		
	NS ³	DO ⁴	DFC ⁵	NS ³	DO ⁴	DFC ⁵
Half-deviation	0.794	0.803	0.798	0.739	0.718	0.744
One-third	0.771	0.760	0.774	0.718	0.691	0.725
Ten-percent	0.629	0.634	0.648	0.636	0.643	0.624
Split-by-mean	0.635	0.636	0.630	0.569	0.548	0.590
K-means	0.816	0.827	0.821	0.749	0.735	0.750

¹Dry Matter Intake

²Residual Feed Intake

³Number of Services

⁴Days Open

⁵Days to First Calving

Cows are clustered into “high”, “medium”, and “low” groups using five different methods.

Note that Split-by-mean results in only “high” and “low” groups.

Table 3.3: Significance (*P*-values) of ANOVA tests run between residual feed intake (RFI) and dry matter intake (DMI) groups for three measures of reproductive performance using five different clustering methods to determine grouping.

Clustering Method	NS ¹	DO ²	DFC
RFI			
Half Deviation	0.006*	0.054	0.002*
One Third	0.005*	0.011*	0.003*
Ten-percent	0.005*	0.016*	0.020*
Split by Means	0.026*	0.003*	0.094
K-means	0.003*	0.054	0.002*
DMI			
Half Deviation	0.277	<0.0001*	0.250
One Third	0.360	<0.0001*	0.057
Ten-percent	0.067	<0.0001*	0.948
Split by Means	0.189	<0.0001*	0.783
K-means	0.199	<0.0001*	0.410

¹Number of Services

²Days Open

³Days to First Calving

*significant *P*-value ($P \leq 0.05$)

Table 3.4: Phenotypic correlations (r_p) \pm SE between residual feed intake (RFI), dry matter intake (DMI), and reproductive parameters¹

Item	$r_p \pm SE$	<i>P</i>-value
RFI		
Number of services	0.18 \pm 0.04	<0.001
Days open (d)	0.18 \pm 0.03	<0.001
Days to first calving (d)	-0.14 \pm 0.04	0.004
DMI		
Number of services	0.17 \pm 0.037	<0.001
Days open (d)	0.22 \pm 0.041	<0.001
Days to first calving (d)	-0.074 \pm 0.047	0.08

¹Pearson correlations were calculated in R based on 1,513 Holstein cows from Virginia Tech and Iowa State University

Table 3.5: Post hoc Tukey's HSD testing for all significant results of ANOVA tests for RFI and DMI based on a Half-deviation clustering method

<i>Residual Feed Intake (RFI)</i>							
Reproductive Trait	High RFI		Medium RFI		Low RFI		P-value
	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	
NS ¹ (serv)	3.95 ^a ± 0.13	375	3.61 ^{ab} ± 0.11	564	3.36 ^b ± 0.13	389	0.006
DO ² (d)	131.27 ± 5.26	175	124.24 ± 3.90	279	114.27 ± 4.99	173	0.054
DFC ³ (d)	719.24 ^a ± 2.53	162	728.44 ^b ± 2.36	238	733.98 ^b ± 3.32	173	0.002

<i>Dry Matter Intake (DMI)</i>							
Reproductive Trait	High DMI		Medium DMI		Low DMI		P-value
	Mean ± SE	n	Mean ± SE	n	Mean ± SE	n	
NS ¹ (serv)	3.78 ± 0.13	306	3.65 ± 0.12	380	3.50 ± 0.12	385	0.277
DO ² (d)	143.85 ^a ± 6.57	210	125.53 ^b ± 4.17	303	107.12 ^c ± 3.36	303	0.006
DFC ³ (d)	706.00 ± 2.76	92	710.62 ± 2.76	143	704.83 ± 2.64	114	0.250

^{abc} Significant ($P < 0.05$) differences between means from ANOVA models comparing RFI and DMI with reproductive traits

¹ Number of services

² Days open

³ Days to first calving

Chapter 4

Genetic parameters between feed efficiency, feed intake, and reproductive performance

ABSTRACT

Holstein cows with decreased residual feed intake (RFI) and dry matter intake (DMI) are desirable for their reduced feed consumption, but selection for these traits may also lead to reduced reproductive performance. We hypothesized that there would be an unfavorable genetic relationship between reproductive traits and feed efficiency and feed intake. In this study, we examined whether DMI and RFI can be genetically selected for independent of number of services (NS), days open (DO), and days to first calving (DFC). To achieve this, the objectives of this study were to estimate heritability and determine genetic correlations between the feed traits (RFI and DMI) and the reproductive traits (NS, DO, and DFC). Daily measurements of DMI, milk yield, weekly milk composition, and monthly body weight were used to calculate RFI on 1,513 Holstein cows at Virginia Tech and Iowa State University. Measures of reproductive performance included number of services (NS; $n = 1,337$), previous days dry (DD; $n = 816$), days open (DO; $n = 860$), and days to first calving (DFC; $n = 572$). Genetic correlations and heritability estimates were calculated in ASReml using a sire model using 2 generation pedigrees. Random and fixed effects included herd, birth season, age, calving season, and dam. There were 190 unique sires with an average of 7 progeny per sire. As expected, heritability estimates for reproductive traits were low ($h^2 \leq 0.09$). Those for RFI and DMI were moderate ($h^2 = 0.24 \pm 0.07$; 0.33 ± 0.08) suggesting opportunity for genetic progress in both of these traits. Genetic correlations were significant and positive for NS with RFI ($r_g \geq 0.22 \pm 0.17$) and DMI ($r_g = 0.12 \pm 0.04$). We observed a moderate positive genetic correlation ($r_g = 0.21 \pm 0.17$) between DO and RFI, but did not detect a relationship with DMI. There was no genetic relationship between DFC and RFI or DMI. Based on these results, we suggest that improvement for RFI and DMI is possible through genetic selection. Additionally, we suggest that genetic selection for decreased RFI or DMI would not unfavorably impact reproductive performance.

INTRODUCTION

Feed is the largest variable operating cost for dairy operations, accounting for roughly 60% of variable costs for typical dairy operations. These input costs may be reduced by selecting for animals with increased feed efficiency or decreased feed consumption. Broadly, an animal is defined as feed efficient when it is able to consume less relative to how much it grows or how much it produces (Van Arendonk et al., 1991). Feed efficiency measure, residual feed intake, is determined using a variety of growth and milk production records (VandeHaar et al., 2016). This inherently allows for decreased feed input costs without impacting production, milk components, or growth. However, there are other areas of performance that are important to dairy producers not included in the prediction model such as health, conformation, temperament, and reproduction. Energy thought to measure true feed efficiency may be in part due to inadequate energy being partitioned for other bodily functions including reproduction (Crowley et al., 2011). Infertility is a primary reason for culling in dairy herds, so its relationship with any trait which may be used in breeding programs must be understood.

Research is being conducted to incorporate RFI, into dairy breeding programs (VandeHaar et al., 2016). Heritability estimates for RFI vary (Table 4.3), but are generally moderate which suggests that RFI could be successfully utilized in breeding programs. However, to safely be used, the genetic relationship between RFI and other relevant traits must be explored. Currently, there is little research on the genetic correlation between RFI and reproductive performance in dairy cows. (Vallimont et al., 2013) determined unfavorable genetic correlations between RFI, daughter pregnancy rate, cow conception rate, and heifer conception rate. Additionally, lower RFI was genetically correlated with later DFC ($r_g = -0.29 \pm 0.14$) in beef cattle (Johnston et al., 2009; Crowley et al., 2011). These researchers hypothesized that this may be due to delayed onset of puberty in low RFI heifers. For either RFI or DMI to be used in dairy breeding programs, this genetic relationship must be better understood. We hypothesized that there would be an unfavorable genetic relationship between reproductive traits with feed efficiency and feed intake. Therefore, the objectives of this study were to estimate heritability and determine genetic correlations between DMI and RFI with reproductive traits.

MATERIALS AND METHODS

Data Collection

All animal procedures were conducted in accordance to each participating University's animal care and use committee. Feed, milk, and reproductive data were collected on 1,513 Holstein cows between 50 and 200 d post-partum at Virginia Tech and Iowa State University for an average of 61 d. Individual daily measurements of DMI, daily milk yield, weekly milk composition, and weekly body weights were collected to calculate RFI. A linear model was created to estimate feed intake and determine individual RFI (VandeHaar et al., 2016):

$$DMI_i = \beta_0 + \beta_1 \times MilkE_i + \beta_2 \times MWWT_i + \beta_3 \times \Delta BodyE_i + Parity + Experiment + Cohort(Experiment) + Diet(Cohort \times Experiment) + \varepsilon_i$$

where DMI_i is the dry matter intake of an individual, β_n are the regression coefficients, $MilkE_i$ is the milk energy output for an individual, $MWWT$ is the metabolic body weight, $\Delta BodyE_i$ is the change in body energy for an individual, and ε_i is the residual error for an individual (aka RFI). Cows with $RFI < 0$ are considered low RFI (i.e., feed efficient) and cows with $RFI > 0$ are considered high RFI (i.e., feed inefficient). Finally, the net energy in milk was calculated based on the gross every per kilogram in fat, protein, and lactose (VandeHaar et al., 2016):

$$MilkE(Mcal) = \left(\begin{array}{l} 0.0929 \times fat\% + 0.0563 \times protein\% \\ + 0.0395 \times lactose\% \end{array} \right) \times \text{daily milk yield}(kg)$$

There were 4 experimental groups that cows belonged to defined by what external experiment, if any, cows were in. Separately from experimental group, each animal also belonged to one herd. Cows were also grouped into cohorts ($n \geq 288$) by when RFI data was collected on them. Cows with $RFI < 0$ were categorized as low RFI animals and were defined as feed efficient. Conversely, cows with $RFI > 0$ were categorized as high RFI and were considered feed inefficient. There were 3 herds in this data: ISU1 ($n = 502$), ISU2 ($n = 446$), and VT ($n = 172$). The ages of the cows ranged from 2 to 9 yrs with an average of 2.65 ± 1.15 yrs. Parity ranged from 1 to 7 with an average of 1.69 ± 1.15 . There were 4 experimental groups that cows in this study were on: A ($n = 105$), B ($n = 533$), C ($n = 382$), and NA ($n = 493$). There were cows born in all four seasons: summer ($n = 281$), fall ($n = 294$), winter ($n = 263$), and spring ($n = 282$). The years the cows were born in ranged from 2000 to 2012 with the average birth year being 2008. Cows also calved in a 4 seasons: summer ($n = 258$), fall ($n = 271$), winter ($n = 320$), and spring ($n = 271$). Cows calved between the years 2008 and 2014 with the majority in 2011.

In addition to the growth and production traits, 3 measures of reproductive performance were examined: number of services (NS) per conception, days open (DO) between calving and conception, and days to first calving (DFC). Reproductive data were gathered from the lactation during in which daily feed intake and weights for RFI were also collected.

Statistical Analyses

All cows with at least 1 reproductive parameter reported were retained within the dataset. Genetic parameters were calculated in ASReml for all feed efficiency and reproductive traits using a sire model. Originally, an animal model was considered because of its effectiveness in evaluating complex traits (Sun et al., 2009). Compared to the animal model, a sire model does not correct for differences between dams (Gilmour et al., 2009). Therefore, calculations were run as though all progeny of sires were from different dams and all dams were from a homogenous population. A sire model was used in this dataset because most dams had only 1 (n = 693) or 2 (n = 213) daughters and all cows were from the same breed.

The following single trait sire model was used to determine heritability for RFI, DMI, NS, DO, and DFC:

$$y = Xb + Zs + e$$

where y was a vector of observations for a trait of interest, b was the vector with fixed effects (selected for each trait), X was an design matrix relating observations y to fixed effects b , s was the vector with random sire effects, Z was an design matrix relating observations y to random sire effects s , and e was a vector of residual errors accounting for the rest of the possible variation. Random effects in sire models are assumed to have zero means. Variances were modeled as follows:

$$\text{var} \begin{bmatrix} s \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_s^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix}$$

where A was the matrix of Wright's numerator relationships and I was the identity matrix with dimensions equal to the height of the vector of observations y . The fixed effects included in each trait's single and multi-trait model were selected using stepwise regression to remove effects that were not significant, until all were significant or none remained. The initial fixed effects for each model were herd, age, parity, ration, birth season, birth year, calving season, and calving year.

Genetic correlations were calculated for each of the 7 trait pairs of interest: RFI with DMI, RFI with each reproductive trait (NS, DO, DFC), and DMI with each reproductive trait

(NS, DO, DFC). This analysis used a bivariate form of the sire model presented above. Heritability estimates and genetic correlations for all traits and their SE were estimated using ASREML (Gilmour et al., 2009). Additive genetic variance was calculated as $4 \times$ the sire variance. Pedigree information included 2 generations: sires, dams, grandsires, and granddams for each cow. There were a total of 190 unique sires used to estimate heritability and determine genetic relationships.

RESULTS AND DISCUSSION

This research demonstrates the genetic relationships between feed efficiency and feed consumption with fertility measures. Heritability estimates are shown in Table 4.1. As expected, there were low heritability estimates for NS, DO, and DFC ($h^2 \leq 0.091 \pm 0.046$), which supports previous literature. A majority of the variation observed in reproductive parameters is attributable to management and(or) environmental factors; making genetic improvement upon these traits difficult (Berry et al., 2014). Researchers performed a meta-analysis on heritability in beef and dairy reproductive traits and found that most female reproductive traits tended to be lowly heritable ($h^2 = 0.02$ to 0.04) (Berry et al., 2014). Number of services and DO in Norwegian reds also had low heritability estimates (Chang et al., 2006). Heritability estimates for NS, calving interval, and DFC in Holsteins were also low (Pritchard et al., 2013). Interestingly, SE associated with our heritability estimates were higher than previous literature. This may be attributed to increased variability or decreased sample sizes within our dataset and not a true deviation from the published literature. Overall, heritability estimates for reproductive traits were low meaning that the rate of genetic change would be slow.

Heritability for RFI and DMI were moderate ($h^2 = 0.24 \pm 0.07$ and $h^2 = 0.33 \pm 0.08$). Table 4.1 contains heritability estimates for both of these traits from the published literature. For RFI in both beef and dairy cattle, these estimates ranged from 0.18 (0.02) to 0.47 (0.12) (Durunna et al., 2013; Templeman et al., 2015). Within dairy animals, heritability estimates ranged from 0.18 (0.02) to 0.38 (0.09) (Pryce et al., 2012; Templeman et al., 2015) Therefore, our heritability estimate for RFI was within the expected range for dairy cows. For DMI in both beef and dairy cattle, the literature had a wide range of heritability estimates from 0.07 ± 0.14 to 0.54 ± 0.15 (Nkrumah et al., 2007; Toshniwal et al., 2008). Two previous studies in dairy cattle had results very similar to those found within this study with heritability estimates of 0.34 ± 0.07

and 0.34 ± 0.11 (De Haas et al., 2012; Spurlock et al., 2012), but another had a lower heritability estimate much less than any other study with 0.07 ± 0.14 (Toshniwal et al., 2008). However, most of the previous studies had results similar to the heritability of DMI (0.33 ± 0.08) that was found within this research. These results provide evidence to suggest that improvement on RFI or DMI is possible through genetic selection.

Though genetic progress is possible for RFI, DMI, and reproductive traits, limited phenotypic information is available on RFI and reproduction. Therefore, repeatability of these traits is expected to be decreased; thereby, decreasing the rate of genetic progress (Henderson, 1963). Potential ways to improve the repeatability of these traits include: the development of standardized recording procedures and access to feed intake measurement systems. However, implementing these strategies could greatly increase production costs and in some cases are not feasible; therefore, we suggest developing genomic breeding values for these traits.

Table 4.2 contains genetic correlations between RFI, DMI and reproductive parameters. With RFI, both NS and DO had moderate, positive genetic correlations ($r_g = 0.22 \pm 0.17$ and $r_g = 0.21 \pm 0.17$, $P = 0.01$). We suggest that genetic selection for low RFI cows (i.e., more feed efficient) will indirectly cause decreases in NS and DO. Decreases in NS and DO would both be beneficial to producers. Decreased NS would result in decreased semen and labor costs since cows would have to be bred fewer times preconception. Decreased DO would result in increased production because producers would be able to dry the cow off while still at acceptable levels of production. However, genetic improvement made for NS and DO will be marginal due to the low heritability of these traits. Therefore, we suggest that selection for RFI will not unfavorably impact NS or DO, but neither will there be a significant beneficial effect. Our results conflict with previous research that determined unfavorable genetic relationships between RFI and fertility (Vallimont et al., 2013). That study used two measures of RFI, but neither were identical to the model used in our research. The first was RFI_{reg} which is calculated by regressing daily DMI on daily milk, fat, and protein yields, body weight (BW), daily body condition score (BCS) gain or loss, the interaction between BW and BCS gain or loss, and days in milk. The second they used was RFI_{NRC} which was estimated by subtracting 305-d DMI predicted according to their fat-corrected milk and BW from actual 305-d DMI. Both utilize similar traits to those components we used, but not identical. Therefore, what exactly RFI measures differs between

these studies which may account for some of the difference seen between our results and those results of Vallimont et al. (2013).

For DFC, Crowley (2011) found that low RFI was genetically correlated with DFC ($r_g = -0.29 \pm 0.14$). Conversely, we determined that DFC was not genetically associated with ($P = 0.36$) with RFI. Our results do not differ greatly from Crowley (2011) as the magnitude of the genetic correlation was fairly low and the variance high. Crowley (2011) hypothesized that selection for RFI was associated with delayed onset of puberty, which was supported by Johnston (2009). Therefore, more directly measuring puberty may expand better on this previously published research than an indirect measure such as DFC. Days to first calving is affected by onset of puberty, but there are other factors that may contribute to variation within this trait such as fertility and ability to maintain pregnancy. Additionally, environmental and management factors both account for a large amount of the phenotypic variation seen within DFC. Overall, our results suggest that selection for RFI will not unfavorably impact DFC.

A possible reason genetic correlations reported between RFI and reproduction may differ from previous research is that SE for our genetic correlations were noticeably high. Additionally, models used to calculate RFI differ between studies, so the trait used here may differ subtly from the RFI trait used in other studies. However, even though SE were increased, mean estimates did not differ greatly from previous research. Additionally, genetic correlations support phenotypic relationships reported in chapter 2. Based on our results we suggest that genetic selection for RFI would not have an unfavorable effect on reproductive performance.

For DMI, only NS had a significant genetic correlation ($r_g = 0.12 \pm 0.04$, $P = 0.05$). This suggests that as feed intake decreases fewer NS would be required to achieve pregnancy. Though favorable, selection for DMI would have a weak impact on NS, the same as the results found for RFI. Contrary to these results, another study on 1,366 Canadian beef cows found no significant genetic correlation between NS and DMI (Mu et al., 2016). The genetic correlation presented in our paper is small and barely reaches the threshold of significance; therefore, our results do not differ largely from the literature. For DFC, the genetic correlation was not significant ($P = 0.21$). Therefore, selection for DMI would likely not have a large effect on DFC. Overall, selection for DMI will not negatively impact reproductive performance.

Neither DMI nor RFI had negative genetic relationships with the reproductive parameters used in this study. Residual feed intake is more independent of growth and production traits than

DMI because RFI is a measure of feed efficiency which takes these traits into account while DMI is only a measure of feed intake. However, the literature shows similarly mixed relationships between both RFI and DMI with fertility. Overall, in terms of reproduction, both of these traits are viable for use as measures in breeding programs, but RFI has the advantage of accounting for additional production traits. Therefore, we suggest that inclusion of RFI into dairy breeding programs would be advantageous as a measure of feed efficiency and would not unfavorably impact reproductive performance.

CONCLUSION

The objective of this study was to find the genetic parameters between RFI and DMI with reproductive traits in dairy cows. The goal was to determine if selection for these feed efficiency traits would detrimentally affect reproductive performance, and to determine how associated the DMI and RFI traits are. As expected, reproductive traits were lowly heritable and feed efficiency and feed consumption was moderately heritable. This suggests that these traits can be improved through genetic selection.

Residual feed intake had no detrimental genetic correlations with the reproductive parameters in this study. Both NS and DO had significant, positive genetic correlations with RFI. This could mean that selection for RFI would have a weak, positive effect for these traits. Low RFI cows requiring fewer services and days to become pregnant would be beneficial for producers, so this is not a detrimental relationship. Additionally, the genetic correlation between RFI and DFC was not significant suggesting that selection for RFI would not have an effect on DFC. Overall, based on the data used for this study, selection for RFI would not negatively impact reproduction.

As is seen with RFI, there were no significant, detrimental genetic correlations between DMI and reproductive performance. Number of services had a significant genetic correlation with DMI; however, the magnitude of this correlation was small. So, selection for DMI may have a weak, positive effect on NS, but not on DO since its genetic correlation was not significant. This would not be detrimental to producers since it is desirable to have a cow who requires fewer services. Days to first calving had no significant genetic correlation with DMI. This suggests that selection for DMI would not impact DFC. Overall, selection for DMI would not negatively impact any of the reproductive traits examined here.

Within this study, both RFI and DMI had neutral to beneficial genetic correlations with NS, DO, and DFC. The heritability estimates of the reproductive traits were also low whereas the feed traits had moderate heritability estimates. Overall, both RFI and DMI may be selected for without unfavorably impacting reproductive performance.

TABLES

Table 4.1: Heritability estimates (h^2) and corresponding SE for RFI, DMI, NS, DO, and DFC¹

Item	$h^2 \pm$ standard error
Residual Feed Intake	0.24 ± 0.070
Dry Matter Intake	0.33 ± 0.08
Number of Services	0.025 ± 0.052
Days Open	0.091 ± 0.046
Days to First Calving	0.072 ± 0.040

¹Heritability estimates are generated using ASReml based on 1,513 Holstein cows from Virginia Tech and Iowa State University

Table 4.2: Genetic correlation (r_g) \pm SE between residual feed intake (RFI) and reproductive parameters¹

	Item	$r_g \pm SE$	<i>P</i>-value
RFI			
	Number of services	0.22 \pm 0.17	0.010
	Days open (d)	0.21 \pm 0.17	0.011
	Days to first calving (d)	-0.04 \pm 0.13	0.360
DMI			
	Number of services	0.12 \pm 0.04	0.050
	Days open (d)	0.06 \pm 0.59	0.290
	Days to first calving (d)	-0.09 \pm 0.16	0.210

¹Genetic correlations were calculated in ASReml based on 1,513 Holstein cows from Virginia Tech and Iowa State University

Table 4.3: Previously published heritability estimates for residual feed intake (RFI) and dry matter intake (DMI) in beef and dairy cattle

Heritability estimate \pm SE	Breed	Citation
RFI		
0.39 \pm 0.03	Post weaning Angus	(Arthur et al., 2001)
0.21 \pm 0.12	Mixed breed beef cattle	(Nkrumah et al., 2007)
0.45 \pm 0.06	Mixed breed beef cattle	(Crowley et al., 2010)
0.22 \pm 0.07	Australian dairy heifers	(Pryce et al., 2012)
0.38 \pm 0.09	New Zealand dairy heifers	(Pryce et al., 2012)
0.47 \pm 0.12	Angus steers	(Durunna et al., 2013)
0.18 \pm 0.02	Holstein cows	(Templeman et al., 2015)
DMI		
0.39 \pm 0.03	Post weaning Angus	(Arthur et al., 2001)
0.54 \pm 0.15	Mixed breed beef cattle	(Nkrumah et al., 2007)
0.07 \pm 0.14	Holstein cows	(Toshniwal et al., 2008)
0.34 \pm 0.07	Dairy cattle	(De Haas et al., 2012)
0.34 \pm 0.11	Holstein cows	(Spurlock et al., 2012)

Chapter 5

Conclusion

The objectives of this study were to determine the phenotypic and genetic relationships between RFI and DMI with reproductive traits in dairy cows. The goal was to determine whether selection for these feed traits would detrimentally affect reproductive performance. There were supplemental goals of determining the relationship between RFI and DMI and heritability estimates for all feed and reproductive traits.

First, these relationships were tested using a series of ANOVA run on NS, DO, and DFC of groups clustered based on RFI and DMI using the Half-deviation method. This method was found to be the most appropriate for clustering in this type of study and is recommended for future work. The results of these ANOVA tests were that NS and DFC both differed significantly ($P = 0.006$; 0.002) when dairy cattle were clustered by RFI, and that DO differed significantly when clustered by DMI ($P = 0.006$). Comparing the means of these groups revealed that low RFI cows had fewer services to become pregnant, but required more days to reach their first calving, and that low DMI cows required fewer DO. Overall, there was no detrimental relationship between RFI and DMI with NS or DO, but lower RFI cows did require more days to reach their first calving.

Heritability estimates were calculated using ASReml to determine how much genetic progress could be made when selecting for these traits. Reproductive traits were lowly heritable ($h^2 \leq 0.091$), which is expected because environmental variation accounts for the majority of the phenotypic variation seen in reproductive traits. This suggests that genetic change for these traits would not be substantial. Both DMI and RFI were moderately heritable ($h^2 = 0.24 \pm 0.07$; 0.33 ± 0.08), suggesting an opportunity for genetic progress in both traits.

The traits were then compared using phenotypic and genetic correlations. Like results found through ANOVA testing, both NS and DO had positive phenotypic correlations with RFI ($r_p = 0.18 \pm 0.04$; 0.18 ± 0.03 , $P < 0.001$) and DMI ($r_p = 0.17 \pm 0.04$; 0.22 ± 0.03 , $P < 0.001$). Also, as in the ANOVA results, DFC had a negative phenotypic correlation with RFI ($r_p = -0.14 \pm 0.04$, $P < 0.001$). However, some of these relationships did not hold true for genetic correlations. Both NS and DO still had significant, positive genetic correlations with RFI ($r_g =$

0.22 ± 0.17 ; 0.21 ± 0.17 , $P \leq 0.011$) meaning that selection for RFI may weakly effect NS and DO. Only NS had a significant genetic correlation with DMI ($r_g = 0.12 \pm 0.04$, $P = 0.05$) meaning that selection for DMI may also weakly effect NS. Days to first calving did have a significant genetic correlation with either RFI or DMI ($P \geq 0.21$). Therefore, despite significant phenotypic differences and negative phenotypic correlations, selection for DMI or RFI should not negatively impact DFC. Therefore, there were no detrimental genetic correlations between DMI or RFI and any of the reproductive parameters used here.

In conclusion, fertility traits are lowly heritable, there were no detrimental genetic correlations. Phenotypically, low RFI and DMI cows had detrimental correlations with DFC, but this was not seen in later genetic testing. Therefore, selection for RFI or DMI would not negatively impact reproduction in Holstein cows.

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