RESIDUAL FEED INTAKE IN LACTATING HOLSTEIN DAIRY COWS FED HIGH AND LOW STARCH DIETS: REPEATABILITY AND RELATIONSHIP WITH DIGESTIBILITY

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ABSTRACT

RESIDUAL FEED INTAKE IN LACTATING HOLSTEIN DAIRY COWS FED HIGH AND LOW STARCH DIETS: REPEATABILITY AND RELATIONSHIP WITH DIGESTIBILITY

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Increased product demand accompanied by a simultaneous reduction in resources has put pressure on livestock producers to improve feed efficiency. Residual feed intake (RFI) is one of many tools used to quantify feed efficiency and is defined as the difference between observed feed consumption and predicted consumption based on performance. Residual feed intake assists in identification of animals that convert consumed energy into energy of product more efficiently than contemporaries. Use of modern selection tools will enable more rapid advancements in feed efficiency; however, it is important that cows that are efficient under current conditions are also efficient when subjected to conditions of the future. Furthermore, there are likely physiological and metabolic mechanisms that differ among high and low efficiency cows. Four separate experiments were conducted to determine the repeatability of RFI across high and low starch diets as well as the relationship between digestive efficiency and RFI. Additionally, the relationships between RFI and blood metabolites that are indicators of carbohydrate metabolism and energy partitioning were studied. We determined that RFI was highly repeatable across high and low starch diets, and that digestibility may account for some variation in RFI. We conclude that cows that are efficient when fed diets common at present will probably also be efficient when fed diets in the future that will likely be higher in byproduct type feeds.

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KEY TO ABBREVIATIONS

ΔBCS = BCS change

ΔBodyE = Body energy change

ΔBW = BW change

BCS = Body condition score

BHBA = β-hydroxybutyrate

BUN = Blood urea nitrogen

BW = Body weight

CP = Crude protein

DE = Digestible energy

DM = Dry matter

DMI = Dry matter intake

FCR = Feed conversion ratio

GE = Gross energy

HI = High starch diet

HRFI = High RFI cows

HS = High starch diet

iNDF = indigestible NDF

IOFC = Income over feed cost

LO = Low starch diet

LRFI = Low RFI cows

LS = Low starch diet

MBW = Metabolic BW

ME = Metabolizable energy

MilkE = Milk energy output

MM = Multiple of maintenance

MRFI = Medium RFI cows

NE = Net energy

NEFA = non-esterified fatty acids

NFC = Non-fibrous carbohydrate

NFFS = Non-forage fiber sources

NDF = Neutral detergent fiber

RFI = Residual feed intake

SCC = Somatic cell count

SNP = Single nucleotide polymorphism

VFA = Volatile fatty acid

CHAPTER 1

LITERATURE REVIEW

ENERGETICS AND FEED EFFICIENCY

Energy Flow

Gross energy (GE), the total combustible energy of the feed consumed by an animal, is converted to digestible energy (DE) after digestion and energy is lost in feces. Digestible energy is used for metabolism that results in the production of urine and gases, such as methane. The energy spared after this conversion is called metabolizable energy (ME). Metabolizable energy becomes net energy (NE) after energy is lost as heat associated with feed intake. Net energy is then partitioned to milk production, body tissue gain, or maintenance. The energetic efficiency for the conversion of ME to NE is assumed to be the same, regardless of whether NE is used for milk production, body reserve gain, or maintenance (NRC, 2001). There are three major energy sinks in a lactating cow (Coppock, 1985). For a 600 kg cow producing 40 kg of 4% fat-corrected milk, fecal output accounts for 35% of GE intake, heat production accounts for 31% of GE intake, and milk production accounts for 26% of GE intake. Of energy dissipated as heat for the same cow, 23.5% is associated with maintenance and 76.5% is due to catabolic, anabolic, fermentation, and digestion processes associated with feed intake (Coppock, 1985). It appears that an increase in the energy partitioned to milk production and a decrease in energy lost in feces and heat will have the greatest impact on feed efficiency.

Dilution of Maintenance

Selection for greater milk yield in the past has enhanced feed efficiency in dairy cattle through the dilution of maintenance (Moe & Tyrrell, 1975; Tyrrell, 1980; Coppock, 1985; VandeHaar, 1998). As an animal produces more milk and consumes more feed to support greater production, a smaller proportion of the feed consumed is partitioned toward energy required for maintenance. Gains in efficiency from diluting maintenance requirements diminish as a cow consumes more as a multiple of maintenance (Tyrrell, 1980). This is partially due to a reduction in digestive efficiency that is associated with greater feed intake (Moe & Tyrrell, 1975; Tyrrell & Moe, 1975). The optimal multiple of maintenance to minimize fecal losses per unit of milk is likely about four or five (VandeHaar, 1998). Many modern high producing dairy cows have met or exceeded intake levels of three to four times maintenance requirement, making it unlikely that future increases in production will facilitate great advances in feed efficiency.

Energy Partitioning

Dairy cows can be more efficient by partitioning a greater proportion of nutrients to milk, increasing digestive ability, having a lower energy requirement for maintenance, and reducing energy losses associated with metabolism (Bauman et al., 1985). Bauman and coworkers (1985) concluded that large variation exists between animals for nutrient partitioning, but that differences for digestive ability and maintenance requirement per unit of BW were unapparent. More recently, others determined that steers and barrows divergent for feed efficiency showed differences in the percent of GE consumed partitioned to product rather than methane or heat (Nkrumah et al., 2006; Barea et al., 2010). There is also a genetic component related to the partitioning of NE to milk, rather than to maintenance and body tissue gain (Veerkamp &

Emmans, 1995; Friggens et al., 2011), which could be related to the dilution of maintenance that accompanies high levels of milk production or an improvement in the conversion of ME to NE. The genetic propensity to partition more energy into milk than into body tissue gain is evident in early to mid-lactation, when cows are in negative energy balance and mobilizing body reserves to support milk production (Coppock, 1985; Yan et al., 2006). In addition to improving efficiency through direct selection for nutrient partitioning, it is also possible to improve gross energetic efficiency by increasing an animal's digestive ability through diet manipulation (Tyrrell, 1980; Bauman et al., 1985; VandeHaar, 1998).

QUANTIFICATION OF FEED EFFICIENCY

Many methods are utilized to quantify feed efficiency in livestock, with the most simple quantification of feed efficiency in the dairy industry being the milk:feed ratio, or the amount of milk produced per unit of feed intake (Hooven et al., 1972; Britt et al., 2003). Milk:feed, although applicable and straightforward, does not account for energy content of milk output, the energy derived from body tissue, or the energy required for maintenance. Milk:feed can be adjusted to an energy basis (Dickinson et al., 1969; Grieve et al., 1976; Custodio et al., 1983; Blake & Custodio, 1984), making it a less biased tool to describe efficiency than the uncorrected ratio.

Both milk:feed and energy-corrected milk:feed fail to account for the mobilization of body reserves, which allows for bias toward animals that mobilize more body tissue to support milk production. Excessive tissue mobilization can lead to metabolic disorders, which can negatively impact future performance. For this reason, accounting for the energy contribution of body reserves to milk production and the energy that a cow partitions to body reserves is of interest when considering ways to assess feed efficiency in lactating cows. Efficiency can also be defined as the amount of energy required by a cow to produce one unit of milk solids after energy for maintenance and tissue gain are considered (Prendiville et al., 2009). Still, another way to define feed efficiency in dairy cattle is gross efficiency, which is the percentage of total energy consumed that is captured in milk and body tissues (VandeHaar and St-Pierre, 2006). The advantage of including the energy of body tissue gain or loss in the quantification of feed efficiency in lactating dairy cattle is obvious; using this approach, it is possible to distinguish the difference between a cow that is efficient due to excessive tissue utilization and one that possess a superior ability to convert feed into product. Despite this advantage, gross efficiency is not a perfect tool for identifying both the most feed efficient and most desirable dairy cows. Cows that are feed efficient, as determined by gross efficiency, may convert feed into product more efficiently, but no distinction is made as to whether that product is milk or body tissue.

Quantification of feed efficiency in beef cattle is less complicated than that for dairy cattle because excessive mobilization of body reserves to support milk production is not an issue in the beef industry. In beef cattle, tools used to examine feed efficiency include: feed conversion ratio (unit of feed intake over unit of gain, FCR), average daily gain (ADG), partial efficiency of growth (ADG divided by feed intake after adjusting for the feed energy partitioned toward maintenance), and gain per unit of $BW^{0.75}$ (Arthur et al., 2001). Regardless of species, the purpose of quantifying feed efficiency is the same: to identify animals that have a superior ability to produce the most product with the least amount of input and waste, without compromising health and well-being.

Although gross efficiency is a less biased method to define feed efficiency than both milk:feed and energy-corrected milk:feed in dairy cattle, both are influenced by level of milk production. Higher producing cows are more efficient because they partition more energy toward milk and body tissue than to maintenance. However, it is not likely that rapid advances in efficiency will be achieved through the dilution of maintenance in the future because some of the highest producing cows already eat at multiples of maintenance of four or five, where marginal improvements in feed efficiency are much lower (VandeHaar, 1998). Further improvements in feed efficiency may be attainable if cows that convert GE to DE, DE to ME, or ME to NE for milk or body gain more efficiently are identified for selection.

RESIDUAL FEED INTAKE

An alternative approach to quantify feed efficiency in livestock is residual feed intake (RFI). Residual feed intake is a tool used to assess feed efficiency independent of growth, body size, and milk production. Residual feed intake was first defined for beef heifers and bulls as feed intake adjusted for growth requirements (Koch et al., 1963). They described efficiency as the difference between observed feed intake and predicted intake based on growth performance and expected maintenance requirement (Koch et al., 1963). Animals that consume less than expected have a low RFI and are more efficient. Unlike milk:feed and gross efficiency, RFI can account for all three fates of ME in a lactating cow: milk production, BW gain or loss, and maintenance. Residual feed intake determines feed efficiency within a production level and thus, is not influenced by the dilution of maintenance. Because it is independent of maintenance requirement, RFI and dilution of maintenance can both be used as tools to improve feed efficiency separately. Residual feed intake can be applied to aid identification of animals that are more efficient due to improved digestive or metabolic potential, or those that have a lower maintenance requirement per unit of BW than predicted. In other words, animals that are more efficient (low RFI) are those that have the ability to convert GE to NE more efficiently than contemporaries. Figure 1.1 shows how RFI fits into the energy flow through a cow. Cows that lose less energy as feces, urine, gas, and heat are those that are most efficient when using RFI to define efficiency.

Residual feed intake is used to characterize feed efficiency in beef cattle (Arthur et al., 1996; Herd et al., 2004; Koch et al., 1963; Nkrumah et al., 2006; Richardson and Herd, 2004) and swine (Arthur et al., 2008; Barea et al., 2010; Nguyen et al., 2005). More recently, the use of RFI to quantify efficiency in dairy cattle production systems is of interest due to rising feed costs and environmental concerns related to animal production systems (Connor et al., 2013; Green et al., 2013).

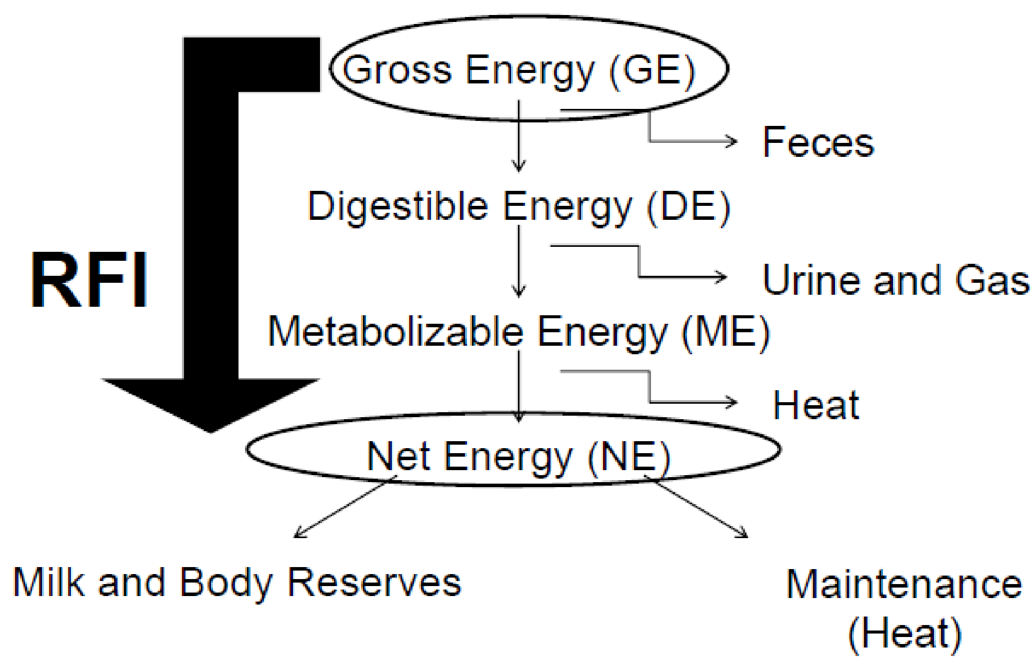

Figure 1.1. Feed energy flow through a cow. Residual feed intake allows for the identification of energetically efficient animals. Efficient animals are those that convert gross energy (i.e. total energy intake) into net energy more efficiently by reducing energy losses in feces, urine, gas, and heat. These animals have superior digestive or metabolic processes or a lower maintenance requirement per unit of BW than expected.

Using RFI to define efficiency is advantageous for many reasons. First, its independence of production level enables the identification of efficient animals without reliance on the dilution of maintenance which may allow for more rapid advances in feed efficiency than a sole reliance on the dilution of maintenance. When incorporated into selection indices, RFI will enable selection for energetic efficiency without altering milk production traits. Residual feed intake allows for the identification of animals that convert GE to NE more efficiently, which gives the livestock industry opportunity to improve sustainability through waste reduction. By definition, RFI is independent of BW gain or loss, and as such should not bias selection toward cows that are too fat or too thin. Furthermore, low RFI cows are economically valuable because they eat less than expected for a given level of production when compared to cohorts and thus daily feed costs for these animals are lower.

RFI and Other Tools to Assess Efficiency

Residual feed intake has been utilized for over fifty years to assess feed efficiency in beef cattle (Koch et al., 1963) and is an alternative tool used to quantify feed efficiency independent of production level. Common tools used to evaluate feed efficiency in beef cattle, such as FCR, unit gain/unit $BW^{0.75}$, the gain:feed ratio, and partial efficiency of growth, and dairy cattle, such as milk:feed and gross efficiency, are not independent of production level. Consequently, selection for these traits parallels selection for greater milk production. Because RFI is independent of production level, its correlation with the more simple efficiency parameters is limited, although not absent (Koch et al., 1963; Arthur et al., 1996; Arthur et al., 2001; Nguyen et al., 2005; Kelly et al., 2010b; Vallimont et al., 2011). Using RFI as a tool to assess feed efficiency can be difficult due to economic costs associated with the collection of individual performance data for feed intake (Nguyen et al., 2005). Correlations between RFI and the more practical methods used to quantify feed efficiency may provide opportunity to identify efficient animals without direct measurement of RFI.

Residual feed intake was negatively correlated with milk:feed and energy-corrected milk:feed in lactating dairy cattle (Vallimont et al., 2011). In agreement, Connor and others (2013) determined that dairy cows with low RFI had greater energy-corrected milk:feed than high RFI cows. Others found that RFI was negatively correlated with gain:feed in beef cattle (Arthur et al., 1996; Arthur et al., 2001; Kelly et al., 2010b) and swine (Nguyen et al., 2005). Data from beef steers separated into high and low RFI groups indicated that FCR was lower and partial efficiency of gain was greater for low RFI animals, but no differences in daily gain per unit of $BW^{0.75}$ were observed (Nkrumah et al., 2006). In contrast, Lawrence et al. (2011) did not identify significant differences in FCR for high and low RFI pregnant heifers. Ratio traits such as FCR and milk:feed favor a reduction in DMI without depression in production. Residual feed intake in both beef and dairy cattle was positively correlated with DMI (Arthur et al., 2001; Mäntysaari, et al., 2012), which could explain its moderate correlation with ratio traits that utilize feed intake in their computation. The lack of relationship between RFI and gain per unit of $BW^{0.75}$ (Nkrumah et al., 2006) is not surprising, given that predicted feed intake is based on performance and predicted maintenance requirement, and therefore, RFI should not be related to either variable considered in this particular ratio.

Selection for Residual Feed Intake

For years livestock producers have attempted to improve feed efficiency through selective mating decisions. Milk production is positively correlated with milk:feed, meaning that selection for either will improve the other (Veerkamp & Emmans, 1995). In the past, selection for greater milk production has been accompanied by increased efficiency due to the dilution of maintenance. Feed intake and milk production are heritable traits in dairy cattle, with estimates ranging from 0.16 to 0.49 and 0.16 to 0.50, respectively (Veerkamp, 1998). Given that both feed intake and milk production are moderately heritable, it seems reasonable to assume that feed efficiency ratios (milk:feed, gain:feed, gross efficiency) will also be heritable. Feed efficiency ratios are heritable in lactating cows with estimates similar to those for milk yield (Van Arendonk et al., 1991; Veerkamp, 1998), although estimates as low as 0.14 are reported (Vallimont et al., 2011). Similar heritability estimates for feed efficiency ratios and feed intake are observed for beef cattle (Schenkel et al., 2004), broilers (Mignon-Grasteau et al., 2004; De Verdal et al., 2011), and swine (Cai et al., 2008).

As a proposed alternative approach for the assessment of feed efficiency, it is imperative that RFI is also heritable such that progress toward superior efficiency will continue in the future. There is overwhelming evidence that RFI is heritable in livestock. Residual feed intake is moderately heritable ($h^2 = 0.15$; Tempelman et al., 2013) in lactating dairy cows, with estimates ranging from 0.01 to 0.38 (Veerkamp et al., 1995; Vallimont et al., 2011). Estimates for the heritability of RFI in beef cattle range from 0.38 to 0.62 (Archer et al., 1997; Schenkel et al., 2004). Residual feed intake is also heritable in swine (Nguyen et al., 2005; Cai et al., 2008), broilers (Mignon-Grasteau et al., 2004; De Verdal et al., 2011), and mice (Archer et al., 1998). The moderate to low heritability of RFI indicates that selection for it will be successful in improving energetic efficiency.

Incorporating a trait like RFI into a selection index is desirable because it is independent of milk production. Because RFI quantifies energetic efficiency within a production level, selection pressure can be applied to improve feed efficiency without placing more emphasis on milk production than is desirable. Too much emphasis on milk production may remove emphasis on other economically important traits such as fertility and health traits. Ratio traits, like milk:feed and gross efficiency, might place extra emphasis on milk production if included in a selection index since they are highly correlated with milk production.

The first step to using any trait in genetic selection is to identify superior animals for that particular trait. To determine RFI, individual production and feed intake performance is recorded during a given period. The ideal test period for an accurate estimate of RFI is between 35 and 70 d, depending on the frequency of performance measurements (Archer et al., 1997; Arthur et al., 2008). Due to facility and economic constraints, it is impractical for most commercial dairy producers to estimate RFI for individual females on the farm. The frequent use of artificial insemination in the dairy industry (Capper et al., 2009) may allow for performance testing of bulls and selection for RFI could be accomplished through breeding all cows to low RFI bulls. With the advent of new genetic technologies, it may be possible to expedite advances in energetic efficiency by using genomics to aid in the identification of low RFI animals. Recent studies suggest that genomic technology may be implemented to successfully identify animals that are superior for RFI. A study using beef steers indicated that 150 single nucleotide polymorphisms (SNPs) were related to RFI, and 23 were highly significant (Sherman et al., 2010), though others found that only 25 SNPs were associated with RFI in beef steers (Karisa et al., 2013). Pryce et al. (2012) determined that 8 SNPS were affiliated with RFI in Holstein heifers. By implementing genomics, not only would bulls be assessed for RFI at a younger age, but low RFI females could also be identified; thus, it would be possible to mate efficient bulls to efficient cows to facilitate more rapid progress for energetic efficiency in the dairy industry.

FEED EFFICIENCY AND ANIMAL HEALTH AND PERFORMANCE

Feed efficiency is important to farm profitability and environmental stewardship; however, it is imperative that selection for improved efficiency does not compromise animal health and reproductive performance, which are also vital to the success of the industry. Feed efficiency is a reduction of input (feed) while increasing output as product (milk and body gain), while minimizing energy losses through feces, gas, urine, and heat. When feed intake is not sufficient to provide the nutrients required for maintenance and performance, animals mobilize body reserves to mitigate the deficit. Milk production is a high priority for animals in early lactation and mobilization of body reserves to support increased energy demand occurs during this time. As body tissue utilization increases and body condition decreases, females are at risk for decreased reproductive performance due to a longer postpartum anestrous period (Butler et al., 1981) and metabolic problems associated with negative energy balance (Collard et al., 2000).

Reproductive Performance

Research in beef cattle (Arthur et al., 2005; Basarab et al., 2007; Blair et al., 2013), swine (Young et al., 2010; Gilbert et al., 2012), and mice (Hughes and Pitchford, 2004) focus on the reproductive performance of animals divergently selected for RFI. Beef cows of a low RFI line (Arthur et al., 2005) and dams of low RFI calves (Basarab et al., 2007) had greater fat thickness and calved 5-6 d later than high RFI cows, though Blair et al. (2013) did not observe differences between high and low RFI lines for calving date. Cows from the low RFI line tended to calve 5 d later than cows in the high RFI line (Arthur et al., 2005), suggesting that these females might have had a longer postpartum anestrous period or took longer to conceive than high RFI cows. However, there was no evidence for differences in pregnancy rate, calving rate, weaning rate

(Arthur et al., 2005; Basarab et al., 2007) or first service conception rate (Blair et al., 2013) among high and low RFI groups. Lactating sows from low RFI lines mobilized more body fat, lost more BW during lactation, and produced more live piglets that grew faster than those from high RFI lines (Young et al., 2010; Gilbert et al., 2012) and no difference in time to rebreeding was determined (Gilbert et al., 2012). In contrast, lower prolificacy was associated with the low RFI line in mice (Huges and Pitchford, 2004). The results from these studies suggest that the relationships between RFI and reproductive performance and body reserve utilization may be present but are variable depending on the species of interest. More research is required to determine if a true relationship between RFI and reproductive traits exists. Studies in dairy cattle have yet to examine the relationship between RFI reproductive performance, although by definition, RFI should be independent of BW change.

Animal Health

Few studies have examined the relationship between feed efficiency and animal health. In lactating dairy cows, Søndergaard et al. (2002) defined feed efficiency as energy requirement over energy intake, and examined its relationship with various other traits including those related to udder health. No phenotypic correlation between efficiency and somatic cell count (SCC) was observed; however, there was a negative genotypic correlation (r=-0.37) between efficiency and SCC. A strong positive genetic correlation between SCC and body tissue mobilization was observed (Søndergaard et al., 2002), which supports the idea that energy deficiency is associated with a weakened immune system. Others (Lawrence et al., 2012) saw a greater white blood cell count in beef heifers with high RFI when compared with medium and low RFI heifers, although lymphocyte, neutrophil, and red blood cell counts were not significantly different among the groups. In contrast, Richardson et al. (2002) measured immune cell parameters for beef steers and determined that sire breeding value for RFI was negatively related to and white blood cell count and lymphocyte percentage, but positively associated with neutrophil percentage.

Animals that are efficient consume less feed to produce the same amount of product as their contemporaries. Ratio measures of feed efficiency (milk:feed or FCR) do not account for body tissue utilization, and thus selection for these may have unfavorable effects on the energy balance of the lactating cow. Residual feed intake, by definition, accounts for body weight change and thus should be independent of body tissue mobilization during lactation.

SOURCES OF VARIATION IN RESIDUAL FEED INTAKE

Because RFI quantifies differences in feed intake independent of production level, it is likely that underlying physiological and biological processes allow some animals to eat less than others. Some animals may have a lower maintenance requirement than expected, have greater digestive efficiency, lose less energy as the heat increment of feeding, or have greater metabolic efficiency and lose less energy as urine and gas. Richardson and Herd (2004) estimated that sources of variation for RFI in beef cattle include: feeding pattern (2%), body composition (5%), protein turnover and tissue metabolism (37%), heat increment of feeding (9%), digestive efficiency (10%), physical activity (10%), and other unknown metabolic processes (27%). Most of these sources of variation largely influence maintenance requirements, but differences in methane production (Hegarty et al., 2007) and digestibility may also be important.

Animal Activity and Behavior

Richardson and Herd (2004) hypothesized that differences in animal activity and behavior may account for 12% of variation in RFI. Many have examined differences in feeding behavior and activity among high RFI and low RFI animals and provide insight as to whether efficient animals are less active than inefficient animals.

Feeding activity. Research in beef steers, pigs, and dairy heifers has been focused on daily eating time and the number of meals per d (De Haer et al., 1993; Nkrumah et al., 2006; Montanholi et al., 2010; Durunna et al., 2011; Williams et al., 2011; Green et al., 2013), although results are conflicting. Inconsistent results are also reported for eating rate among high and low RFI beef and dairy animals (Golden et al., 2008; Kelly et al., 2010a; Kelly et al., 2010b; Montanholi et al., 2010; Durunna et al., 2011; Williams et al., 2011; Green et al., 2013). Diurnal variation in feed consumption among high and low RFI lines has also been examined in beef and dairy animals (Montanholi et al., 2010; Lawrence et al., 2011; Green et al., 2013), with high RFI cattle consuming more feed during afternoon and night hours. These results suggest that there may be differences among high and low RFI animals in regard to feeding patterns and behavior, although consistent results among species are lacking.

General Activity. In addition to feeding behavior, high and low RFI animals may also differ in general activity levels, such as standing, walking, and lying times. Low RFI Bos indicus beef steers tended to spend more time more time lying and less time standing than high RFI steers (Gomes et al., 2013), but high and low RFI periparturient Bos taurus heifers RFI did not differ in total standing, lying, or active time (Lawrence et al., 2011). Furthermore, Luiting and coworkers (1994) suggested that animals with low RFI may be less susceptible to stress and demonstrate less anxiety and nervous behavior, which would reduce energy losses from activity. It is likely that animals that have low RFI spend less energy for activity than those with high RFI, thus decreasing their maintenance requirement (Luiting et al., 1994).

Body Composition

Richardson and Herd (2004) estimated that differences in body composition account for ~5% of the variation in RFI, although body composition should already be considered in the determination of RFI due to differences in the energy content of fat and protein. For beef cattle, residual feed intake is calculated by regressing DMI on MBW and ADG, and the composition of gain is often not considered. Beef cattle with low RFI are reportedly leaner than animals with high RFI (Basarab et al., 2003; Kelly et al., 2010a; Kelly et al., 2011), and plasma leptin concentration was positively correlated with RFI (Richardson and Herd, 2004), indicating that high RFI cattle had more body fat. The influence body composition has on RFI may be dependent on an animal's maturity and physiological state when RFI is measured (Herd and Arthur, 2009). Gain:feed for growing animals is expected to be greater than that of finishing animals because growing animals deposit more lean than fat. For accurate determination of RFI, composition of body gain should be quantified and energy content of gain should be used in the model, rather than ADG.

Heat and Methane Production

Heat and methane production can influence an animal's efficiency because an increase in either results in decreased efficiency of conversion of DE to NE for production. It is estimated that heat production related to feeding accounts for 9% of the variation in RFI for beef cattle (Richardson and Herd, 2004), but methane production was not considered in that assessment.

Heat production. As might be expected, heat production associated with maintenance, activity, and the heat increment of feeding was greater for high RFI steers (Richardson et al.,

2001) and total heat production was greater for high RFI steers (Basarab et al., 2003; Nkrumah et al., 2006). Furthermore, body surface temperature was positively correlated with RFI for beef steers (Montanholi et al., 2010). During both fasting and re-feeding, low RFI chickens produced less heat than high RFI chickens (Swennen et al., 2007), suggesting that low RFI birds have a lower heat increment of feeding. These results support the hypothesis that animals that have high RFI lose more energy as heat that could have otherwise been used for production.

Methane production. Differences among high and low RFI cattle for methane production are also reported, with low RFI steers producing less methane per day than high RFI steers (Nkrumah et al., 2006; Hegarty et al., 2007). These results suggest that selection for animals with lower RFI may also reduce methane production which would further improve the environmental sustainability of livestock production.

Digestibility

It is estimated that digestibility accounts for up to 10% of the variation in RFI for beef cattle (Richardson and Herd, 2004) and it is hypothesized that digestibility may be more important in ruminants than monogastrics (Luiting et al., 1994; Herd and Arthur, 2009). Differences in rumen microbial population and rumen environment are reported for high and low RFI cattle (Lawrence et al., 2011; Carberry et al., 2012; Hernandez-Sanabria et al., 2012), which may influence digestive efficiency.

Digestibility and RFI in cattle. Some publications have shown that efficient beef cattle have improved digestibility (Richardson and Herd, 2004; Nkrumah et al., 2006; McDonald et al., 2010), while others reported no differences for digestibility (Lawrence et al., 2012). Compared to low RFI steers, high RFI steers lost 16% more energy in feces as a percent of GE intake (*P*=0.14; Nkrumah et al., 2006). Furthermore, digestibility of DM was negatively correlated with RFI for beef steers and cows (Richardson and Herd, 2004; Nkrumah et al., 2006; McDonald et al., 2010), indicating that animals that were efficient had improved digestibility. Residual feed intake also tended to be correlated with digestibility of CP but not NDF (Nkrumah et al., 2006). In contrast, digestibility was not different between high and low RFI lines of gestating beef heifers (Lawrence et al., 2012), which was attributed to the type of diet (high forage) that was fed.

The relationship of digestibility and overall feed efficiency is complicated by the fact that feed intake as a multiple of maintenance influences digestive efficiency, with digestibility decreasing as intake increases (NRC, 2001). Thus, animals that eat less per unit of production (low RFI animals) would be expected to have greater digestibility simply because they eat less. Do these animals eat less because they are better at digesting food? Or do they digest food better because they eat less? McDonald et al. (2010) reported that DMI was not related to digestibility, but very few studies have examined the relationship of digestive and overall efficiency.

Interaction between digestive efficiency and diet. One study of broilers divergent for digestive efficiency indicated that the high digestive efficiency line had lower RFI than the low digestive efficiency line (Mignon-Grasteau et al., 2004). A later generation of these broiler lines was studied to determine the influence of diet particle size on digestive efficiency (Rougière et al., 2009). Results from Rougière and coworkers (2009) showed that the broilers selected for high digestive efficiency had lower feed intake, higher gain:feed, and greater digestion than those selected for low digestive efficiency for all of the diets fed. However, when a coarse-particle diet was fed to the low line, an increase in gizzard and pancreas mass was observed and digestive efficiency increased (Rougière et al., 2009). Rougière et al. (2009) concluded that the low digestive efficiency line required stimulation by coarse particles to increase mass of these organs in order to improve digestive efficiency, whereas the high efficiency line had already achieved superior digestive efficiency and did not require such stimulation. These results suggest that digestive efficiency may be influenced by the type of diet fed and that animals may differ in their response to a particular diet depending on their efficiency status.

Rumen microbial population. Differences in the rumen microbial population may influence digestive efficiency and the amount of energy that an animal can extract from its feed. Some (Carberry et al., 2012; Hernandez-Sanabria et al., 2012) determined differences in rumen population among high and low RFI cattle, while others (Rius et al., 2012) did not. Thus, rumen microbial population may influence RFI, but this influence could be altered depending on the type of diet fed (Carberry et al., 2012). Rumen microbial population may also be modulated by factors specific to an individual animal, such as genetics (Hernandez-Sanabria et al., 2013). Thus, it seems reasonable that microbial populations among high and low RFI cattle may be different, although whether or not these differences influence digestive efficiency is unknown.

Physiology and Metabolism

Richardson and Herd (2004) suggested that physiology and metabolism may account for up to 64% of the variation in RFI in beef cattle. These biological processes have a large influence on the maintenance requirement of an animal, which is hypothesized to be the greatest source of variation in RFI (Luiting et al., 1994). Alterations in mitochondrial function, tissue metabolism, and organ size may modify an animal's maintenance requirement. However, the proportion of consumed energy that is required for maintenance is much lower for a lactating dairy cow than that of a growing beef animal. Thus, differences in maintenance requirements may be less influential in determining RFI for a lactating cow.

Mitochondrial function. Animals with more efficient mitochondrial function may be more feed efficient since mitochondria produce 90% of the energy needs for a cell (Bottje and Carstens, 2009). Low RFI steers had better mitochondrial coupling, improved efficiency of electron transport, and an increase in electron flux through the respiratory chain than high RFI steers (Kolath et al., 2006). Improved coupling activity would increase the proportion of energy that is harnessed as ATP rather than lost as heat, thus increasing the proportion of ME that is captured as NE in low RFI animals.

Oxidative stress is also related to RFI, with greater oxidative stress in high RFI animals (Bottje et al., 2002). Bottje and Carstens (2009) showed that the concentration of protein carbonyls, which can indicate oxidative stress, was elevated for high RFI broilers. Up-regulation of certain genes associated with oxidative stress and coping with this stress in high RFI cattle (Chen et al., 2011) further supports the idea that inefficient animals produce more reactive oxygen species. A reduction of oxidative stress among low RFI animals could improve the efficiency of mitochondrial function by reducing oxidative damage to mitochondrial components.

Tissue metabolism. Protein turnover and tissue metabolism are estimated to account for 37% of the variation in RFI (Richardson and Herd, 2004). Protein turnover is energetically expensive (Herd et al., 2004), and therefore, increased turnover could be expected to increase maintenance requirements. Castro Bulle et al. (2007) provided evidence for this relationship in beef steers. They determined that the degradation rate of myofibrillar protein was positively related to maintenance requirement. Inconsistent results for the relationship between protein turnover and RFI in beef cattle have been reported. High RFI cattle may (Richardson et al., 2001; Richardson et al., 2004) or may not (Castro Bulle et al., 2007; Lawrence et al., 2012) have a greater rate of protein turnover than low RFI cattle.

Changes in energy partitioning may also influence RFI, and analysis of plasma metabolites could provide insight to these changes and how partitioning may be different among cattle with high and low RFI. Conflicting relationships between RFI and plasma metabolites have been reported. Plasma insulin concentration was positively correlated with RFI in finishing heifers and steers (Richardson et al., 2004; Kelly et al., 2010b), but insulin concentration was not related to RFI and was not different between RFI lines of growing heifers (Kelly et al., 2010a; Lawrence et al., 2012). Increased plasma insulin could result in greater fat deposition, which is consistent with the greater backfat thickness of high RFI growing heifers (Kelly et al., 2010a). Plasma NEFA was negatively correlated with RFI (Kelly et al., 2010a) or positively correlated with RFI (Lawrence et al., 2012) for growing beef heifers, and was not related to RFI for finishing heifers (Kelly et al., 2010b). Plasma concentration of β-hydroxybutyrate (BHBA) was positively correlated with RFI (Richardson and Herd, 2004; Kelly et al., 2010a; Kelly et al., 2010b), suggesting increased lipolysis in high RFI animals.

Organ size. Various results for the differences between high and low efficiency animals for organ size are reported. For growing steers, one group reported that liver weight and gastrointestinal tract weight were both 8% greater for high RFI steers than low RFI steers (Basarab et al., 2003). Richardson et al. (2001) observed that internal organs mass, as a percent of live weight, was not different between high and low RFI steers, but external organ (head, hide, hooves, tail) mass and bone mass, as percentages of live weight, were greater for low RFI steers. Gomes and coworkers (2012) did not determine any differences for organ weights between efficiency groups of Bos indicus steers. Differences in organ size and weight could influence their function and activity, which may play a role in determining RFI. A larger gastrointestinal tract could improve digestive efficiency by increasing retention time, or it could decrease protein efficiency by increasing the amount of protein turnover that must occur to accommodate the increased maintenance demands of the greater tissue area.

REPEATABILITY OF RESIDUAL FEED INTAKE

Residual feed intake is a heritable trait in lactating dairy cows and other livestock species (Veerkamp, 1998; Schenkel et al., 2004). As such, it is desirable to incorporate RFI into a selection index to improve feed efficiency. Using RFI as a genomic tool to select for more feed efficient animals is promising; however, it is important that animals within the test population are unbiased to ensure that selection will progress in a desirable direction. Estimates for RFI may vary depending on the age of the animal, its physiological state, and the type of diet fed during the test period. Investigation of the repeatability of RFI across different scenarios will help to resolve the most ideal method for an accurate and unbiased assessment.

Repeatability of RFI and Stage of Maturity

There are several studies that have considered the repeatability of RFI across different stages of maturity. Jensen and others (1992) observed low repeatability of RFI (r=0.10) in dairy bulls assessed during two different growing periods. Others (Archer et al., 1994) determined that RFI was moderately repeatable across four different growth periods in beef bulls. Durunna et al.

(2012) found that RFI was repeatable (r=0.52) in growing beef heifers across two consecutive RFI test periods, though 50% of the animals changed their efficiency grouping (high, medium, or low) from one period to another. Some studies indicate that phenotypic correlations are lower than genotypic correlations either when animals are assessed for RFI as weaned heifers and subsequently as lactating beef cows (Archer et al., 2002) or when the relationship between RFI as growing heifers and RFI as lactating dairy cows is examined (Nieuwhof et al., 1992). Phenotypic and genotypic correlations for the repeatability of RFI in these studies ranged from 0.07 to 0.40 and 0.58 to 0.98, respectively (Nieuwhof et al., 1992; Archer et al., 2002). In two studies of beef cattle (Arthur et al., 1999; Strobehn and Dahlke, 2012), the correlations between RFI estimated for weaned calves and that for dry or lactating cows were 0.36 and 0.24, respectively. Currently, the repeatability of RFI for growing dairy heifers and RFI during their subsequent lactation is being studied (Williams et al., 2011; Waghorn et al., 2012). In growing mice, weekly RFI estimates were highly repeatable (r=0.8) in mature animals, but less repeatable (r=0.27) in younger animals (Archer and Pitchford, 1996). From these data, it is evident that RFI is moderately repeatable at different stages of maturity which suggests that perhaps stage of maturity may not be a crucial component in the accurate determination of RFI.

Repeatability of RFI and Physiological State

Residual feed intake is moderately repeatable when measured throughout an entire lactation in grazing dairy cows (Prendiville et al., 2011). Prendiville and coworkers (2011) estimated RFI for each cow six times throughout a whole lactation cycle. The correlation between whole lactation RFI and RFI estimated for any one period during the lactation cycle ranged from 0.40 to 0.71. Residual feed intake measured during late lactation (>230 DIM) had a strong relationship (r=0.71) with whole lactation RFI (Prendiville et al., 2011). The repeatability of DMI is also moderate throughout different stages of lactation (Kramer et al., 2008), which likely impacts the repeatability of RFI. Connor et al. (2013) determined that the repeatability of RFI across different lactations was 0.56 in early lactation dairy cows. This group also observed that weekly estimates for RFI were moderately correlated with each other (r=0.47) throughout the first 90 DIM, suggesting that during early lactation, RFI is moderately repeatable. Although it is uncertain which stage of lactation would be ideal to obtain the most accurate estimate for a 305-d RFI prediction, Prendiville et al. (2011) suggested that estimates obtained between 60 and 230 DIM might be most reflective of whole lactation RFI. Measuring RFI during this period of lactation may reduce error due to large changes in BW, since BW change is difficult to quantify. Furthermore, error due to energetic demands for pregnancy will be minimal between 60 and 230 DIM (NRC, 2001).

Repeatability of RFI and Type of Diet

There is a paucity of data for the repeatability of RFI when animals are fed different types of diets. To be a useful in genetic selection, RFI must be repeatable across different types of diets such that selection decisions made at the present do not negatively impact efficiency of future generations subjected to different feeding regimes. Kelly and coworkers (2010b) investigated the repeatability of RFI for beef heifers across growing and finishing stages. During the growing phase (Kelly et al., 2010a), heifers were fed a 70% forage, 30% concentrate diet; during the finishing phase (Kelly et al., 2010b), cattle were fed a 30% forage, 70% concentrate diet. Residual feed intake was moderately repeatable (r=0.62) across the two phases (Kelly et al., 2010b). Although the objective of the study was to examine the repeatability of RFI across different growth phases of the heifers, it indicates that RFI could be repeatable across two markedly different diets. Durunna et al. (2011) examined the repeatability of RFI in steers across growing and finishing diets. The grower diets were 20% forage, 80% concentrate, and the finisher diets were 100% concentrate, with 10% in the form of alfalfa pellets (Durunna et al., 2011). The repeatability of RFI across the two stages was lower (r=0.33) than results reported by Kelly et al. (2010b).

HIGH AND LOW STARCH DIETS FOR DAIRY CATTLE

Formulation Strategies and Considerations

Non-fibrous carbohydrates (NFC) are important components of lactating dairy cow rations and are included to increase the energy density of diets to enable greater energy intake, which is necessary to sustain high levels of milk production. Sugar, starch, pectin, and organic acids make up the four major fractions of NFC and the proportion of each component within a feed varies depending on feed type (NRC, 2001). Corn is a major component in livestock rations fed throughout the United States, and its largest NFC fraction is starch (NRC, 2001). The digestible energy content of starch is greater than that of forage (NRC, 2001). Although ruminal starch digestibility is highly variable, apparent total tract digestibility of starch is more uniform (Allen, 2000) and is unrelated to ruminal starch digestibility (Firkins, 1997). In addition to their greater digestible energy content, concentrates high in starch are less bulky than forage, which enables greater feed intake when compared with diets composed mostly of forage that may limit intake because of their filling effect and slower rate of passage from the rumen. Starch fermentation enhances the production of glucose precursors in the rumen (Allen, 2000), which are vital to high levels of milk production. Non-fibrous carbohydrates are also important for microbial protein synthesis, which also influences cow performance (Clark et al., 1992). The typical starch concentration of dairy cattle rations in the United States ranges from 15 to 30%

(Dann and Grant, 2009). This range reflects the diversity in the types of rations formulated for the various sectors of the U. S. dairy herd, which is influenced primarily by the availability and cost-effectiveness of certain feeds in different regions.

Feeding low starch diets by replacing high-cost concentrates, such as corn, with byproducts may be an economical alternative for dairy producers. Many of these byproducts are non-forage fiber sources (NFFS) which include byproduct feeds such as soybean hulls, distillers grains, wheat middlings, beet pulp, and corn gluten feed. The availability and price of byproducts will likely determine the cost-effectiveness of their inclusion in rations. Byproduct feeds, though often cheaper than corn, can be highly variable from load to load (Bradford and Mullins, 2012), and thus, profitability may be altered if the changes in nutrient profile of these feeds negatively impact animal performance. In some situations, feeding NFFS to reduce dietary starch concentrations can improve milk:feed (Voelker and Allen, 2003a) such that income over feed cost (IOFC) is improved (Ranathunga et al., 2010). If the cost of byproduct per unit of nutrient increases or if production is reduced then profitability of feeding low starch diets high in byproduct feeds may decrease.

The recommended starch concentration for dairy cows throughout lactation is between 23 and 30% (Grant, 2005). Because concentrates are usually more expensive, it may be desirable to reduce the amount of concentrate fed to lactating cows by feeding reduced starch diets. There are three approaches to formulating low starch diets (Dann and Grant, 2009). The first approach involves substituting NFFS for high starch concentrate. Non-forage fiber sources are low in starch, high in digestible NDF, and typically similar in particle size to concentrates, and thus, replacement of grain with NFFS will not likely limit intake due to fill and will allow for greater feed intake by early lactation cows (Bradford and Mullins, 2012). Decreasing the starch content of lactating cow rations is also accomplished by replacing high starch feeds with high quality, digestible forages (Oba and Allen, 2000), though doing so might result in lower DE intake because forage is less digestible than NFC (NRC, 2001). Replacement of high starch concentrate with sugar and pectin is the third strategy that can be implemented to reduce the starch concentration in lactating cow diets (Broderick and Radoff, 2004; Hall et al., 2010).

Lactation Performance

It is imperative that a reduction of dietary starch does not compromise milk production. Many have investigated the effects of feeding low starch diets on production performance of lactating cows. Different approaches used to reduce dietary starch concentration show various effects on milk and milk component concentrations and yields.

Feeding nonforage fiber sources. Some studies show that protein production is altered when feeding low starch diets that are high in byproduct feeds. Boddugari et al. (2001) observed lower milk protein concentration when a corn milled product replaced portions of ground corn at four different levels (0, 50, 75, and 100%) in the diet of mid-lactation cows. Similarly, milk protein concentration tended to decrease when soyhulls or wheat middlings and whole cottonseed replaced ~8-10% of ground corn in low starch diets (22 vs. 27% starch; Gencoglu et al., 2010; Ferraretto et al., 2011). Ferraretto et al. (2011) also observed a trend for reduced protein yield. Others have reported no significant change in milk protein yield or concentration when reduced starch diets were formulated with NFFS (Lechartier and Peyraud, 2011; Zhang et al., 2010; Beckman and Weiss, 2005; Ipharraguerre et al., 2002a; Bhattacharya and Lubbadah, 1971).

Milk fat concentration and yield can also be altered by feeding reduced starch diets that are high in NFFS. Beckman and Weiss (2005) manipulated the dietary NDF:starch ratio of diets fed to mid-lactation cows by substituting ground corn with cottonseed hulls and soybean hulls, creating diets that differed in starch concentration (33, 30, and 25% starch) and observed a linear increase in milk fat concentration as dietary starch was reduced. Lechartier and Peyraud (2011) replaced ground corn with citrus pulp, beet pulp, and soybean hulls to achieve diets differing in starch concentration (25 v. 41% starch), and cows had significantly greater milk fat concentration and yield when fed the low starch diet. Similarly, milk fat concentration and yield increased linearly as soybean hulls replaced up to 40% of diet DM at the expense of ground corn (Ipharraguerre et al., 2002a), and fat yield increased linearly as beet pulp replaced high moisture corn at increasing levels, with starch concentrations ranging from 35-17% (Voelker and Allen, 2003a). However, others did not observe significant differences for milk fat yield or concentration when low starch diets were fed (Bhattacharya and Lubbadah, 1971; Boddugari et al., 2001; Gencoglu et al., 2010; Zhang et al., 2010; Ferraretto et al., 2011).

Effects of feeding low starch diets that are high in NFFS on milk yield were examined (Boddugari et al., 2001; Ipharraguerre et al., 2002a; Voelker and Allen, 2003a; Gencoglu et al., 2010; Ferraretto et al., 2011), but no significant changes in milk yield occurred. Varying results for milk production performance observed when feeding low starch diets is likely due to the variation in the type and amount of byproduct included in the diets, as well as associative interactions between dietary ingredients.

Feeding high quality forage. Replacing high starch ingredients with high quality forage is another approach that can be used to reduce the starch concentration of rations. This method should be approached with caution, as voluntary DMI may be depressed by distension if too much forage is included in the diet (Allen, 2000). Boguhn et al. (2010) replaced corn silage with beet pulp silage at 11% of diet DM, resulting in diets that were 27 or 19% starch. No effect on milk production or milk components was observed for early to mid-lactation cows fed these diets, although DMI was significantly reduced when the low starch diet was fed (Boguhn et al., 2010). Oba and Allen (2000) compared brown midrib 3 (BMR) corn silage and conventional corn silage (CCS) among high and low forage NDF diets. The average starch concentrations for the low and high NDF diets were 37% and 26%, and BMR corn silage diets contained 11 and 14% more digestible NDF in the low and high NDF diets, respectively. Milk yield, milk component yields, and DMI were similar between the low NDF (high starch) diet with CCS and the high NDF (low starch) diet with BMR corn silage (Oba and Allen, 2000). Oba and Allen (2000) concluded that the BMR corn silage enabled cows to consume more feed because of a reduction in gut fill, and that its incorporation into high fiber, low starch diets will yield the most favorable results. These results support the idea that high fiber, low starch diets may not greatly compromise DMI and production if high quality and digestible forage sources are included in place of high starch concentrates or forages.

Feeding other NFC. Low starch diets may also be formulated by replacing starch with other types of NFC that contain a smaller proportion of starch and larger proportions of sugar or pectin. In a study by Hall et al. (2010), citrus pulp or molasses and sucrose replaced ground corn to include 20 or 10% of diet DM, and resulted in 3 diets that were ~24, 14, or 12.5% starch. Milk yield was not significantly altered and DMI tended to decrease when the 24% starch diet was fed compared with the two lower starch diets (Hall et al., 2010). Milk protein concentration, fat and protein yield, and MUN were reduced, but milk fat concentration was increased when the lower starch diets were fed (Hall et al., 2010). In another study, high moisture corn was replaced with either dried or liquid molasses at 4 different levels, resulting in diets that were 32 to 23% starch or 31 to 26% starch (Broderick and Radloff, 2004). When the dried molasses was fed, DMI increased linearly and there was a significant quadratic effect for milk fat yield, with the lowest yields occurring at the highest and lowest inclusion rates of molasses (Broderick and Radloff, 2004). When the liquid molasses was substituted for high moisture corn, a quadratic effect for milk yield was observed, with the lowest yields occurring at the highest and lowest inclusion rates of molasses, though milk fat yield and concentration was not different among treatments (Broderick and Radloff, 2004). These data suggest that reducing dietary starch concentration through replacement of high starch NFC with low starch NFC may maintain adequate production by dairy cows, although the type and amount of low starch NFC included may influence results.

Low starch diets may be formulated through the replacement of concentrate with NFFS which are low in starch and high in digestible NDF, the exchange of high starch ingredients for high quality forage, or by the substitution of high starch NFC for NFC that are lower in starch and higher in sugar and pectin. Studies that investigate the results of these strategies provide insight to the effects that low starch diets have on production performance of dairy cows. Conflicting results are likely due to the variation between and within types of feeds used as starch substitutes, in addition to their inclusion rate in low starch diets. Low starch diets must be adjusted based on observed cow performance in order to yield optimal results.

Feed Efficiency

Feed efficiency is influenced by production and DMI. Reducing the starch concentration of diets fed to lactating dairy cows may decrease (Ipharraguerre et al., 2002a; Voelker and Allen, 2003a; Boguhn et al., 2010), increase (Zhang et al., 2010; Lechartier and Peyraud, 2011), or have no effect (Beckman and Weiss, 2005; Ferraretto et al., 2011) on DMI. As described above, varying results for milk yield and milk components are observed when feeding low starch diets. Because of this, reducing dietary starch concentration produces a variety of results for feed efficiency when it is defined as milk:feed. This is likely due to the fact that dietary starch concentration alters BW gain, which will bias the assessment of efficiency if only ratio traits like milk:feed are considered. The effect of low starch diets on DMI and production is likely dependent on the type of feed used to replace high starch feedstuffs, the amount of the feed that is included in the diet, and associative effects between dietary ingredients.

Nutrient digestibility. Nonforage fiber sources are low in starch and high in digestible NDF, and have a particle size similar to that of many concentrates (Bradford and Mullins, 2012). When replacing starch with NFFS, the overall diet NDF digestibility will increase because a greater proportion of total NDF will be made up of highly digestible NDF from NFFS. Oba and Allen (1999) determined that a 1-unit increase in forage NDF digestibility would increase 4% fat corrected milk yield by 0.25 kg/d and DMI by 0.17 kg/d. The authors also determined that diets that contained more digestible forage resulted in numerically greater BW gain per d (P=0.16; Oba and Allen, 1999). This increased efficiency through increasing the total amount of digestible NDF may provide some explanation as to why the replacement of concentrate with NFFS may result in improved milk:feed; however, increased milk:feed does not provide an accurate assessment of true feed efficiency since BW changes are not considered in its computation.

Feed intake and energy partitioning. Dietary starch concentration influences the rumen microenvironment, which may affect feed efficiency when cows are fed high and low starch diets because changes in the rumen affect feed intake and nutrient absorption and partitioning. Increasing the ruminal digestion of concentrates in dairy cattle rations is typically associated with increased propionate production and decreased acetate production (Kaufman, 1976). Increased propionate is associated with an increase in gluconeogenesis and insulin secretion that can decrease DMI (Allen, 2000) and increase glucose uptake by adipose tissue.

Lechartier and Peyraud (2011) reported greater DMI when cows were fed low starch diets. Reduced DMI by cows fed high starch diets in that study could have been the result of the greater propionate production observed when cows were fed the high starch diets, which might have amplified diet differences for DMI. In contrast, Voelker and Allen (2003a) observed a decrease in DMI as beet pulp replaced high moisture corn independent of ruminal propionate concentration, ruminal pH, and acetate:propionate ratio, and because DMI decreased with little reduction in milk yield, milk:feed was increased. However, gain in body condition score tended to be reduced when low starch diets were fed (Voelker and Allen, 2003a). Similarly, when soyhulls replaced ground corn, Ipharraguerre et al. (2002a) observed a linear decrease in daily BW gain as inclusion rate of soyhulls increased. These data support the idea that greater production of glucose precursors in the rumen, observed when cows are fed higher starch diets, is indirectly related with increased glucose uptake by adipose tissue.

Rumen environment and fermentation. When compared with high starch diets, low starch diets (25% vs. 41.5% starch) reduced mean ruminal pH, resulted in a greater ruminal pH range, and increased the acetate:propionate ratio as soyhulls, citrus pulp, and beat pulp replaced ground corn (Lechartier and Peyraud, 2011). Similarly, when beet pulp replaced high moisture corn and 4 inclusion rates (35 to 18% starch), the acetate:propionate ratio increased linearly, but ruminal pH range tended to decrease linearly and mean ruminal pH was not affected (Voelker and Allen, 2003b). As soyhulls replaced ground corn at increasing rates (0 to 40%; estimated dietary starch concentration of 37 to 9%), the acetate:propionate ratio increased linearly as the inclusion rate of soybean hulls increased (Ipharraguerre et al., 2002b). Furthermore, Ipharraguerre et al. (2002b) reported a tendency for a quadratic effect for mean ruminal pH, with the lowest pH at the highest inclusion rate of soyhulls. The altered acetate:propionate ratio that occurred for the low starch diets in all three studies coincide with the increased milk fat yield observed (Ipharraguerre et al., 2002a; Voelker and Allen, 2003a; Lechartier and Peyraud, 2011).

The rate of ruminal fermentation of starch and other concentrates can alter the rumen environment by through the production of lactic acid, which may reduce rumen pH if produced in excess (Kaufman 1976; Russell and Hino, 1985). Rumen pH influences the rumen microbe population which affects the digestion of substrates, such as fiber (Kaufman, 1976). Decreased pH is associated with rumen acidosis, which can depress intake, cause milk fat depression, and lead to health problems such as laminitis and body condition loss (Kleen et al., 2003). Both low starch and high starch concentrates may be rapidly fermented in the rumen to yield lactic acid (Cullen et al., 1986). Lechartier and Peyraud (2011) observed that ruminal fermentation products are dependent on the degradability of feedstuffs in addition to the overall starch concentration of the diet. In that study, cows were fed high or low starch diets, and within each starch concentration, there were three levels of rumen degradable DM. The pH range increased linearly and both DMI and the acetate:propionate ratio decreased linearly as the degradability of the diets increased, regardless of starch content (Lechartier and Peyraud, 2011). These data show diet fermentability, rather than starch concentration alone, is more important to determining rumen fermentation products. Because high concentrate diets reduce rumen pH, they may also alter rumen microbial processes and effectively shift biohydrogenation pathways in the rumen (Bauman and Griinari, 2003). Intermediates resulting from altered rumen biohydrogenation (specifically *trans*-10, *cis*-12 conjugated linoleic acid) reduce milk fat production (Bauman and Griinari, 2003) and may increase lipogenesis (Harvatine et al., 2009), consequently shifting energy partitioning to body tissue gain.

The fermentation profile of different feeds in the rumen can indirectly alter feed efficiency by affecting DMI and nutrient partitioning to milk or body tissue. Depending on the definition of feed efficiency (i.e. milk:feed, gross efficiency, or RFI) and the amount and type of ingredients included in the ration, animals may be more efficient, less efficient, or indifferent when fed high and low starch diets. By definition, RFI is independent of BW gain or loss so that dietary induced BW changes should not affect its determination.

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CHAPTER 2

RESIDUAL FEED INTAKE IS REPEATABLE FOR LACTATING HOLSTEIN COWS FED HIGH AND LOW STARCH DIETS

ABSTRACT

Residual feed intake (RFI) is a tool to quantify feed efficiency in livestock and is commonly used to assess efficiency independent of production level, BW, or BW change. Forty-four primiparous and 65 multiparous lactating Holstein cows, averaging (mean ± SD) 665 ± 77 kg of BW, 42 ± 9 kg of milk/d, and 120 ± 30 d postpartum, were fed diets of high (HI) or low (LO) starch content in four cross-over experiments with 4-wk periods. The LO diets were ~40% NDF and ~14% starch and the HI diets were ~26% NDF and ~30% starch. Individual dry matter intake (DMI) of a cow was modeled as a function of milk energy output (MilkE), metabolic BW (MBW), body energy change (ΔBodyE), and fixed effects of parity, experiment, cohort nested within experiment, and diet nested within cohort and experiment; RFI for each cow was the residual error term. Cows were classified as high (>0.5 SD), medium (±0.5 SD), or low (<0.5 SD) RFI. For the model, each unit increase in MilkE, MBW, or ΔBodyE was associated with 0.35, 0.09, or 0.05 kg increase in DMI, respectively. When compared with LO diets, HI diets increased energy partitioning to body energy gain (8.3 vs. 4.5%; P<0.01) and tended to increase DMI (P=0.09). The correlation between RFI when cows were fed HI diets and RFI when cows were fed LO diets was 0.73 (P<0.01) and was similar within each parity and experiment. Fifty-six percent of cows maintained the same RFI classification (high, medium, or low RFI) and only 4 cows changed from high RFI to low RFI or vice versa when diets were changed. Milk:feed, income over feed cost, and DMI were also highly repeatable. We achieved significant changes

in milk production and energy partitioning between HI and LO diets and still determined RFI to be repeatable across diets. We conclude that RFI is reasonably repeatable for a wide range of dietary starch concentrations fed to mid-lactation cows, so that cows that are most efficient when fed high corn diets are likely also most efficient when fed diets high in non-forage fiber sources.

INTRODUCTION

Residual feed intake (RFI) is calculated as the difference between an individual's observed feed consumption and it's predicted feed consumption. An animal with a negative RFI consumes less than expected for its given level of production and thus is more efficient. Because it is independent of production level, using RFI as a tool to assess feed efficiency in dairy cattle for the purposes of genetic selection has become increasingly popular in recent years (Connor et al., 2013; Green et al., 2013; Macdonald et al., 2014). The heritability of RFI in lactating dairy cattle is ~0.15 (Tempelman et al., 2013). If RFI is to be used in selection strategies, it is vital that it be repeatable across environmental conditions.

Residual feed intake was moderately repeatable across two consecutive feeding periods in beef heifers classified as high (>0.5 SD), medium (±0.5 SD), and low (<0.5 SD) RFI (Durunna et al., 2012). However, in that study, only 49% of heifers maintained their efficiency classification from one period to the next; 28% of heifers changed their RFI ranking by more than ± 1 SD and 72% of heifers changed their RFI ranking by less than ± 1 SD. Connor et al. (2013) determined that RFI was repeatable across weeks (r = 0.47) for Holstein dairy cows in early lactation. Others investigated repeatability of RFI in beef heifers across growing and finishing stages when fed grower and finisher diets (Kelly et al., 2010a; Kelly et al., 2010b) and determined that RFI measured during the growing period and RFI measured during the finishing period were moderately correlated (r=0.62). However, Durunna et al. (2011) examined the repeatability of RFI between two consecutive periods for beef steers fed a grower diet, and subsequently a finisher diet, and observed that RFI was less repeatable (r=0.33).

Many of the cows used in current estimates of RFI for dairy cows were fed diets that are high in concentrate. In the future, competition for feed grains might limit their availability for feeding cows. Our goal in animal selection is to find cows that are efficient across many types of diets, so that those efficient when fed the high starch diets, typical of the Midwest United States at present, will also be efficient when consuming lower starch diets that might be fed in the future. The objective of this experiment was to determine if RFI is repeatable when lactating dairy cows are fed diets that differ markedly in starch content. We hypothesized that RFI and other measures of feed efficiency would be repeatable across high and low starch diets fed to lactating dairy cows.

MATERIALS AND METHODS

Cows, Experimental Design, and Diets

Experimental procedures were approved by the Institutional Animal Care and Use Committee of Michigan State University. Data from four separate cross-over experiments were used to determine the repeatability of RFI across high and low starch diets. Lactating Holstein cows were fed diets that differed in starch content in experiments 1 (n=32; 22% primiparous), 2, (n=25; 40% primiparous) 3 (n=32; 50% primiparous), and 4 (n=20; 55% primiparous). Mean DIM, BW, and milk yield for all cows (mean ± SD) were 120 ± 30 d, 665 ± 77 kg, and 42 ± 9 kg/d, respectively, at the start of the experiments. For all experiments, the two experimental periods lasted 28 d. Within each experiment, cows were blocked based on milk yield and parity and randomly assigned to treatment sequence. All cows were housed in individual tie stalls and milked twice daily (0300 and 1430 h). Water was available ad libitum and feed was offered once daily at 1000 h (experiments 2 and 4) or 1200 h (experiments 1 and 3) at >110% of expected intake based on intake of the previous day. Tie stalls were equipped with a double-cupped watering system to prevent contamination of feed with water and with side panels and a front gate to prevent other cows from stealing feed during cow movements.

During experimental periods, cows were fed high (HI) or low (LO) starch diets, which were formulated to be markedly different in starch content. Ingredient and nutrient composition of all diets are shown in Table 2.1. All HI diets contained about 30-35% corn grain and were measured to be about 26% NDF and 30% starch. The LO diet in experiment 1 was formulated by replacing ground corn with soybean hulls to be 12% starch. For the LO diet in experiment 2, soybean hulls replaced ground corn and wheat straw and the diet was 16% starch. The LO diet in experiment 3 was 16% starch and was formulated by replacing ground corn and portions of high moisture corn and wheat straw with legume silage, soybean hulls, whole cottonseed, and a palmitic acid enriched fatty acid supplement (98% total FA). In experiment 4, the LO diet was 12% starch, being derived by including soybean hulls and whole cottonseed at the expense of ground corn, wheat straw, and portions of both corn and legume silages. Although diets across experiments were formulated with different concentrations of ingredients, distinct differences in starch content between HI and LO were achieved within experiment, and in all cases milk production or nutrient partitioning were altered by diet. Diets were adjusted for changes in forage DM concentration twice weekly.

Table 2.1. Composition of high and low starch diets fed during each experiment[1,2].

	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	HI	LO	HI	LO	HI	LO	HI	LO
Ingredient, % of DM								
Corn silage	23.9	24.3	23.6	23.8	23.7	24.2	23.5	20.9
Legume silage	21.9	22.1	21.2	21.4	11.1	22.6	20.6	18.4
Wheat straw	4.97	5.04	5.19	--	3.79	1.94	4.82	--
Soybean hulls	--	28.9	--	30.5	--	10.6	--	32.1
Cottonseed, whole	--	--	--	--	7.45	9.07	--	9.22
Corn, ground	29.6	3.61	21.4	--	13.1	--	30.8	7.18
Corn, high moisture	--	--	8.28	8.16	21.5	11.0	--	--
Soybean meal	16.6	13.5	17.17	12.9	15.9	14.6	17.2	9.08
Fat supplement[3]	--	--	--	--	--	2.51	--	--
Vitamin & mineral[4]	2.03	2.06	2.06	2.09	2.02	2.05	2.08	2.08
Limestone	0.50	--	0.50	--	0.75	0.76	0.52	--
Sodium bicarbonate	0.51	0.52	0.49	0.50	0.75	0.76	0.51	0.51
Dicalcium phosphate	--	0.25	0.18	0.50	--	--	--	0.51
Nutrient, % of DM								
DM	53.9	53.6	55.9	55.7	55.8	51.7	49.5	52.2
NDF	27.2	43.9	25.9	39.4	25.1	32.8	27.6	44.2
Starch	30.1	12.2	30.3	15.5	32.5	16.1	28.2	11.8
CP	16.4	15.9	16.6	16.0	17.0	18.3	16.9	15.2
Ash	11.8	14.1	6.5	7.3	5.4	6.8	6.1	6.5
Ether Extract	2.52	1.90	2.15	1.95	3.24	5.61	2.30	3.41
NE_L, Mcal/kg[5]	1.62	1.56	1.68	1.62	1.80	1.75	1.72	1.62
GE, Mcal/kg[6]	4.15	4.14	4.16	4.11	4.26	4.34	4.19	4.21

[1]High (HI) and low (LO) starch diets fed to lactating cows during experiments 1, 2, 3, and 4 (n=32, 25, 32, 20, respectively).
[2]Nutrient composition was determined from feed ingredients sampled during the last 5 d of each 28-d experimental period.
[3]Fat supplement was palmitic acid enriched.
[4]Vitamin and mineral mix contained 34.1% dry ground shell corn, 25.6% white salt, 21.8% calcium carbonate, 9.1% Biofos, 3.9% magnesium oxide, 2% soybean oil, and < 1% of each of the following: manganese sulfate, zinc sulfate, ferrous sulfate, copper sulfate, iodine, cobalt carbonate, vitamin E, vitamin A, vitamin D, and selenium.
[5]Mean apparent net energy concentration of diets, based on average cow performance. For each diet, $DietNE_L$ = the average of (MilkE + 0.08 x MBW + ΔBodyE) / DMI for all cows on the diet.
[6]Gross energy concentration, calculated from nutrient profile of individual feed ingredients, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0; Michigan State University, East Lansing, MI): 4.20 kcal/g carbohydrate, 5.65 kcal/g crude protein, 9.50 kcal/g fatty acid estimated from ether extract, 3.95 kcal/g sugar (Watt and Merrill, 1973).

Sample Collection and Analysis

Cows were fed once per day and orts were removed and weighed daily prior to feeding. Milk yield was recorded electronically at each milking, and milk samples were obtained from 4 consecutive milkings per wk (d 6, 7, 13, 14, 20, 21, 27, 28 of each period in experiments 1, 2, and 4; d 4, 5, 11, 12, 18, 19, 25, 26 of each period in experiment 3). Milk samples were analyzed for fat, protein, lactose, somatic cell count, and milk urea nitrogen (MUN) with infrared spectroscopy by Michigan DHIA (East Lansing). Body weight for each cow was recorded three (experiments 2, 3, and 4) or five (experiment 1) days per wk immediately after the morning milking. Body condition score (BCS) for each cow was recorded at the beginning and end of each period.

Collection and analyses of diet ingredients were the same for all four experiments. During the last 5 d of experimental periods, samples of feed ingredients were obtained daily to determine the nutrient profile of the diets. All samples were frozen after collection until analysis. Samples were composited to obtain one sample per period and dried in a forced air oven (135°C for > 72 h) before grinding through a Wiley mill (1-mm screen; Arthur H. Thomas Co., Philadelphia, PA). The reported nutrient and ingredient composition of diets was determined by the average of both periods for each experiment. In all cases, the treatment diets for periods 1 and 2 were very similar (CV < 8% for nutrient concentrations).

Samples of feed were analyzed for crude protein (CP), starch, neutral detergent fiber (NDF), ether extract, and ash. Crude protein was determined according to Hach et al. (1987), and starch was analyzed by an enzymatic method after gelatinization with sodium hydroxide (Karkalas, 1985). Glucose concentration was determined via glucose oxidase method (Glucose kit #510; Sigma Chemical Co., St. Louis, MO), and absorbance was measured with a micro-plate reader (SpectraMax 190; Molecular Devices Corp., Sunnyvale, CA). Neutral detergent fiber was determined according to Mertens (2002) and ether extract was determined using a modified Soxhlet apparatus (AOAC, 1990). Ash was determined after 5 h combustion at 500°C, and concentrations of nutrients are expressed as a percentage of DM.

Calculations

Milk energy output (MilkE; MCal/d) for a cow was estimated by the following equation (NRC, 2001; from Equation 2-15):

$$\text{MilkE} = [9.29 \text{ x fat (kg)} + 5.63 \text{ x true protein (kg)} + 3.95 \text{ x lactose (kg)}],$$

where each component is based on the average output of a cow during a 28-d period. Metabolic BW for a cow (MBW; $kg^{0.75}$) was estimated as $BW^{0.75}$, where BW was the mean BW for the cow during the 28-d period. Mean daily BW change (ΔBW; kg) was calculated for each cow within a period by linear regression after two iterations of outlier removal. After the first regression, records >3.5 SD were removed before the second regression was performed; records >3.5 SD were removed after the second regression before determining ΔBW, which was the slope from the third regression. Energy expended for body tissue gain (ΔBodyE; Mcal/d) was estimated by an equation derived from NRC (2001; Table 2-5):

$$\Delta\text{BodyE} = [(2.88+1.036 \text{ x BCS}) \text{ x } \Delta\text{BW}],$$

where BCS is the average BCS for a cow during a 28-d period. Energy partitioning was predicted based on observed performance:

$$\% \text{ to milk, maintenance, or body tissue} = [\text{MilkE}, 0.08 \times \text{MBW}, \text{ or } \Delta\text{BodyE} / (\text{MilkE} + 0.08 \times \text{MBW} + \Delta\text{BodyE}) \times 100],$$

where % to milk, maintenance, or body tissue is the percent of apparent energy absorbed partitioned to milk production, maintenance requirement, or body tissue gain, respectively. Adjusted BW, which adjusts a cow's BW to the BW that she would be if she had a BCS of 3.0, was used as an indicator of body size and was defined as:

$$\text{Adjusted BW} = [\text{BW} / (0.137 \times \text{BCS} + 0.589)].$$

The milk:feed ratio for a cow during a period was determined as the average daily energy-corrected milk yield (ECM; ECM = [0.327 × milk (kg) + 12.95 × fat (kg) + 7.20 × protein (kg)]; Tyrell and Reid, 1965) over the average daily DMI. Gross energy efficiency, or the percent of energy consumed captured in milk and body tissue gain, was calculated as the average MilkE and ΔBodyE divided by the average gross energy intake during a 28-d period. Individual feed nutrient analyses were used to calculate gross energy, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0; Michigan State University, East Lansing, MI). Energy values for each nutrient were assigned according to Merrill and Watt (1973): 4.20 kcal/g carbohydrate, 5.65 kcal/g crude protein, 9.50 kcal/g fatty acid estimated from ether extract, 3.95 kcal/g sugar, and 3.62 kcal/g fermented acid.

Daily feed cost for each diet was calculated using economic values for commodities in the Midwest United States in the Fall of 2013. Commodity prices ($/kg DM) used were: $0.22/kg corn silage, $0.11/kg legume silage, $0.10/kg wheat straw, $0.22/kg soybean hulls, $0.41/kg whole cottonseed, $0.34/kg ground corn, $0.33/kg high moisture corn, $0.56/kg soybean meal, $1.55/kg fat supplement, $0.13/kg vitamin and mineral mix, $0.22/kg limestone,

\$0.22/kg sodium bicarbonate, and \$0.45/kg dicalcium phosphate. Milk income was determined for a cow based on individual production of protein (\$7.11/kg), fat (\$3.46/kg), lactose (\$0.87/kg), and milk (\$0.04/kg). Based on average production for all cows and the economic values for components, average milk price was determined to be \$17.47 per 45.4 kg. Gain of BW was assigned an economic value of \$1.78/kg, which was based on the value of a cull cow.

Apparent diet energy content ($DietNE_L$; Mcal/kg) was calculated for each diet as the average NE_L required by each cow divided by her average daily intake for the diet:

$$DietNE_L = \text{Average } [(MilkE + 0.08 \text{ x } MBW + \Delta BodyE)/DMI],$$

where DMI is the average DMI for a cow when she was fed the diet. Multiple of maintenance was calculated based on 1) production and on 2) actual intake. Multiple of maintenance (MM) based on requirements for observed production was calculated as:

$$MM_R = [(MilkE + 0.08 \text{ x } MBW + \Delta BodyE)/0.08 \text{ x } MBW].$$

Multiple of maintenance based on actual intake was calculated as:

$$MM_I = [(DMI \text{ x Diet Energy Density})/(MBW \text{ x } 0.08)],$$

where diet energy density was the mean $DietNE_L$ for each diet (1.7 and 1.6 Mcal NE_L/kg for HI and LO diets, respectively).

Statistical Analysis

Dry matter intake for an individual cow during each 28-d period was regressed as a function of major energy sinks using GLM Procedure in SAS (v. 9.3; SAS Institute, Cary, NC). To define RFI, DMI was modeled as follows: $DMI_i = \beta_0 + \beta_1 \text{ x } MilkE_i + \beta_2 \text{ x } MBW_i + \beta_3 \text{ x}$

$\Delta BodyE_i$ + *Parity* + *Experiment* + *Cohort(Experiment)*+ *Diet(Cohort x Experiment)*+ ε_i, where DMI_i was the observed DMI, $MilkE_i$ was the observed milk energy output, MBW_i was the average $BW^{0.75}$, and $\Delta BodyE_i$ was the predicted change in body energy, based on measured BW and BCS, for ith cow. Parity (1 or 2+), experiment (1, 2, 3, or 4), cohort nested within experiment, and diet (HI or LO) nested within cohort and experiment were fixed effects, where a cohort was a group of cows that ate the same diet at the same time. Residual feed intake was defined as the error term in the model (ε_i). To determine the number of animals that changed their efficiency ranking when they were switched from one diet to another, cows were grouped into high (HRFI), medium (MRFI), and low (LRFI) RFI groups. Cows >0.5 SD of the mean RFI for a cohort were classified as HRFI, cows <-0.5 SD were classified as LRFI, and those ±0.5 SD were classified as MRFI. Weekly estimates of RFI for a cow were also computed using data collected during each week (8 weeks per experiment) according to the model previously stated except the fixed effect of experimental week nested within cohort and experiment replaced the fixed effect of diet nested within cohort and experiment. Weekly RFI estimates from weeks 1 through 4 and weeks 5 through 8 were averaged to determine within-diet repeatability of RFI.

To determine differences in performance between most efficient and least efficient animals, 11 cows with the lowest RFI (lowest 10%) and 11 cows with the highest RFI (highest 10%) for each diet (HI or LO) were compared to each other. The effect of efficiency status was determined using the GLM Procedure of SAS according to the model: $Y_i = \mu + R_i + \varepsilon_i$, where μ is the overall mean, R_i is the fixed effect of efficiency group (i=efficient or inefficient) and ε_i is the residual error. The PDIFF option was used to compare least square means between the two efficiency groups. Production, efficiency, and energy partitioning responses to HI and LO diets were analyzed using the MIXED Procedure in SAS, with fixed effects of experiment, diet, parity, and period nested within experiment, all interactions of fixed effects, and the random effect of cow nested within experiment and parity. The full model was always used because $P<0.20$ for the three-way interaction for some responses of interest.

Pearson and Spearman correlation coefficients were obtained using the CORR Procedure of SAS. For correlations of traits with whole-period RFI, data from both treatments for each cow were used, so that performance from both diets was included. Correlations and main effects were considered significant at $P<0.05$ and trends at $P<0.10$. Interactions were considered significant at $P<0.10$ and trends at $P<0.15$.

RESULTS

Repeatability of Feed Efficiency

In general, cows that were efficient within a production level (low RFI) when they were fed one diet were still efficient when they were fed the other diet. Pearson and Spearman correlation coefficients were similar for the repeatability of RFI, so only Pearson correlation coefficients are reported. Pearson correlations for the repeatability of RFI, milk:feed, IOFC, gross efficiency, and DMI across HI and LO diets are listed in Table 2.2. For all cows, RFI (r=0.73; P<0.01), milk:feed (r=0.72; $P<0.01$), IOFC (r=0.84; $P<0.01$), and DMI (r=0.92; $P<0.01$) were repeatable across HI and LO diets for the 4-wk periods. However, the repeatability of gross feed efficiency across diets was low (r=0.15; $P=0.13$). Figure 2.1 illustrates the relationship between RFI when cows were fed HI diets and RFI when cows were fed LO diets. When diets were switched, 61 cows (56%) maintained their RFI group (HRFI, MRFI, or LRFI), and of the 48 cows that changed groups, only 4 cows changed from LRFI to HRFI or HRFI to LRFI. Repeatabilities of RFI, milk:feed, IOFC and DMI were similar across experiments and parity. Weekly RFI was also repeatable across experimental week (Table 2.3). Average repeatability of weekly RFI within-diet (weeks 1 through 4 and weeks 5 through 8) was 0.65 and across diet (weeks 1 through 4 compared with 5 through 8) was 0.56. Thus, across diet repeatability of weekly RFI was ~86% of within-diet repeatability.

Table 2.2. Pearson correlations for the repeatability of feed efficiency traits across high (HI) and low (LO) starch diets[1].

	Trait[2]					P-values[3]				
Group [4]	RFI	Milk: feed	Gross Efficiency	IOFC	DMI	RFI	Milk: feed	Gross Efficiency	IOFC	DMI
All Cows	0.73	0.72	0.15	0.84	0.92	<0.01	<0.01	0.13	<0.01	<0.01
Primiparous	0.69	0.72	-0.19	0.89	0.72	<0.01	<0.01	0.22	<0.01	<0.01
Multiparous	0.74	0.73	0.30	0.78	0.87	<0.01	<0.01	0.02	<0.01	<0.01
Experiment 1	0.71	0.72	0.44	0.75	0.88	<0.01	<0.01	0.01	<0.01	<0.01
Experiment 2	0.81	0.74	0.16	0.94	0.97	<0.01	<0.01	0.46	<0.01	<0.01
Experiment 3	0.73	0.68	-0.17	0.83	0.95	<0.01	<0.01	0.35	<0.01	<0.01
Experiment 4	0.61	0.58	-0.55	0.88	0.93	<0.01	<0.01	0.01	<0.01	<0.01

[1]Correlations are the relationships between animal performance when fed a high starch diet and animal performance when fed a low starch diet.
[2]RFI = residual feed intake, kg DM/d; Milk:feed = energy-corrected milk per unit of feed; IOFC = income over feed cost, $/d.
[3]P-values for repeatability correlations reported for animal groups.
[4]Animals included for each analysis included all cows (n=109), primiparous cows (n=44), multiparous cows (n=65), experiment 1 cows (n=32), experiment 2 cows (n=25), experiment 3 cows (n=32), and experiment 4 cows (n=20).

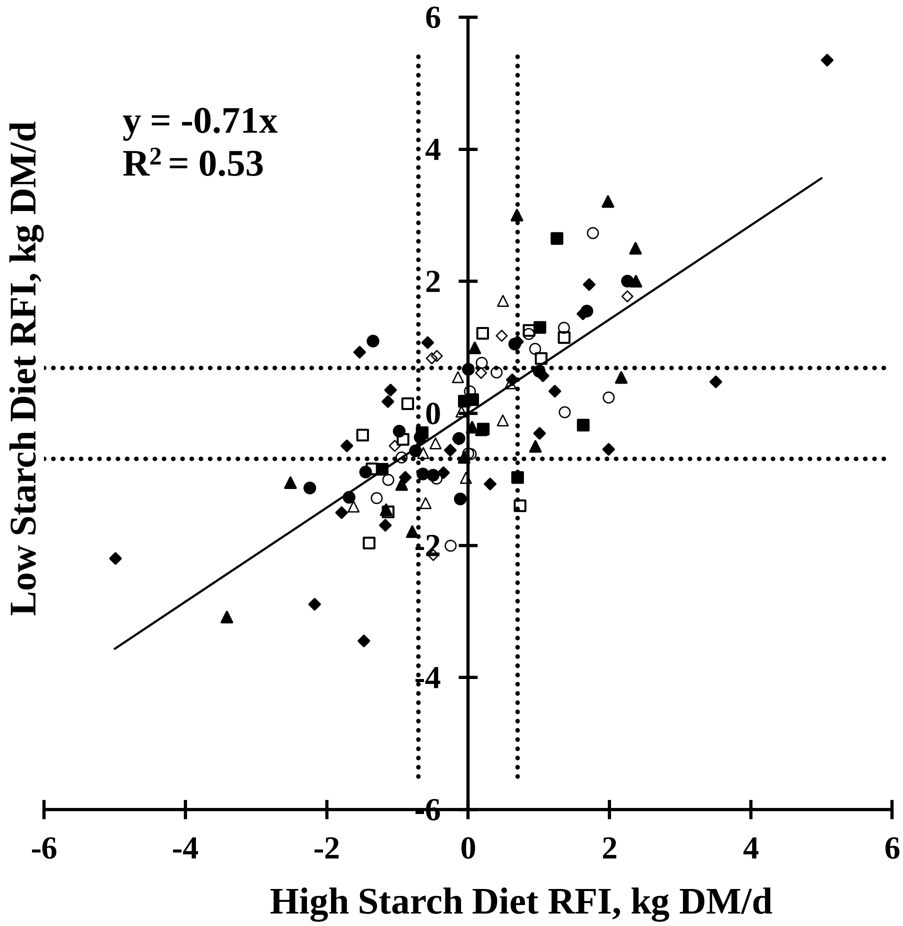

Figure 2.1. The relationship between RFI when cows were fed a low starch diet and RFI when cows were fed a high starch diet. Each data point represents an individual cow (n=109) and her performance when she was fed each diet. Open diamonds (◇) indicate experiment 1 primiparous cows (n=7); closed diamonds (◆) indicate experiment 1 multiparous cows (n=25); open triangles (△) indicate experiment 2 primiparous cows (n=10); closed triangles (▲) indicate experiment 2 multiparous cows (n=15); open circles (○) indicate experiment 3 primiparous cows (n=16); closed circles (●) indicate experiment 3 multiparous cows (n=16); open boxes (□) indicate experiment 4 primiparous cows (n=11); and closed boxes (■) indicate experiment 4 multiparous cows (n=9). Dotted lines represent ±0.5 SD from the mean RFI for each diet.

Table 2.3. Pearson's and Spearman's correlations for the repeatability of weekly RFI across experimental week for cows (n=109) fed high and low starch diets[1].

Week[2,3]	1	2	3	4	5	6	7	8
1	**1.00**	0.66	0.66	0.54	0.48	0.59	0.38	0.42
2	0.62	**1.00**	0.75	0.69	0.60	0.61	0.54	0.54
3	0.64	0.67	**1.00**	0.66	0.68	0.63	0.48	0.55
4	0.54	0.66	0.65	**1.00**	0.61	0.64	0.61	0.61
5	0.49	0.55	0.64	0.62	**1.00**	0.73	0.62	0.57
6	0.53	0.54	0.59	0.61	0.70	**1.00**	0.63	0.67
7	0.37	0.51	0.50	0.63	0.64	0.62	**1.00**	0.67
8	0.44	0.54	0.54	0.57	0.53	0.66	0.64	**1.00**

[1]Pearson's correlation coefficients are above the diagonal; Spearman's correlation coefficients are below the diagonal. All correlation coefficients were highly significant (P<0.01).
[2]Week of experiment. Diet change occurred after completion of week 4, so all cows were fed the same diet (either HI or LO) for wk 1 through 4, and then the other diet for wk 5 through 8.
[3]Weekly RFI was estimated from performance of each cow for the specified week, with ΔBodyE being calculated using ΔBW defined as the difference between average BW for the week minus the average BW for the previous week.

Dry Matter Intake Model

Among the four experiments, coefficients for MilkE, MBW, and ΔBodyE ranged from 0.28 to 0.41, 0.02 to 0.13, and -0.03 to 0.11, respectively. When animals from all experiments were included in the model, coefficients for MilkE, MBW, ΔBodyE and parity 1 were 0.35, 0.09, 0.05, and -1.96, respectively, and the model R^2 was 0.86. Milk energy output was always significant (P<0.01), and MBW was significant for all models (P<0.01) except for experiment 4 (P=0.46), which was likely due to the greater parity effect in that experiment. When parity was removed from the model, coefficients for MilkE, MBW, and ΔBodyE were 0.42, 0.13, and 0.04, respectively, and the model R^2 was 0.83. For our analysis, we utilized the full model which included the fixed effect of parity.

Animal Performance

Table 2.4 shows performance and efficiency least square means when cows were fed HI and LO diets. Gross efficiency was greater when cows were fed HI diets (*P*<0.01) and DMI tended to be greater for HI diets (*P*=0.09), but milk:feed and IOFC were not different between diets (*P*=0.80 and *P*=0.65, respectively). Milk yield was greater when cows were fed HI diets (*P*=0.03), but MilkE was not affected by diet (*P*=0.27). Milk fat concentration was greater (3.88 vs. 3.63%; *P*<0.01) and milk protein concentration was lower (3.01 vs. 3.13%; *P*<0.01) when cows were fed LO diets, respectively. When cows were fed HI diets, ∆BW, ∆BCS, and ∆BodyE were greater than when fed LO diets (*P*<0.01). Cows partitioned a greater proportion of energy toward body tissue gain and less energy toward milk when fed HI diets (*P*<0.02). There was a diet by experiment interaction for ∆BCS (*P*=0.01), milk fat concentration (*P*<0.01), milk:feed (*P*=0.04), ∆BodyE (*P*=0.07), and energy partitioned to milk (*P*=0.06).

Table 2.4. Least square means of performance and efficiency of cows fed high (HI) and low (LO) starch diets.

	Diet			P-value[1]				
Item[3]	HI	LO	SEM	Diet	Exp[2]	Parity	Period (Exp)	Diet x Exp
Intake and Production								
DMI, kg/d	25.7	25.2	0.24	0.09	<0.01	<0.01	0.80	0.21
Milk Yield, kg/d	42.3	40.2	0.67	0.03	<0.01	<0.01	0.17	0.69
MilkE, Mcal/d	29.6	28.9	0.45	0.27	<0.01	<0.01	0.16	0.39
Milk fat, %	3.63	3.88	0.05	<0.01	<0.01	<0.01	0.76	<0.01
Milk protein, %	3.13	3.01	0.03	<0.01	<0.01	<0.01	0.05	0.99
BW and ΔTissue								
MBW, $kg^{0.75}$	131	130	0.92	0.77	0.02	<0.01	0.88	1.00
ΔBW, kg/d	0.63	0.35	0.05	<0.01	0.49	0.49	<0.01	0.12
ΔBCS, pt/28 d	0.16	0.06	0.02	<0.01	0.53	<0.01	<0.01	0.01
ΔBodyE, Mcal/d	3.76	2.04	0.32	<0.01	0.41	0.35	<0.01	0.07
Energy Partitioning[4]								
% to milk	67.5	69.7	0.66	0.02	0.01	<0.01	<0.01	0.06
% to maintenance	24.2	25.8	0.35	<0.01	<0.01	<0.01	0.01	0.79
% to body tissue	8.30	4.48	0.74	<0.01	0.87	0.05	<0.01	0.13
Efficiency								
Milk:feed	1.66	1.65	0.02	0.80	<0.01	0.05	<0.01	0.04
Gross Efficiency, %	31.0	29.1	0.39	<0.01	<0.01	0.45	<0.01	0.98
IOFC, $/d	10.6	10.5	0.21	0.65	<0.01	<0.01	0.06	0.72
RFI, kg DM/d	-0.01	0.03	0.15	0.86	0.99	0.83	1.00	0.99

[1]P-value associated with main effects of diet, experiment, parity, period nested within experiment, and the interaction between diet and experiment.
[2]Exp = experiment.
[3]MilkE = milk energy output; MBW = $BW^{0.75}$; ΔBW = change in BW; ΔBCS = change in BCS per 28-d period; ΔBodyE = change in body energy; Milk:feed = energy-corrected milk per unit of feed; IOFC = income over feed cost; RFI = residual feed intake.
[4]Energy partitioning: % to milk = percent of apparently absorbed energy partitioned to milk production; % to maintenance = percent of apparently absorbed energy partitioned to maintenance; percent of apparently absorbed energy partitioned to body tissue gain.

Table 2.5. Pearson correlations of efficiency and performance with 4-wk period residual feed intake[1].

			Parity[2]				Diet			
	All Cows		Primiparous		Multiparous		HI		LO	
Item[3]	r	P-value[4]	r	P-value	r	P-value	r	P-value	r	P-value
Intake and Production										
DMI, kg/d	0.38	<0.01	0.56	<0.01	0.54	<0.01	0.36	<0.01	0.40	<0.01
MilkE, Mcal/d	0.00	1.00	0.12	0.27	-0.03	0.72	-0.06	0.56	0.05	0.59
BW, BCS, and ΔTissue										
MBW, $kg^{0.75}$	0.00	1.00	-0.01	0.92	0.00	0.96	0.02	0.81	-0.02	0.80
BCS	-0.11	0.09	-0.10	0.33	-0.13	0.15	-0.06	0.57	-0.17	0.07
ΔBW, kg/d	0.00	0.95	0.20	0.06	-0.08	0.40	-0.09	0.37	0.11	0.24
ΔBodyE, Mcal/d	0.00	1.00	0.19	0.08	-0.08	0.37	-0.08	0.41	0.10	0.30
Energy partitioning[5]										
% to milk	-0.01	0.89	-0.11	0.29	0.03	0.74	0.02	0.85	-0.04	0.67
% to body tissue	0.01	0.88	0.16	0.13	-0.06	0.50	-0.06	0.50	0.10	0.32
Efficiency										
Milk:feed	-0.39	<0.01	-0.34	<0.01	-0.40	<0.01	-0.45	<0.01	-0.32	<0.01
Gross Efficiency, %	-0.35	<0.01	-0.14	0.19	-0.44	<0.01	-0.46	<0.01	-0.25	0.01
IOFC, $/d	-0.13	0.05	-0.08	0.48	-0.17	0.05	-0.21	0.03	-0.06	0.54

[1]Performance and efficiency of cows (n=109) fed high (HI) and low (LO) starch diets. Two records per cow (one for performance on high starch diets and one for performance on low starch diets) were included for all analyses except those that examine correlations within diet.

[2]Correlations including only primiparous cows (n=44) or multiparous cows (n=65).

[3]MilkE = milk energy output; MBW = $BW^{0.75}$; BCS = body condition score; ΔBW = change in BW; ΔBodyE = change in body energy; Milk:feed = energy-corrected milk per unit of feed; IOFC = income over feed cost.

[4]P-value associated with the preceding correlation of production and efficiency traits with residual feed intake.

[5]Energy partitioning: % to milk = percent of apparently absorbed energy partitioned to milk production; percent of apparently absorbed energy partitioned to body tissue gain.

Production and Residual Feed Intake

Correlations between RFI and production and other measures of efficiency are listed in Table 2.5. Residual feed intake was not correlated with production and BW variables, which was expected because RFI was estimated based on observed performance. Income over feed cost, gross efficiency, and milk:feed correlated negatively with RFI (r=-0.13, r=-0.35, r=-0.39; *P*=0.05, *P*<0.01, and *P*<0.01, respectively), though IOFC was not related to RFI when cows were fed LO diets (r=-0.06; *P*=0.54). Multiple of maintenance based on requirements was not related to RFI (r=0.01; *P*=0.87), but MM_I correlated positively with RFI (r=0.47; *P*<0.01; data not shown). Body condition score tended to correlate negatively with RFI (r=-0.11, *P*=0.09), but was not related to RFI when cows were fed HI diets (r=-0.06; *P*=0.57). Importantly, energy partitioning was not associated with RFI (*P*>0.80) and MilkE, MBW, and ΔBodyE were also not related to RFI (*P*=1.0). Figure 2.2 illustrates the relationship between daily feed cost and product value for HRFI, MRFI, and LRFI cows. The slopes for HRFI and LRFI cows were similar, but the y-intercept was smaller for LRFI cows, indicating a savings in feed cost of about $0.75/day for the same amount of product produced regardless of level of production.

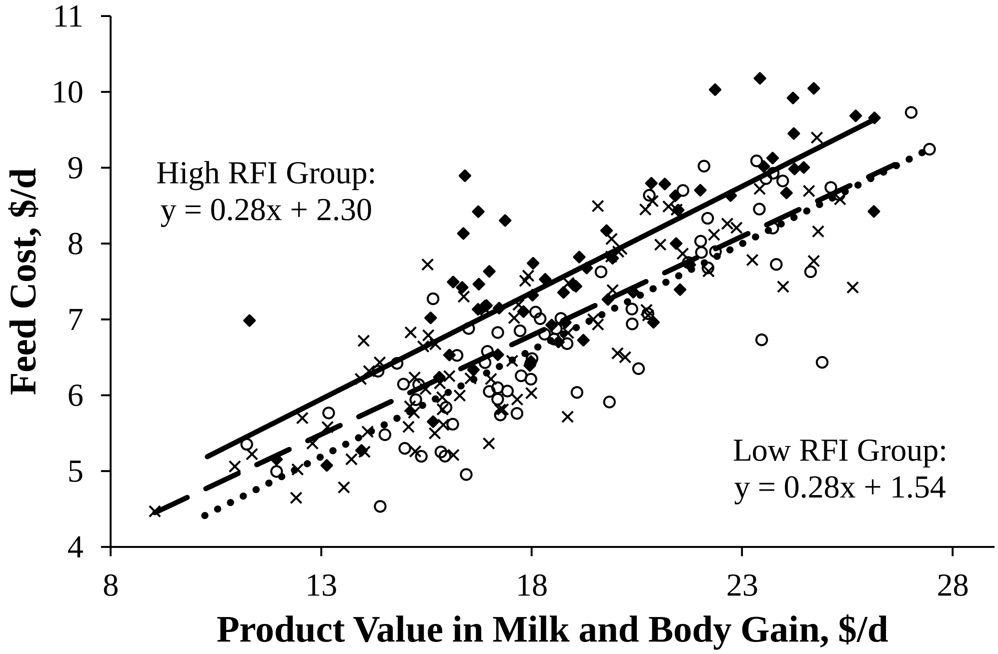

Figure 2.2. Relationship between daily feed cost and product value by RFI groups for cows fed high and low starch diets. Product value was determined by the sum of mean daily milk income and mean daily body weight gain value. Milk income was determined for a cow based on individual production of protein ($7.11/kg), fat ($3.46/kg), lactose ($0.87/kg), and milk ($0.04/kg). Gain of BW was assigned an economic value of $1.78/kg. Feed cost was determined using the following values for feeds ($/kg DM): $0.22/kg corn silage, $0.11/kg legume silage, $0.10/kg wheat straw, $0.22/kg soybean hulls, $0.41/kg whole cottonseed, $0.34/kg ground corn, $0.33/kg high moisture corn, $0.56/kg soybean meal, $1.55/kg fat supplement, $0.13/kg vitamin and mineral mix, $0.22/kg limestone, $0.22/kg sodium bicarbonate, and $0.45/kg dicalcium phosphate. RFI groups were defined as >, <, or ±0.5 SD of the mean RFI of each cohort. LRFI = low RFI group, HRFI = high RFI group, MRFI = medium RFI group. Animals in the HRFI group are denoted by ◆. Animals in the LRFI group are denoted by ○. Animals in the MRFI group are denoted by x. The solid line is the regression line for the HRFI group, the dashed line is the regression line for the MRFI group, and the dotted line is the regression line for the LRFI group.

Most Efficient vs. Least Efficient Cows

There were no significant differences for milk and component yields (data not shown), MilkE, MBW, adjusted BW, ΔBodyE, ΔBW, BCS, ΔBCS, or energy partitioning between the most efficient cows (top 10% of cows for RFI; n=11) and least efficient cows (bottom 10% of cows for RFI; n=11; Table 2.6). When compared with the most efficient cows, DMI was greater for the least efficient cows when fed HI (29.6 vs. 25.4 kg/d; *P*<0.01) and LO diets (28.8 vs. 23.0 kg/d; *P*<0.01). The most efficient cows had significantly greater milk:feed when fed the HI (1.83 vs. 1.51; *P*<0.01) and LO diets (1.71 vs. 1.49; *P*=0.01). Gross efficiency was also greater for the most efficient cows when fed HI diets (34.2 vs. 27.5%; *P*=0.01). Though not significant, IOFC was greater for the most efficient cows when HI diets were fed ($12.4 vs. $10.4; *P*=0.15), but was similar between the most efficient and least efficient cows when LO diets were fed ($11; *P*=0.89). When compared with the least efficient cows, the most efficient cows had lower daily feed cost for HI ($7.1 vs. $8.3; *P*=0.01) and LO diets ($5.7 vs. $7.3; *P*<0.01), but similar product output value (value of milk and body gain; *P*>0.2).

Table 2.6. Performance of the most efficient and least efficient cows fed high (HI) and low (LO) starch diets[1].

	Diet							
	HI				LO			
Item[2]	Most Efficient	Least Efficient	SE	P-value[3]	Most Efficient	Least Efficient	SE	P-value
Intake and Production								
DMI, kg/d	25.4	29.6	1.02	<0.01	23.0	28.8	1.06	<0.01
MilkE, Mcal/d	32.4	30.9	1.98	0.60	27.6	29.9	1.84	0.39
Feed cost, $/d	7.13	8.30	0.30	0.01	5.66	7.31	0.31	<0.01
Product value, $/d	20.7	19.7	1.17	0.56	16.7	18.8	1.16	0.22
BW, BCS, and ΔTissue								
MBW, $kg^{0.75}$	136	137	3.25	0.83	133	133	2.93	1.00
Adjusted BW, kg	714	734	27.7	0.62	699	714	24.6	0.67
BCS	2.90	2.74	0.16	0.48	2.84	2.68	0.13	0.42
ΔBW, kg/d	0.65	0.56	0.24	0.77	0.22	0.54	0.14	0.12
ΔBCS, pt/28 d	0.15	0.17	0.08	0.83	0.04	0.17	0.06	0.18
ΔBodyE, Mcal/d	3.82	3.30	1.35	0.79	1.29	3.02	0.80	0.14
Energy partitioning[4]								
% to milk	68.8	68.3	2.33	0.88	70.0	68.2	1.71	0.47
% to maintenance	23.4	25.1	1.44	0.42	27.6	25.1	1.26	0.17
% to body tissue	7.7	6.6	2.84	0.77	2.4	6.7	2.21	0.18
Efficiency								
Milk:feed	1.83	1.51	0.07	<0.01	1.71	1.49	0.05	0.01
Gross Efficiency, %	34.2	27.5	1.66	0.01	30.0	27.2	1.27	0.14
IOFC, $/d	12.4	10.4	0.94	0.15	10.7	10.5	0.86	0.89
RFI, kg DM/d	-2.87	2.52	0.31	<0.01	-2.20	2.63	0.26	<0.01

[1]Most efficient cows (n=11) and least efficient cows (n=11) were selected based on their ranking among all cows (n=109) for residual feed intake when fed high and low starch diets separately.
[2]MilkE = milk energy output; Product value = daily income from milk and body gain; MBW = $BW^{0.75}$; Adjusted BW = BW adjusted to a body condition score of 3, defined as [BW/(0.137 x body condition score + 0.589)]; BCS = body condition score; ΔBW = change in BW; ΔBCS = change in BCS per 28-d period; ΔBodyE = change in body energy; M:F = energy-corrected milk per unit of feed; GEFF = gross efficiency; IOFC = income over feed cost; RFI = residual feed intake.
[3]P-value associated with differences in efficiency group (efficient or inefficient).
[4]Energy partitioning: % to milk = percent of apparently absorbed energy partitioned to milk production; % to maintenance = percent of apparently absorbed energy partitioned to maintenance; percent of apparently absorbed energy partitioned to body tissue gain.

DISCUSSION

We observed that RFI was repeatable across HI and LO diets, and that few cows changed their efficiency ranking drastically. Differences between the HI and LO diets in each of the four studies were great enough to cause significant differences in milk production, feed intake, body weight gain, or all three. Thus, these findings provide support for the use of RFI as a tool to identify efficient animals, independent of the type of diet fed. Although there was some re-ranking that occurred when cows moved from one diet to the other, this re-ranking was minor, so that selection for the most efficient cows on a high starch diet should result in cows that also are more efficient on a low starch diet. As expected, RFI was independent of production and BW, and cows with low RFI ate less feed to produce the same amount of product as contemporaries.

Repeatability of RFI

The repeatability of RFI across diet in this study was greater than that shown for beef cattle during growing and finishing phases; however, our diets were not as different as the diets in those studies. Durunna et al. (2011) examined the repeatability of RFI in beef steers (n=331) fed consecutive grower (80% concentrate) and finisher diets (100% concentrate) across growing and finishing periods. They determined that RFI was moderately repeatable (r=0.33) and 55% of animals changed feed efficiency ranking (RFI >0.5 SD, RFI <0.5 SD, or RFI ±0.5 SD) from period one to period two. Kelly et al. (2010a, 2010b) also fed high forage diets to beef heifers in the growing period followed by high concentrate diets during the finishing period and found RFI to be more repeatable (r=0.62). Reasons that the repeatability of RFI in our study was greater than in the studies of Kelly et al. (2010b) and Durunna et al. (2011) could be that their diets differed in forage:concentrate ratio, while our HI and LO diets had similar forage:concentrate, and that the cattle in both of those studies were at different stages of growth between measurement periods. Poor growth during the first period could have a compensatory effect of growth and efficiency in the second period.

An animal's stage of maturity and physiological state can influence the repeatability of RFI probably because changes in BW are difficult to quantify. Residual feed intake was repeatable when measured in older mice, but less repeatable in younger mice (Archer and Pitchford, 1996). Arthur et al. (1999) determined that RFI was moderately repeatable (r=0.36) for beef cattle measured just after weaning and at maturity. Macdonald et al. (2014) determined RFI for Holstein heifer calves and evaluated the most and least efficient calves (n=183) as first lactation cows, and alluded to some re-ranking of animals for RFI across the two measurement periods. In a study by Connor et al. (2013), repeatability of weekly RFI measurements was 0.47 through 90 DIM, and after 42 DIM, weekly estimates of RFI were highly correlated with RFI measured through 90 DIM (r~0.8). These studies support the hypothesis that the repeatability of RFI may be dependent on an animal's physiological state during each test period.

Estimation of RFI across different periods may be more repeatable if measurements are obtained from periods when animals are in similar physiological states. In any case, the diets fed in the current study elicited quite different responses in milk yield and component concentration, in addition to energy partitioning. Because changes in BW are difficult to quantify, shifting energy partitioning to BW gain might have been expected to introduce more error into the estimation of RFI when cows were fed HI diets. However, production differences and changes in energy partitioning observed between HI and LO diets in this study did not seem to impact the repeatability of RFI. Residual feed intake for each 4-wk period was highly repeatable (r=0.73) across the diets, suggesting that our ability to identify the most efficient cows was not impeded by diets that altered performance and shifted energy partitioning. When RFI was calculated weekly, we observed that weekly RFI was fairly repeatable within diet, as indicated by the average repeatability of RFI across weeks 1 through 4 and weeks 5 through 8 of experiments (r=0.65). Furthermore, using weekly RFI estimates, we observed an average across-diet repeatability of 0.56 indicating that across-diet repeatability made up 86% of the repeatability observed within-diet. Repeatability of weekly RFI was expected to be lower than the repeatability of whole-period RFI because each period averaged data for 4-wk and therefore had less measurement error. That RFI was not perfectly repeatable between HI and LO diets or across weeks within diet suggests that genotype by environment interactions may be important or that there is error associated with the measurement of RFI from one week to another.

Repeatability of Other Efficiencies

Milk:feed was highly repeatable across diets for the current study, which was higher than the repeatability for gain:feed reported by Kelly et al. (2010b) and Durunna et al. (2011). The repeatability of IOFC across HI and LO diets also was high (r=0.84; $P<0.01$), suggesting that cows that are most profitable within a group will likely still be the most profitable even when expensive, high starch concentrates, like corn grain, are replaced with cheaper non-forage fiber sources, like soybean hulls. Repeatability for DMI was 0.92, which is higher than results reported by Kelly et al. (2010b). The high repeatability of DMI may have played a role in determining the repeatability of RFI and milk:feed since both traits are calculated based on observed DMI. The repeatability of MilkE was also high (r=0.89; $P<0.01$; data not shown), which may have also influenced the repeatability of milk:feed. Cows in this study were probably in similar physiological states across both 28-d treatment periods, which may have enhanced repeatabilities that we observed for DMI, MilkE, and milk:feed. The low repeatability of

ΔBodyE might have influenced the low overall repeatability of gross efficiency across HI and LO diets. The low repeatability of ΔBodyE suggests that there is much more error associated with determining ΔBodyE. The repeatability of gross efficiency for cows that were fed the HI diet in period one followed by the LO diet in period two was 0.15 (P=0.27). For cows fed the LO diet in period one followed by the HI diet in period two, repeatability of gross efficiency was 0.24 (P=0.07). These findings suggest that perhaps the sequence in which diets were fed did not significantly alter the repeatability of gross efficiency across HI and LO diets.

RFI and Performance

As expected, DMI correlated positively with RFI. These results are similar to other reports for beef and dairy animals (Castro Bulle et al., 2007; Kelly et al., 2010b; Green et al., 2013). Consistent with these results, the most efficient cows ate ~5 kg DM/d less than the least efficient cows in our study. Milk:feed correlated negatively with RFI, indicating that cows with low RFI also had enhanced milk:feed which suggests that selection for RFI could improve this trait concurrently. Others reported negative correlations of RFI with gain:feed in beef cattle (Castro Bulle et al., 2007; Kelly et al., 2010b, Arthur et al., 2001). When all cows and both diets were considered, IOFC correlated negatively with RFI. However, when looking at relationships for each diet, IOFC was not associated with RFI when cows were fed LO diets. One reason for this could be that when compared to the most efficient cows, the least efficient cows had a mean daily product value that was numerically greater (P=0.2) when fed LO diets which would have offset their greater daily feed cost, causing IOFC to be similar among the most and least efficient cows. Multiple of maintenance based on energy requirements was not related to RFI, but was highly correlated with both gross efficiency and milk:feed (r=0.8 and r=0.7, respectively; data not shown). These results confirm that selection for RFI would be independent of the dilution of maintenance, unlike milk:feed and gross efficiency. Both gross efficiency and milk:feed rely on diluting out maintenance through the partitioning of a greater proportion of NE to milk production rather than to maintenance. In contrast, RFI is independent of the dilution maintenance because it quantifies efficiency within a production level and allows for the identification of animals the convert gross energy into metabolizable energy more efficiently by reducing energetic losses in feces, urine, gas, and heat. Unlike MM_R, MM_I correlated positively with RFI (r=0.47) because observed DMI is used to determine both variables. Thus, RFI is independent of the dilution of maintenance only when multiple of maintenance is calculated based on requirements for observed production (MM_R).

When compared with the least efficient cows, the most efficient cows had similar MilkE, MBW, ΔBW, ΔBodyE, ΔBCS, and average BCS for both HI and LO diets, and RFI was not correlated with any of these traits, as was expected since the model used to derive RFI accounted for these variables. However, RFI tended to correlate negatively with BCS when cows were fed LO diets but not HI diets. Since BCS was not directly included in the model to estimate RFI, it was not surprising that the most efficient and least efficient cows were a little different. Adjusted BW, which adjusts a cow's BW to the BW that she would be if she had a BCS of 3.0 was used as an indicator of body size and was not correlated with RFI (data not shown), and was similar between the most and least efficient cows across both diets. Although the similarity between the most efficient and least efficient cows for adjusted BW is not unexpected since a form of BW (MBW) is accounted for in the prediction of RFI, it confirms that selection for RFI will not bias toward large or small cows. Energy partitioning was also not different between efficiency groups and not correlated with RFI. Because body energy change is accounted for in the prediction of RFI, it is expected that cows with low RFI will not be any more likely to mobilize body tissue to support production than cows with high RFI. The independence of RFI from BW loss is important because excessive tissue mobilization is related to metabolic diseases and poor fertility (Butler et al., 1981; Collard et al., 2000). When BW change was included in the model to derive RFI, RFI was not associated with reproductive performance of beef cattle (Arthur et al., 2005; Basarab et al., 2007; Blair et al., 2013). However more research needs to be conducted to determine if selection for RFI will influence fertility in dairy cattle.

Production Responses to High and Low Starch Diets

Similar to results shown by others (Ipharraguerre et al., 2002; Ranathunga et al., 2010; Ferraretto et al., 2011; Weiss et al., 2011), feeding diets that differed in starch content in this study altered DMI, milk yield, and milk component concentration. We also saw differences in energy partitioning, with more energy partitioned to milk and less to body gain when cows were fed LO diets. Cows fed HI diets had greater ΔBW and ΔBCS, which are similar to results reported by Ipharraguerre et al. (2002) and Voelker and Allen (2003), respectively. There was a significant interaction of diet and experiment for energy partitioned to milk because diets for experiments 3 and 4 resulted in large shifts in partitioning, but diets in experiments 1 and 2 did not alter energy partitioning. The interaction of diet and experiment was also significant for ΔBCS and ΔBodyE, with cows in all experiments having numerically greater ΔBCS and ΔBodyE when fed HI diets, but differences between diets were only significant for experiment 3. One reason that differences were significant for experiment 3 and not experiments 1, 2, and 4 could be that the LO diet for experiment 3 was formulated by replacing starch with forage, non-forage fiber, and supplemental fat; in experiments 1, 2, and 4, non-forage fiber replaced starch to formulate LO diets. That cows gained more body condition when they were fed HI diets suggests that HI diets resulted in the production of more glucose precursors (Allen et al., 2009) that caused increased insulin secretion, which enhanced glucose uptake by adipose tissue. Milk:feed was not significantly different between HI and LO diets, but gross efficiency was greater when cows were fed HI diets. This could have been due to the greater energy content of HI diets or to increased lipogenesis that was observed for HI diets (as indicated by increased ΔBodyE and ΔBW), but similar MilkE for both diets. As expected, RFI was not different between HI and LO diets. Regardless of whether or not energy partitioning was significantly altered by diet, RFI was still repeatable across diet within each individual experiment.

Since feed accounts for a large proportion of production costs, it is of interest whether RFI is related to profitability. Animals with low RFI consume less feed than contemporaries to yield the same amount of product. In this study, the most efficient cows had significantly lower daily feed cost than the least efficient cows, but product value (milk + body gain) was similar. Compared with high RFI cows, cows with low RFI cost ~$0.75 less to feed per day for the same value of product produced regardless of level of production (Figure 2.2). Although IOFC was not strongly correlated with RFI, the most efficient cows had numerically greater IOFC for HI (~$2.00) and LO diets (~$0.20) than the least efficient cows (Table 2.5). Our results indicate that profitability is mostly independent of RFI when using IOFC as an indicator of profit, because MM_R is independent of RFI and MM_R is a major determinant of profitability (VandeHaar and St-Pierre, 2006).

CONCLUSION

We conclude that RFI is repeatable across high and low starch diets fed to mid-lactation dairy cows. Our results suggest that cows that are efficient when eating diets that are high in starch content, as is typical for the Midwest United States, will also still be efficient when consuming diets that are high in non-forage fiber sources, such as soybean hulls. Residual feed intake, unlike milk:feed and gross efficiency, is independent of multiple of maintenance on a requirement basis, so it will be useful for identifying efficient animals independent of the dilution of maintenance. Profitability, as estimated by IOFC, was not significantly different between the lowest and highest RFI cows for either diet, suggesting that it may be independent of an animal's RFI status; however, IOFC was ~$2 greater for low RFI cows when fed high starch diets. Although IOFC may be independent of RFI, cows with low RFI will likely cost less to feed on a daily basis because DMI is reduced for cows with low RFI.

APPENDIX

Table A. 1. Characterization of animals for experiments 1, 2, 3, and 4.

Item[1]	Experiment 1[2,3]	Experiment 2	Experiment 3	Experiment 4
DIM	144 ± 26	104 ± 28	120 ± 26	107 ± 25
Milk, kg/d	38 ± 8	41 ± 10	46 ± 9	42 ± 8
BW, kg	694 ± 74	650 ± 73	672 ± 80	655 ± 71

[1]DIM = days in milk at start of experiment.
[2]Mean ± standard deviation.
[3]Experiment 1: n=32 (7 primiparous, 25 multiparous); Experiment 2: n=25 (10 primiparous, 15 multiparous); Experiment 3: n=32 (16 primiparous, 16 multiparous); Experiment 4: n=20 (11 primiparous, 9 multiparous).

Table A. 2. Ingredient and milk component prices used to determine income over feed cost.

Ingredient/Component[1]	Price, $/kg DM
Feed Ingredients	
Corn silage	0.22
Legume silage	0.11
Wheat straw	0.10
Soybean hulls	0.22
Cottonseed, whole	0.41
Corn, ground	0.34
Corn, high moisture	0.33
Soybean meal	0.56
Fat supplement	1.55
Vitamin & mineral	0.13
Limestone	0.22
Sodium bicarbonate	0.22
Dicalcium phosphate	0.45
Milk Components and BW Gain	
Fat	3.46
Protein	7.11
Other solids	0.87
Producer price differential	0.04
BW gain	1.78

[1]Feed ingredient prices are based on prices in the Midwest United States in September, 2013.

Table A. 3. Re-ranking of cows between RFI groups when changed from high starch to low starch diets.

RFI Group Change[1]	Number of Cows
LRFI to HRFI	2
HRFI to LRFI	2
LRFI to MRFI	10
HRFI to MRFI	10
MRFI to LRFI	12
MRFI to HRFI	10

[1]RFI groups were defined as ±0.5 SD for the mean RFI of each cohort. LRFI = low RFI group, HRFI = high RFI group, MRFI = medium RFI group.

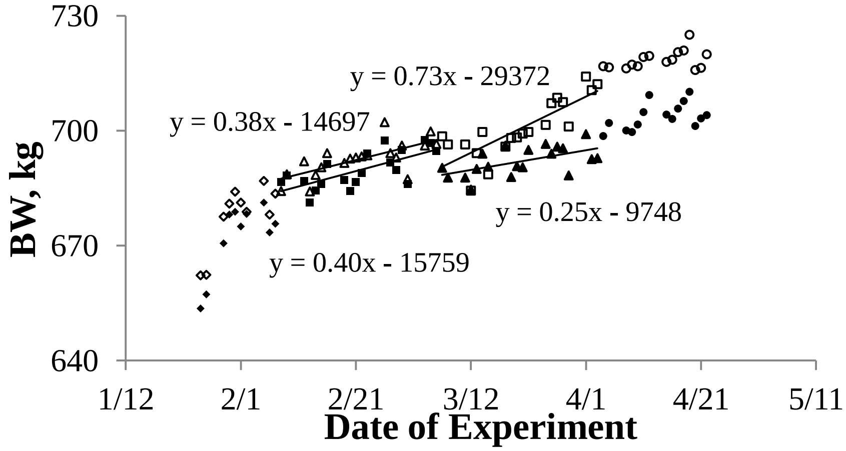

Figure A. 1. Mean cohort BW vs. date of experiment for cows in experiment 1 to determine if gut fill effects on the prediction of ΔBW. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

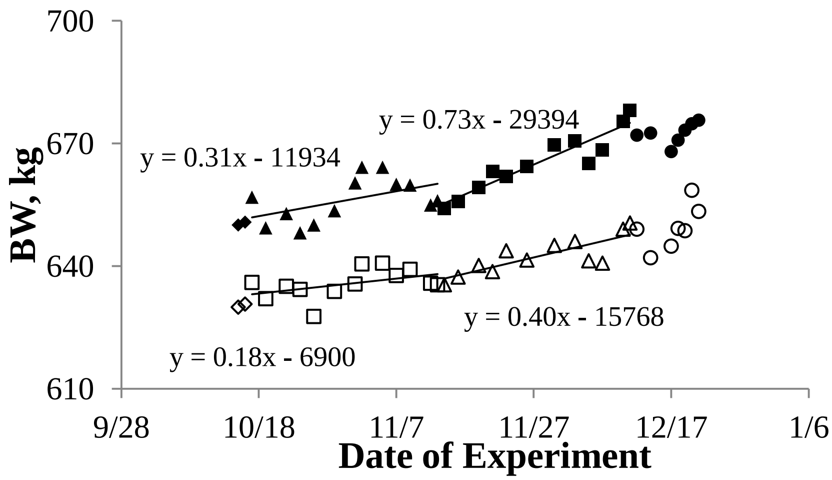

Figure A. 2. Mean cohort BW vs. date of experiment for cows in experiment 2 to determine gut fill effects on the prediction of ΔBW. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

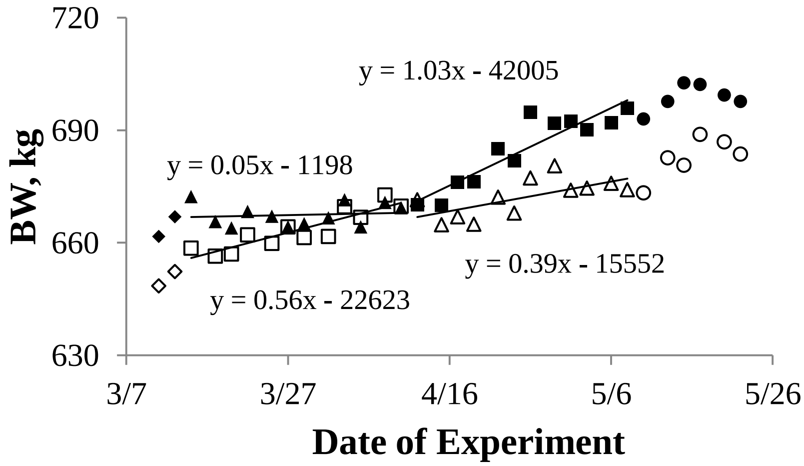

Figure A. 3. Mean cohort BW vs. date of experiment for cows in experiment 3 to determine gut fill effects on the prediction of ΔBW. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

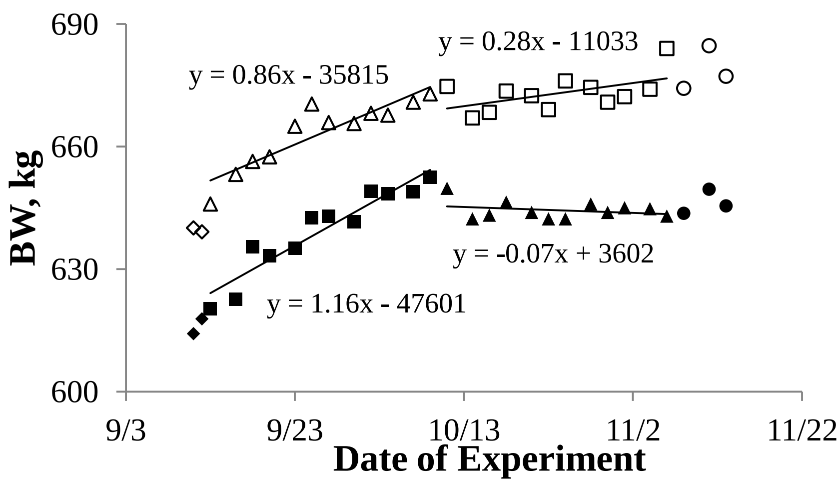

Figure A. 4. Mean cohort BW vs. date of experiment for cows in experiment 4 to determine gut fill effects on the prediction of ΔBW. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

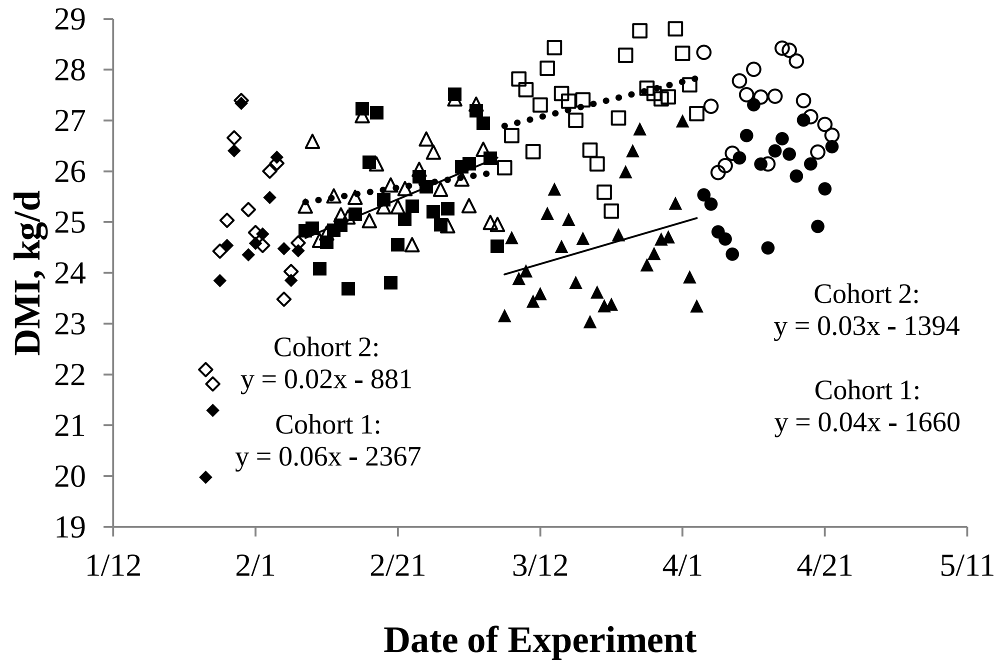

Figure A. 5. Mean cohort DMI vs. date of experiment for cows in experiment 1 to determine if feed intake may have influenced gut fill effects when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

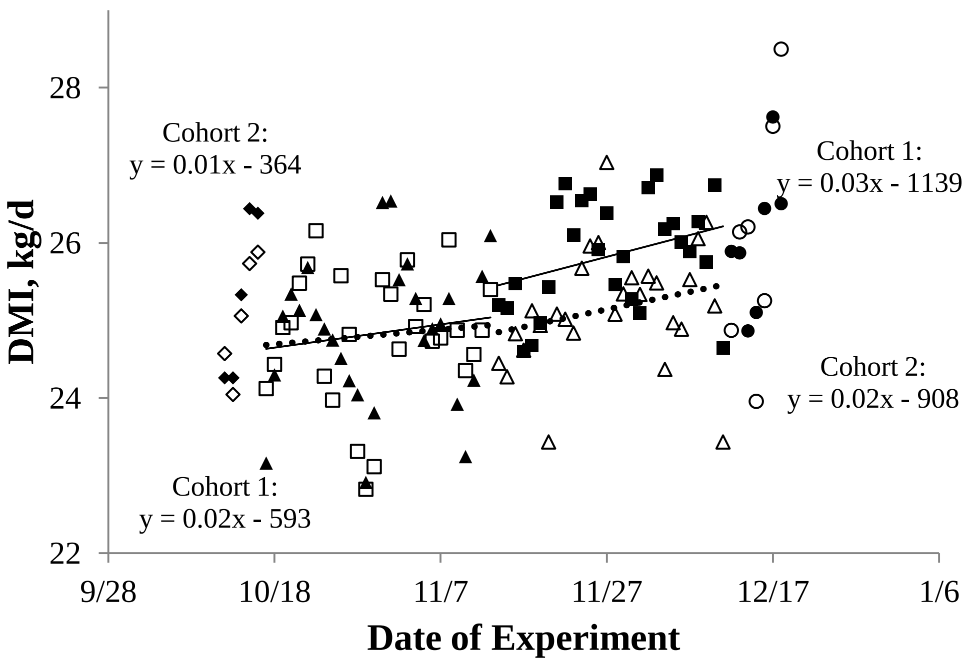

Figure A. 6. Mean cohort DMI vs. date of experiment for cows in experiment 2 to determine if feed intake may have influenced gut fill effects when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

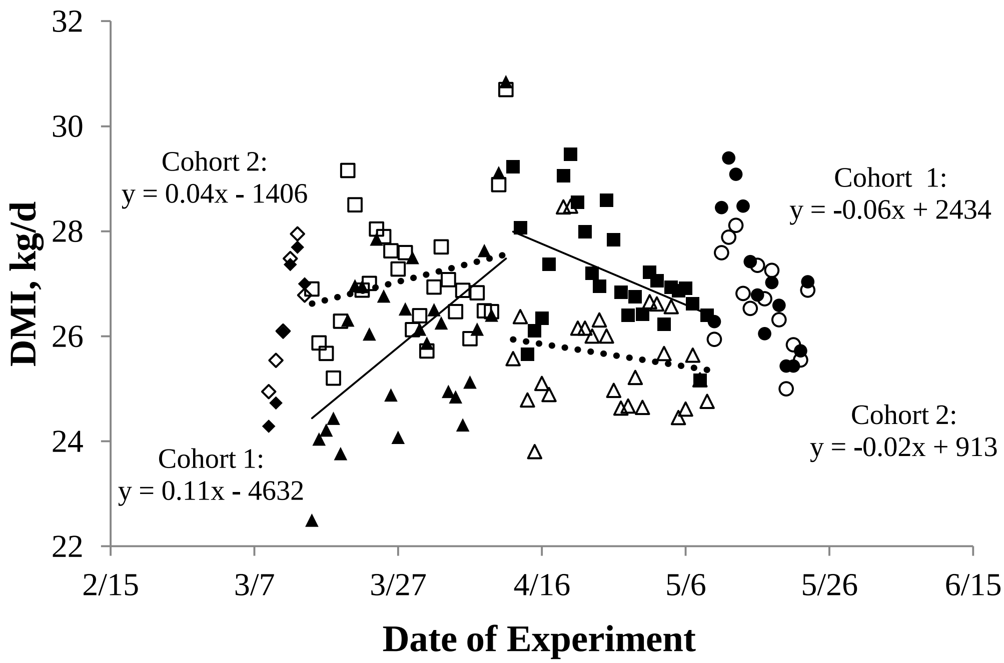

Figure A. 7. Mean cohort DMI vs. date of experiment for cows in experiment 3 to determine if feed intake may have influenced gut fill effects when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

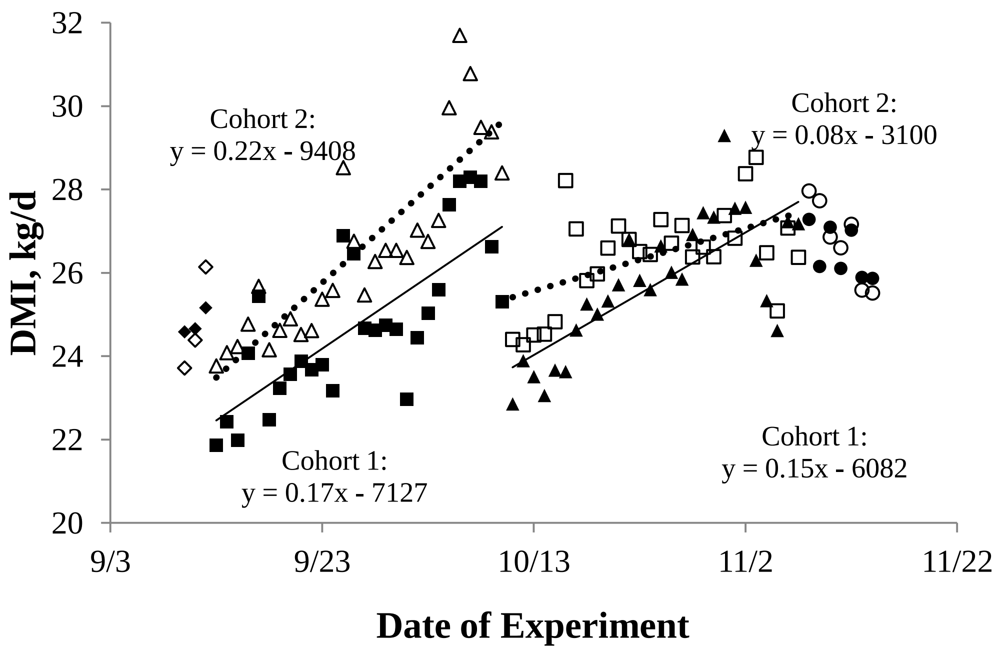

Figure A. 8. Mean cohort DMI vs. date of experiment for cows in experiment 4 to determine if feed intake may have influenced gut fill effects when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

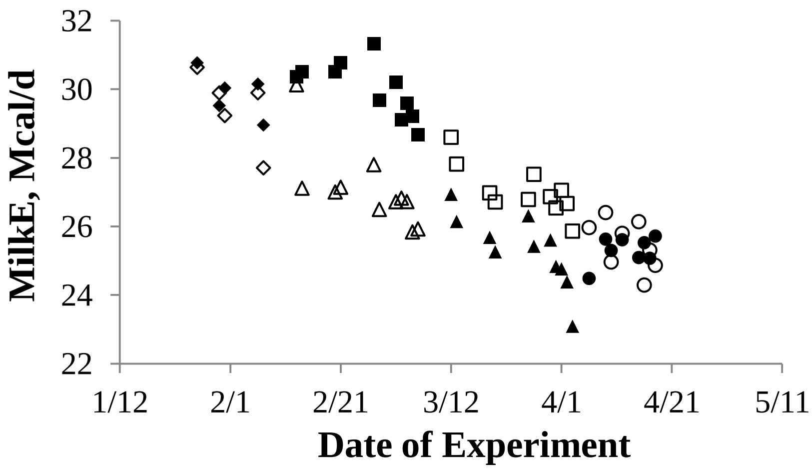

Figure A. 9. Mean cohort MilkE vs. date of experiment for cows in experiment 1 to determine if MilkE was altered when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

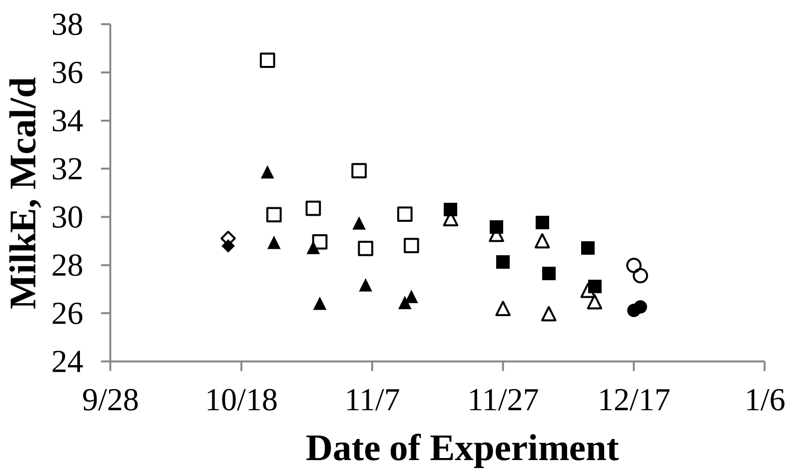

Figure A. 10. Mean cohort MilkE vs. date of experiment for cows in experiment 2 to determine if MilkE was altered when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

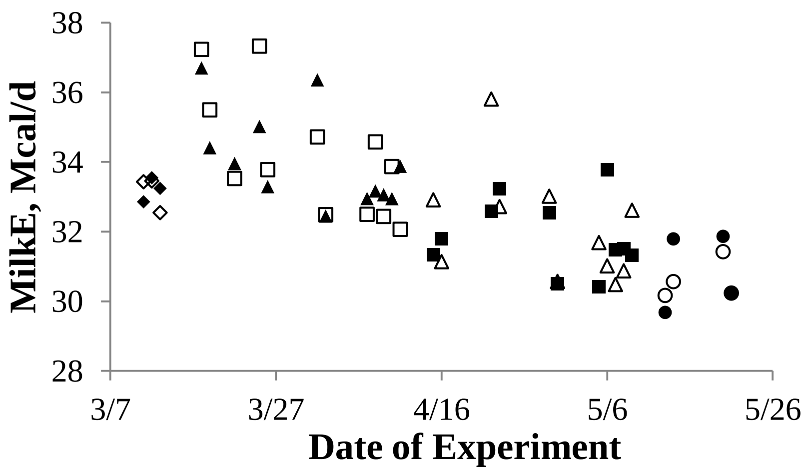

Figure A. 11. Mean cohort MilkE vs. date of experiment for cows in experiment 3 to determine if MilkE was altered when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

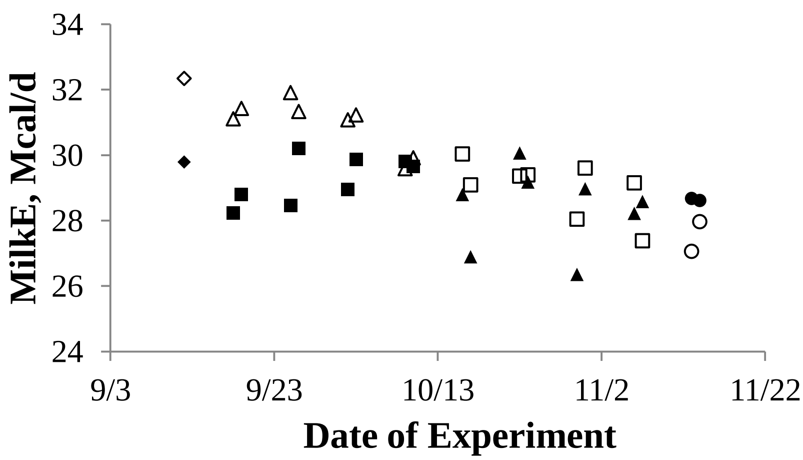

Figure A. 12. Mean cohort MilkE vs. date of experiment for cows in experiment 4 to determine if MilkE was altered when diet changes occurred. Closed diamonds (◆) represent cows in cohort 1 fed the preliminary control diet; open diamonds (◇) represent cows in cohort 2 fed the preliminary control diet; closed boxes (■) represent cows in cohort 1 fed the high starch diet; open boxes (□) represent cows in cohort 2 fed the high starch diet; closed triangles (▲) represent cows in cohort 1 fed the low starch diet; open triangles (△) represent cows in cohort 2 fed the low starch diet; closed circles (●) represent cows in cohort 1 fed the post-experiment control diet; and open circles (○) represent cows in cohort 2 fed the post-experiment control diet.

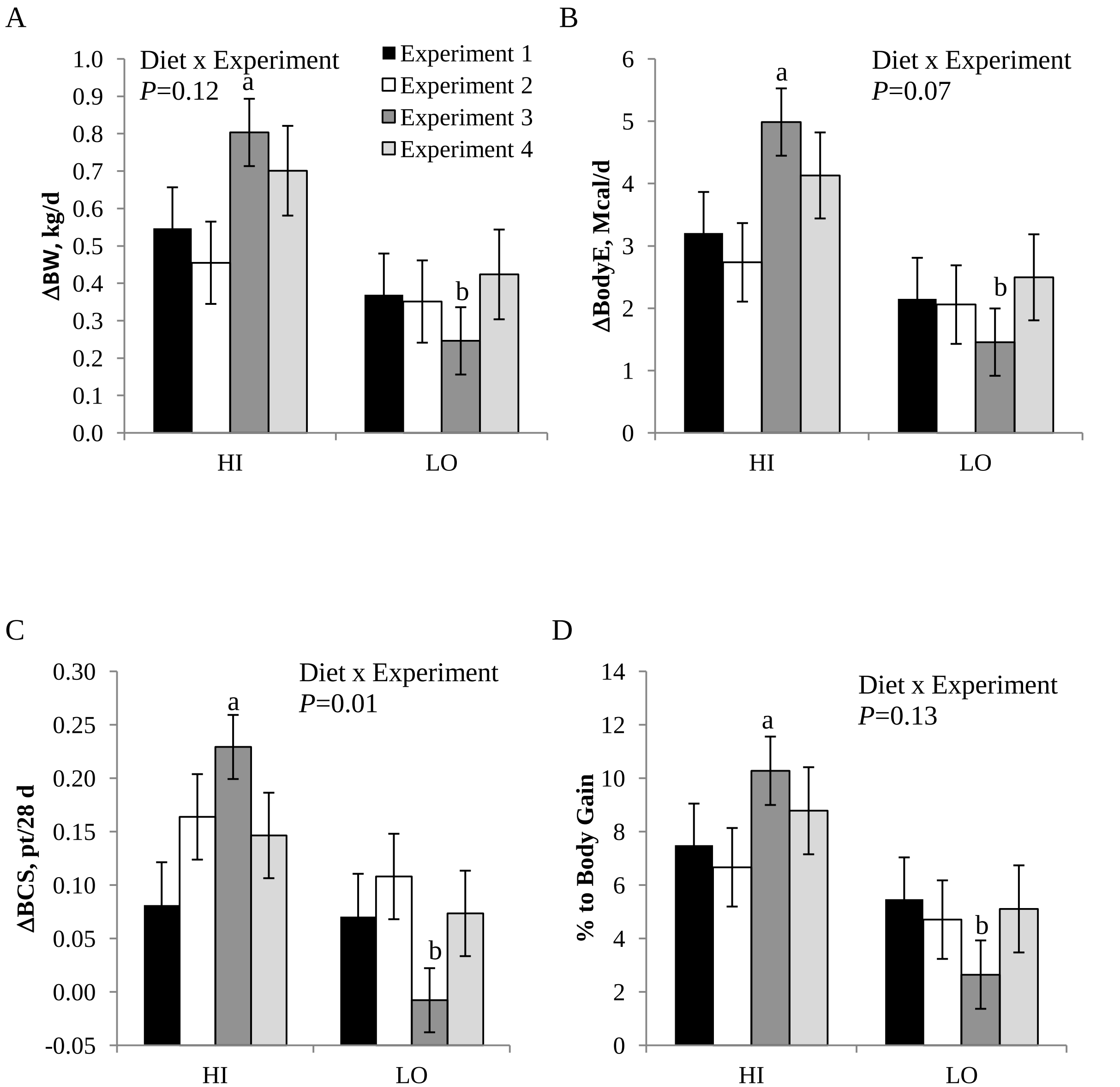

Figure A. 13. Least square means for ΔBW (change in BW; A), ΔBodyE (change in body energy; B), ΔBCS (change in BCS; C) and % of energy partitioned to body gain (D) by experiment and diet. Diets were high (HI) or low (LO) starch. Experiments 1, 2, 3, and 4, utilized 32, 25, 32, and 20 cows, respectively. Bars with different superscripts within an experiment are significantly different ($P<0.05$).

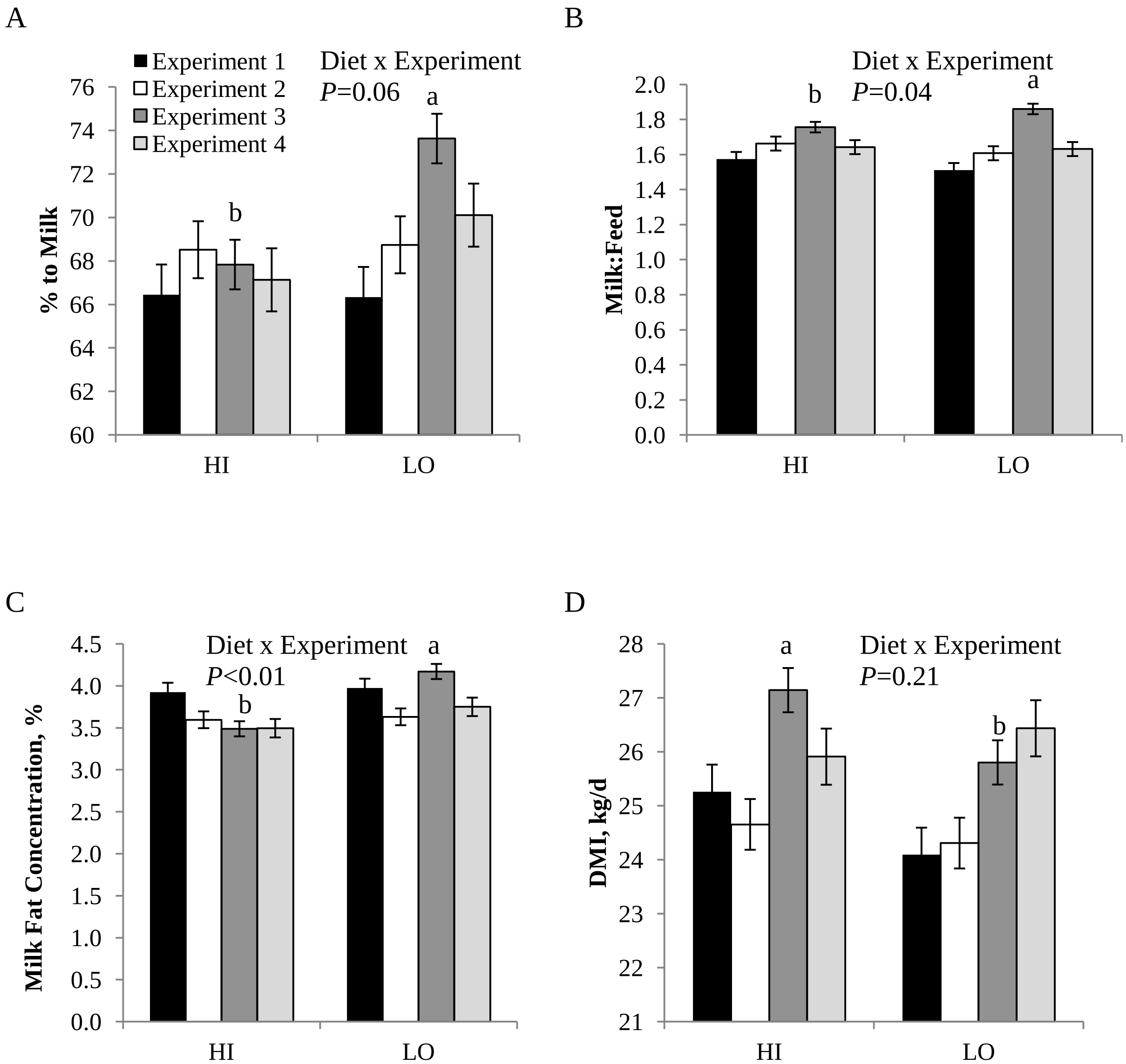

Figure A. 14. Least square means for % of energy partitioned to milk (A), milk:feed (B), milk fat concentration (C) and DMI (D) by experiment and diet. Diets were high (HI) or low (LO) starch. Experiments 1, 2, 3, and 4, utilized 32, 25, 32, and 20 cows, respectively. Bars with different superscripts within an experiment are significantly different (P<0.05).

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CHAPTER 3

RELATIONSHIP BETWEEN RESIDUAL FEED INTAKE AND DIGESTIBILITY FOR LACTATING HOLSTEIN COWS FED HIGH AND LOW STARCH DIETS

ABSTRACT

We determined if differences in digestibility among cows explained variation in residual feed intake (RFI) in 4 cross-over design experiments. Lactating Holstein cows (n=109; 120±30 DIM; mean ± SD) were fed diets high (HS) or low (LS) in starch. LS diets were ~40% NDF and ~14% starch; HS diets were ~26% NDF and ~30% starch. Each experiment consisted of two 28-d treatment periods, with digestibility measured during the last 5 d. Individual DMI and milk yield were recorded daily, BW was measured 3-5 times per wk, and milk components were analyzed 2 d/wk. Individual DMI was regressed on milk energy output, metabolic BW, body energy gain, and fixed effects of parity, experiment, cohort nested within experiment, and diet nested within cohort and experiment, with the residual being RFI. High RFI cows eat more than expected and were deemed less efficient. RFI correlated negatively with digestibility of starch for both HS (r=-0.31; P<0.01) and LS diets (r=-0.23; P=0.02), and with digestibilities of DM (r=-0.30; P<0.01) and NDF (r=-0.23; P=0.02) for LS diets but not HS diets (P>0.3). For each cohort, cows were classified as high RFI (HRFI; >0.5 SD), medium RFI (MRFI; ±0.5 SD), and low RFI (LRFI; <-0.5 SD). Digestibility of DM was similar (~66%) among HRFI and LRFI cows for HS diets but greater for LRFI cows when fed LS diets (64 vs. 62%; P<0.05). For LS diets, digestibility of DM accounted for 33% of the differences among HRFI and LRFI for apparent diet energy density, as determined from individual cow performance, suggesting that digestibility accounts for some of the between-animal differences for the ability to convert gross energy into

net energy. Although digestibility was different between HRFI and LRFI cows for LS diets, some of the differences were expected because cows with high RFI eat at a higher multiple of maintenance, which could depress digestibility. Based on these data, we conclude that a cow's digestive ability explains none of the variation in RFI for cows eating high starch diets but 9-33% of the variation in RFI when cows are fed low starch diets. Because cows with low RFI eat less than high RFI cows, it might be expected that their digestive efficiency would be greater simply due to differences in intake; however, it is possible that low RFI cows may in fact eat less than cows with high RFI because of a superior ability to convert gross energy into digested energy.

INTRODUCTION

Residual feed intake (RFI) has been used to assess efficiency in beef cattle (Richardson et al., 2004; Nkrumah et al., 2006; Lawrence et al., 2011), swine (Harris et al, 2012), poultry (Luiting et al., 1994; Mignon-Grasteau et al., 2004), and dairy cattle (Rius et al., 2012; Green et al., 2013; Macdonald et al., 2014; Tempelman et al., 2013). Residual feed intake is the difference between what an animal consumes and what it is predicted to consume based on production and maintenance requirements (Koch et al., 1963). Residual feed intake quantifies efficiency within a production level, and thus is independent of the dilution of maintenance based on requirements for maintenance and production. Cows with low RFI have improved digestive and metabolic efficiencies, or have lower maintenance requirements than expected for a given BW; they eat less than contemporaries per unit of apparent net energy consumed and efficiently convert gross energy to net energy.

The underlying biological mechanisms to explain differences in RFI among animals are not clear. Richardson and Herd (2004) hypothesized that 2% of the variation in RFI was due to feeding patterns, 10% was due to activity level, 37% was due to protein turnover and tissue metabolism, 5% was due to body composition, 9% was due to the heat increment of feeding, 10% was due to digestibility, and 27% was due to unknown metabolic processes.

Animals with improved digestive efficiency lose less energy in feces and are expected to be more feed efficient. In dairy cattle, calves identified as low RFI tended to have improved DM digestibility as early lactating cows (Rius et al., 2012). Nkrumah et al. (2006) determined that RFI was correlated (r =-0.3) with DM digestibility in beef steers and that steers with low RFI had 6% greater digestion of DM. In agreement, Richardson et al. (1996) reported that low RFI beef cattle tended to have greater DM digestibility than high RFI cattle. Broilers selected divergently for digestive efficiency differed in RFI, with birds with high digestive efficiency having lower RFI than birds with low digestive efficiency (Mignon-Grasteau et al., 2004). Sixth generation broilers out of the same selection lines were fed diets that differed in particle size (Rougière et al., 2009). Birds of high digestive efficiency line always had greater nutrient digestibility than the low line regardless of diet; however, a diet by line interaction indicated that coarse particle diets stimulated greater digestive efficiency in the low line, but not the high line (Rougière et al., 2009). Cattle that differ in RFI have diverse rumen environments (Lawrence et al., 2011) and microbial populations (Carberry et al., 2012; Hernandez-Sanabria et al., 2012), which suggest that there could be differences in digestibility between these groups. However, both Carberry et al. (2012) and Hernandez-Sanabria et al. (2012) indicated that these relationships may be influenced by diet type. These studies suggest that diet may affect the digestive efficiency of high and low RFI animals differently.

The objective of this study was to determine if digestibility accounts for variation in RFI in lactating dairy cows fed high and low starch diets. We hypothesized that 1) digestibility would account for some of the variation in RFI and that more efficient cows would have improved digestive ability; and 2) that differences in digestibility among high and low RFI cows would be more apparent when fed low starch, high NDF diets.

MATERIALS AND METHODS

Cows, Experimental Design, and Diets

Experimental procedures were approved by the Institutional Animal Care and Use Committee of Michigan State University. Data from four separate cross-over experiments were used to determine the relationship between RFI and digestibility. Lactating Holstein cows were fed diets that differed in starch concentration in experiments 1 (n=32), 2 (n=25), 3 (n=32), and 4 (n=20). Cows (n=109) averaged (mean ± SD) 120 ± 30 DIM, 42 ± 9 kg of milk/d, and 665 ± 77 kg BW at the beginning of the experiments. Each experiment consisted of two experimental periods of 28 d each. Cows were blocked based on milk yield and parity and randomly assigned to treatment sequence. Cows were housed in individual tie stalls and milked twice daily (0300 and 1430 h). Water was available ad libitum, and tie stalls were equipped with a double-cupped watering system to prevent contamination of feed with water and a front gate to prevent other cows from stealing feed during cow movements.

Cows were fed high (HS) or low (LS) starch diets, which were formulated to distinctly differ in starch content. Ingredient and nutrient composition of diets are shown in Table 3.1. Although diets were formulated with different ingredients for each experiment, marked differences in starch content between HS and LS were achieved within experiment. High starch diets were about 30% starch and 26% NDF, and contained 30-35% corn grain. The LS diet in experiment 1 was formulated by replacing ground corn with soybean hulls and was 12% starch and 44% NDF. For experiment 2, the LS diet was 15% starch and 40% NDF, and was derived by replacing ground corn and wheat straw with soybean hulls. In experiment 3, soybean hulls, whole cottonseed, legume silage, and a palmitic acid-enriched fatty acid supplement replaced ground corn and portions of wheat straw and high moisture corn to create a LS diet that was 16% starch and 33% NDF. The LS diet in experiment 4 was formulated by including whole cottonseed and soybean hulls at the expense of ground corn, wheat straw, and portions of legume and corn silages and was 12% starch and 44% NDF. The reported ingredient and nutrient composition of diets was determined by an average from the two periods within each experiment. Diets were adjusted for changes in forage DM concentration twice weekly.

Data and Sample Collection

Cows were fed once daily at 1000 h (experiments 2 and 4) or 1200 h (experiments 1 and 3) for >110% of expected intake based on intake from the previous day, and orts were removed and weighed daily prior to feeding. Milk yield was recorded electronically at each milking, and milk samples were obtained from 4 consecutive milkings per wk. Milk samples were analyzed for fat, protein, lactose, somatic cells, and milk urea nitrogen (MUN) with infrared spectroscopy by Michigan DHIA (East Lansing). Body weight for each cow was recorded three (experiments 2, 3, and 4) or five (experiment 1) times per wk immediately after the morning milking. Body condition score (BCS) was determined on a 5-point scale, where 1=thin and 5=fat, as described by Wildman et al. (1982) by 3 trained investigators and recorded for each cow at the beginning and end of each period.

For each experiment, samples of feces, orts, and feed ingredients were collected during the last 5 d of each experimental period to estimate nutrient digestibility and sampling procedures were the same for all four experiments. Samples of feces were collected every 15 h (2400, 0230, 0600, 0900, 1200, 1500, 1800, 2100 h) to obtain 8 samples per cow to represent every 3 h during a 24-h period. Samples of orts (12.5%) from each cow per day and diet ingredients (~0.5 kg) were obtained each day during the collection periods. All samples were stored at -20°C until analyses.

Table 3.1. Composition of high and low starch diets fed during each experiment[1,2].

	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	HS	LS	HS	LS	HS	LS	HS	LS
Ingredient, % of DM								
Corn silage	23.9	24.3	23.6	23.8	23.7	24.2	23.5	20.9
Legume silage	21.9	22.1	21.2	21.4	11.1	22.6	20.6	18.4
Wheat straw	4.97	5.04	5.19	--	3.79	1.94	4.82	--
Soybean hulls	--	28.9	--	30.5	--	10.6	--	32.1
Cottonseed, whole	--	--	--	--	7.45	9.07	--	9.22
Corn, ground	29.6	3.61	21.4	--	13.1	--	30.8	7.18
Corn, high moisture	--	--	8.28	8.16	21.5	11.0	--	--
Soybean meal	16.6	13.5	17.17	12.9	15.9	14.6	17.2	9.08
Fat supplement[3]	--	--	--	--	--	2.51	--	--
Vitamin & mineral[4]	2.03	2.06	2.06	2.09	2.02	2.05	2.08	2.08
Limestone	0.50	--	0.50	--	0.75	0.76	0.52	--
Sodium bicarbonate	0.51	0.52	0.49	0.50	0.75	0.76	0.51	0.51
Dicalcium phosphate	--	0.25	0.18	0.50	--	--	--	0.51
Nutrient, % of DM								
DM	53.9	53.6	55.9	55.7	55.8	51.7	49.5	52.2
NDF	27.2	43.9	25.9	39.4	25.1	32.8	27.6	44.2
Starch	30.1	12.2	30.3	15.5	32.5	16.1	28.2	11.8
CP	16.4	15.9	16.6	16.0	17.0	18.3	16.9	15.2
Ash	11.8	14.1	6.5	7.3	5.4	6.8	6.1	6.5
Ether Extract	2.52	1.90	2.15	1.95	3.24	5.61	2.30	3.41
NE_L, Mcal/kg[5]	1.62	1.56	1.68	1.62	1.80	1.75	1.72	1.62
GE, Mcal/kg[6]	4.15	4.14	4.16	4.11	4.26	4.34	4.19	4.21

[1]High (HS) and low (LS) starch diets fed to lactating cows during experiments 1, 2, 3, and 4 (n=32, 25, 32, 20, respectively).
[2]Nutrient composition was determined from feed ingredients sampled during the last 5 d of each 28-d experimental period.
[3]Fat supplement was palmitic acid enriched.
[4]Vitamin and mineral mix contained 34.1% dry ground shell corn, 25.6% white salt, 21.8% calcium carbonate, 9.1% Biofos, 3.9% magnesium oxide, 2% soybean oil, and < 1% of each of the following: manganese sulfate, zinc sulfate, ferrous sulfate, copper sulfate, iodine, cobalt carbonate, vitamin E, vitamin A, vitamin D, and selenium.
[5]Mean apparent net energy concentration of diets, based on average cow performance. For each diet, $DietNE_L$ = the average of (MilkE + 0.08 x MBW + ΔBodyE) / DMI for all cows on the diet.
[6]Gross energy concentration, calculated from nutrient profile of individual feed ingredients, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0; Michigan State University, East Lansing, MI): 4.20 kcal/g carbohydrate, 5.65 kcal/g crude protein, 9.50 kcal/g fatty acid estimated from ether extract, 3.95 kcal/g sugar (Merrill and Watt, 1973).

Sample Analysis

Diet ingredient (~0.5kg/d) and orts samples (12.5%/d) were composited by period. Diet ingredients, orts, and feces were dried in a forced air oven (135°C for >72 h) before grinding through a Wiley mill (1-mm screen; Arthur H. Thomas Co., Philadelphia, PA). Feces obtained from a cow during a period (8 samples per cow) were composited on an equal DM basis. Samples of diet ingredients, orts, and feces were analyzed for CP, starch, NDF, indigestible NDF (iNDF), and ash. Diet ingredients were also analyzed for ether extract which was determined using a modified Soxhlet apparatus (AOAC, 1990). Crude protein was determined according to Hach et al. (1987), and starch was analyzed by an enzymatic method after gelatinization with sodium hydroxide (Karkalas, 1985). Glucose concentration was determined via glucose oxidase method (Glucose kit #510; Sigma Chemical Co., St. Louis, MO), and absorbance was measured with a micro-plate reader (SpectraMax 190; Molecular Devices Corp., Sunnyvale, CA). Neutral detergent fiber and iNDF were determined according to Mertens (2002) and Goering and Van Soest (1970), respectively. Indigestible NDF, which was used as an internal marker to estimate fecal output and nutrient digestibility (Cochran et al., 1986), was estimated as NDF residue after 240 h in vitro fermentation (Goering and VanSoest, 1970); flasks were reinoculated at 120 h to ensure a viable microbial population. Ruminal fluid for the in vitro incubations was collected from a nonpregnant dry cow fed dry hay only. Ash was determined after 5 h combustion at 500°C, and concentrations of nutrients are expressed as a percent of DM.

Calculations

Milk energy output (MilkE; MCal/d) for a cow was estimated by the following equation (NRC, 2001; from Equation 2-15):

$$\text{MilkE} = [9.29 \text{ x fat (kg)} + 5.63 \text{ x true protein (kg)} + 3.95 \text{ x lactose (kg)}],$$

where each component is based on the average output of a cow during a 28-d period. Metabolic BW for a cow (MBW; $kg^{0.75}$) was estimated as $BW^{0.75}$, where BW was the mean BW for the cow during a specified period. Mean daily BW change (ΔBW; kg) was calculated for each cow within a period by linear regression after two iterations of outlier removal. Energy partitioned to body tissue gain (ΔBodyE; Mcal/d) was estimated by an equation derived from NRC (2001; Table 2-5):

$$\Delta\text{BodyE} = [(2.88 + 1.036 \text{ x BCS}) \text{ x } \Delta\text{BW}],$$

where BCS is the average BCS for a cow during a 28-d period.

The milk:feed ratio for a cow during a period was determined as the average daily energy-corrected milk yield (ECM; ECM = [0.327 × milk (kg) + 12.95 × fat (kg) + 7.20 × protein (kg)]; Tyrell and Reid, 1965) over the average daily DMI. Gross efficiency, or the percent of consumed energy captured in milk and body tissue gain, was calculated as the average MilkE and ΔBodyE divided by the average gross energy intake during a 28-d period. Individual feed nutrient analyses were used to calculated gross energy, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0; Michigan State University, East Lansing, MI). Energy values for each nutrient were assigned according to Merrill and Watt (1973): 4.20 kcal/g carbohydrate, 5.65 kcal/g crude protein, 9.50 kcal/g fatty acid estimated from ether extract, 3.95 kcal/g sugar, and 3.62 kcal/g fermented acid.

Apparent diet energy content (DietNE_L; Mcal/kg) was calculated for each diet as the average NE_L required for each cow divided by the average intake:

$$DietNE_L = \text{Average } [(MilkE + 0.08 \text{ x } MBW + \Delta BodyE)/DMI],$$

where DMI is the average DMI for a cow when she was fed the diet. Multiple of maintenance was calculated based on 1) requirements for production and on 2) actual intake. Multiple of maintenance (MM) based on requirements for observed production was calculated as:

$$MM_R = [(MilkE + 0.08 \text{ x } MBW + \Delta BodyE)/0.08 \text{ x } MBW].$$

Multiple of maintenance based on actual intake was calculated as:

$$MM_I = [(DMI \text{ x Diet Energy Density})/(MBW \text{ x } 0.08)],$$

where diet energy density was the mean Diet NE_L for each diet (1.7 and 1.6 Mcal NE_L/kg for HS and LS diets, respectively).

Statistical Analysis

Data from all four experiments were compiled for analysis. Two cows from experiment 3 were not included in the analysis due to a displaced abomasum and severe mastitis infection during collection periods 1 and 2, respectively. Dry matter intake for an individual cow during each 28-d period was regressed as a function of major energy sinks using GLM Procedure in SAS (v. 9.3; SAS Institute, Cary, NC). To define RFI, DMI was modeled as follows: $DMI_i = \beta_0 + \beta_1 \text{ x } MilkE_i + \beta_2 \text{ x } MBW_i + \beta_3 \text{ x } \Delta BodyE_i + Parity + Experiment + Cohort(Experiment) + Diet(Cohort \text{ x } Experiment) + \varepsilon_i$, where DMI_i was the observed DMI, $MilkE_i$ was the observed milk energy output, MBW_i was the average $BW^{0.75}$, and $\Delta BodyE_i$ was the predicted change in body energy, based on measured BW and BCS, for ith cow. Parity (1 or 2+), experiment (1, 2, 3, or 4), cohort within experiment, and diet within cohort and experiment were fixed effects, where a cohort was defined as a group of cows that consumed the same diet at the same time. The error term in the model was used to define RFI. To determine if DM digestibility was important to the determination of RFI, we also regressed DMI according to the previous model with the addition of DM digestibility and the interaction of DM digestibility and diet (HS or LS) as covariates.

Cows were grouped based on RFI status and classified as high RFI (HRFI), low RFI (LRFI), or medium RFI (MRFI). Cows with RFI >0.5 SD of the mean RFI for a cohort were considered HRFI, those <-0.5 SD were considered LRFI, and those ±0.5 SD were considered MRFI. The effect of efficiency group (HRFI, MRFI, or LRFI) was determined using the MIXED Procedure of SAS according to a model that included the fixed effects of efficiency group (HRFI, MRFI, or LRFI) and experiment (1, 2, 3, or 4), their interaction, and the random effect of cow nested within experiment. Additionally, to account for differences in feed intake as a multiple of maintenance among efficiency groups, nutrient digestibilities were analyzed according to a mixed model that included the fixed effects of efficiency group (HRFI, MRFI, or LRFI) and experiment (1, 2, 3, or 4), MM_I as a covariate, all two- and three-way interactions of variables, and the random effect of cow nested within experiment. For all analyses, nutrient digestibilities for each cohort were standardized to the overall mean of each diet. The REG Procedure was used to determine regression equations, and Pearson correlations were obtained using the CORR Procedure of SAS. For relationships among nutrient digestibilities and RFI, partial correlations, which accounted for effects of parity, cohort, and experiment, were obtained using the PARTIAL option of the CORR Procedure. To illustrate these relationships, residuals for RFI and nutrient digestibilities obtained after each was regressed on parity, cohort, and experiment were plotted.

Production, efficiency, and digestibility responses to HS and LS diets were analyzed using a mixed model in SAS that included the fixed effects of experiment (1, 2, 3, or 4), diet (HS or LS), period (1 or 2) nested within experiment , parity (1 or 2+), all two- and three-way interactions of fixed effects, and the random effect of cow nested within parity and experiment. Main effects and correlations were considered significant at *P*<0.05 and trends were defined as *P*<0.10. Interactions were considered significant at *P*<0.10 and trends at *P*<0.15.

RESULTS

Performance

High starch diets resulted in similar MilkE (*P*=0.34), but greater ΔBodyE (*P*<0.01) than LS diets (Table 3.2), and energy captured as milk output plus body tissue gain was greater for HS than LS (*P*<0.01). Estimated NE_L intake was greater for HS than LS (44 vs. 42 Mcal/d; *P*<0.01), but GE intake was similar (~107 Mcal/d; *P*=0.16). Multiple of maintenance based on intake (MM_I) and multiple of maintenance based on requirements (MM_R) were both greater when cows were fed HS diets (*P*<0.01). Gross efficiency was greater when cows were fed HS compared with LS diets (31 vs. 29%; *P*<0.01), but milk:feed was not different (*P*=0.87) between HS and LS. Residual feed intake was not different between HS and LS diets. Digestibilities of starch and DM were greater for HS diets (*P*<0.01), but NDF digestibility was greater for LS diets (*P*<0.01). High RFI and LRFI cows had similar MilkE, MBW, and ΔBodyE, but LRFI cows had significantly lower DMI, and significantly greater milk:feed, gross efficiency, and apparent $DietNE_L$ than HRFI cows for both diets (Table 3.3).

Table 3.2. Production, efficiency, and digestibility for cows (n=107) fed high (HS) and low (LS) starch diets.

	Diet			P-Value[1]				
Item	HS	LS	SEM	Diet	Period (Exp)	Parity	Exp	Diet*Exp
Intake and Performance[2]								
DMI, kg/d	25.8	25.2	0.24	0.11	0.78	<0.01	<0.01	0.26
GE Intake, Mcal/d	108	106	1.00	0.16	0.78	<0.01	<0.01	0.31
NE_L Intake, Mcal/d	43.8	41.6	0.53	<0.01	<0.01	<0.01	<0.01	0.80
MM, based on intake	4.18	3.87	0.04	<0.01	0.77	<0.01	<0.01	0.25
MM, based on requirements	4.20	3.99	0.05	<0.01	<0.01	<0.01	<0.01	0.83
MilkE, Mcal/d	29.6	29.0	0.45	0.34	0.17	<0.01	<0.01	0.32
ΔBodyE, Mcal/d	3.74	2.16	0.31	<0.01	<0.01	0.51	0.26	0.20
MBW, $kg^{0.75}$	131	130	0.94	0.78	0.88	<0.01	0.02	1.00
Efficiency								
NE captured in milk and body tissue, Mcal/d[3]	33.4	31.2	0.52	<0.01	<0.01	<0.01	<0.01	0.79
Gross Efficiency, %	31.0	29.3	0.39	<0.01	<0.01	0.55	<0.01	0.98
Milk:feed	1.66	1.65	0.02	0.87	<0.01	0.06	<0.01	0.04
RFI, kgDM/d	0.00	0.04	0.15	0.87	0.99	0.92	0.99	0.99
Digestibility, %								
DM	66.8	63.4	0.26	<0.01	1.00	<0.01	0.81	1.00
Starch	95.3	94.7	0.15	<0.01	0.90	0.06	0.77	0.97
NDF	36.7	48.6	0.45	<0.01	0.91	<0.01	0.58	0.92
CP	66.1	64.9	0.31	0.01	1.00	0.99	0.98	0.99

[1]P-value associated with fixed effects of diet, period nested within experiment, parity, experiment (exp), and the interaction of diet and experiment.

[2]GE Intake = gross energy intake; NE_L Intake = apparent NE_L intake based on performance; MM = multiple of maintenance (estimated from requirements for performance or estimated from actual intake); MilkE = milk energy output; ΔBodyE = body energy change; MBW = metabolic BW.

[3]NE captured in milk and body tissue = MilkE + ΔBodyE.

Table 3.3. Performance, efficiency, and digestibility of cows (n=107) fed high and low starch diets by RFI grouping.

	High Starch Diet				Low Starch Diet			
	RFI Group[1] (Mean ± SE)				RFI Group (Mean ± SE)			
	HRFI	MRFI	LRFI	P-value	HRFI	MRFI	LRFI	P-value
n	33	40	34		32	39	36	
Performance[2,3]								
DMI, kg/d	28.7 ± 0.56[a]	25.6 ± 0.56[b]	25.2 ± 0.55[b]	<0.01	27.4 ± 0.64[a]	25.1 ± 0.59[b]	24.4 ± 0.60[b]	<0.01
MM_R	4.29 ± 0.08	4.11 ± 0.08	4.26 ± 0.08	0.29	4.12 ± 0.10	3.96 ± 0.10	3.93 ± 0.10	0.35
MM_I	4.54 ± 0.06[a]	4.17 ± 0.06[b]	4.02 ± 0.06[b]	<0.01	4.20 ± 0.07[a]	3.84 ± 0.06[b]	3.67 ± 0.06[c]	<0.01
MilkE, Mcal/d	31.5 ± 0.95	29.4 ± 0.95	30.5 ± 0.94	0.30	30.2 ± 1.06	28.3 ± 0.98	29.8 ± 1.01	0.39
ΔBodyE, Mcal/d	3.51 ± 0.63	3.02 ± 0.63	4.30 ± 0.63	0.36	2.36 ± 0.52	2.57 ± 0.48	1.38 ± 0.49	0.19
MBW, $kg^{0.75}$	134 ± 1.93	130 ± 1.93	133 ± 1.91	0.31	130 ± 2.05	131 ± 1.89	133 ± 1.94	0.66
$DietNE_L$, Mcal/kg	1.60 ± 0.03[b]	1.67 ± 0.03[b]	1.80 ± 0.03[a]	<0.01	1.57 ± 0.03[c]	1.64 ± 0.02[b]	1.71 ± 0.02[a]	<0.01
Efficiency								
Milk:feed	1.59 ± 0.03[b]	1.66 ± 0.03[ab]	1.74 ± 0.03[a]	<0.01	1.59 ± 0.03[b]	1.62 ± 0.03[b]	1.75 ± 0.03[a]	<0.01
Gross Efficiency, %	29.3 ± 0.68[b]	30.1 ± 0.68[b]	32.9 ± 0.67[a]	<0.01	28.2 ± 0.69[b]	29.0 ± 0.63[ab]	30.3 ± 0.65[a]	0.09
RFI, kg DM/d	1.60 ± 0.12[a]	-0.01 ± 0.12[b]	-1.46 ± 0.12[c]	<0.01	1.65 ± 0.12[a]	-0.06 ± 0.11[b]	-1.40 ± 0.12[c]	<0.01
Digestibility, %								
Starch	94.9 ± 0.26[b]	95.4 ± 0.26[ab]	95.7 ± 0.26[a]	0.07	94.4 ± 0.25	94.7 ± 0.23	95.1 ± 0.24	0.17
NDF	36.8 ± 0.84	37.1 ± 0.84	35.1 ± 0.86	0.21	47.3 ± 0.71[b]	48.0 ± 0.66[ab]	49.6 ± 0.67[a]	0.05
DM	66.6 ± 0.44	67.1 ± 0.44	65.9 ± 0.44	0.15	62.4 ± 0.45[b]	63.1 ± 0.42[ab]	64.2 ± 0.43[a]	0.02
CP	65.9 ± 0.52	66.6 ± 0.52	65.2 ± 0.51	0.17	64.2 ± 0.50	64.8 ± 0.46	65.5 ± 0.47	0.18

[1]HRFI = high RFI cows (>0.5 SD), MRFI = medium RFI cows (±0.5 SD), LRFI = low RFI cows (<-0.5 SD).
[2]MM_R = multiple of maintenance estimated from requirements for performance; MM_I = multiple of maintenance estimated from actual intake; MilkE = milk energy output; ΔBodyE = body energy change; MBW = metabolic BW; $DietNE_L$ =apparent energy density of the diet, calculated from mean cow performance for each diet, as (MilkE + ΔBodyE + 0.08xMBW) / DMI for each cow.
[3]Means within a row and diet with different superscripts are significantly different (P<0.05).

Digestibility and RFI

The partial correlations between RFI and digestibilities of DM, starch, NDF, and CP are illustrated in Figure 3.1. Digestibility of DM correlated negatively with RFI (r=-0.30; P<0.01) when cows were fed LS diets, but not when cows were fed HS diets (r=-0.01; P=0.90). Starch digestibility correlated negatively with RFI when cows were fed both HS and LS (r=-0.31 and r=-0.23; P<0.01 and P=0.02, respectively). Digestibilities of NDF and CP correlated negatively with RFI when cows were fed LS diets (r=-0.23 and r=-0.23; P=0.02 and P=0.02, respectively), but not when cows were fed HS diets (P>0.5). Starch digestibility was significantly greater for LRFI cows than HRFI cows (P<0.05) for HS diets but not LS diets (Table 3.3). Digestibilities of NDF and DM were significantly greater for LRFI cows than HRFI cows for LS diets (49.6 vs. 47.3% and 64.2 vs. 62.4%, respectively; P<0.05) but not HS diets. Digestibility of CP was similar among HRFI, MRFI, and LRFI cows for both HS and LS diets (P>0.05). Apparent $DietNE_L$ was greater for LRFI than HRFI cows for HS (1.80 vs. 1.60 Mcal/kg; P<0.05) and LS diets (1.71 vs. 1.57 Mcal/kg; P<0.05). Because apparent $DietNE_L$ was 8.36% (1.57 / 1.71) greater and DM digestibility was 2.75% greater (62.4 / 64.2) for LRFI cows fed LS diets, 33% of the differences (2.75 / 8.36) in apparent $DietNE_L$ could have been accounted for by differences in DM digestibility. When DM digestibility and the interaction of DM digestibility and diet were incorporated as covariates in the linear model used to predict DMI and determine RFI, both were significant (P=0.04 and P=0.03, respectively; Table B.2).

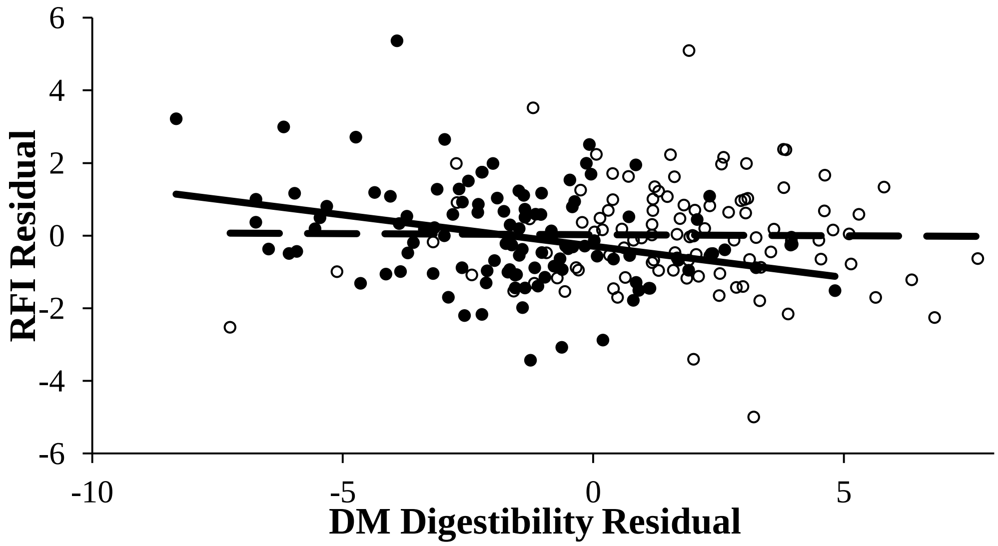

Figure 3.1a. Residuals for RFI vs. residuals for DM digestibility when cows were fed high (HS) and low (LS) starch diets after both variables were regressed on cohort, experiment, and parity. Each point represents an individual cow when fed each diet. Performance for HS diets is indicated by ○ and performance for LS diets is indicated by ●. The dashed line indicates the linear regression for HS (y = 0.01x + 0.03; R^2 = 0.00) and the solid line indicates the linear regression for LS diets (y = -0.17x - 0.29; R^2 = 0.09). Slope of the regression for LS diet was significant (P<0.05).

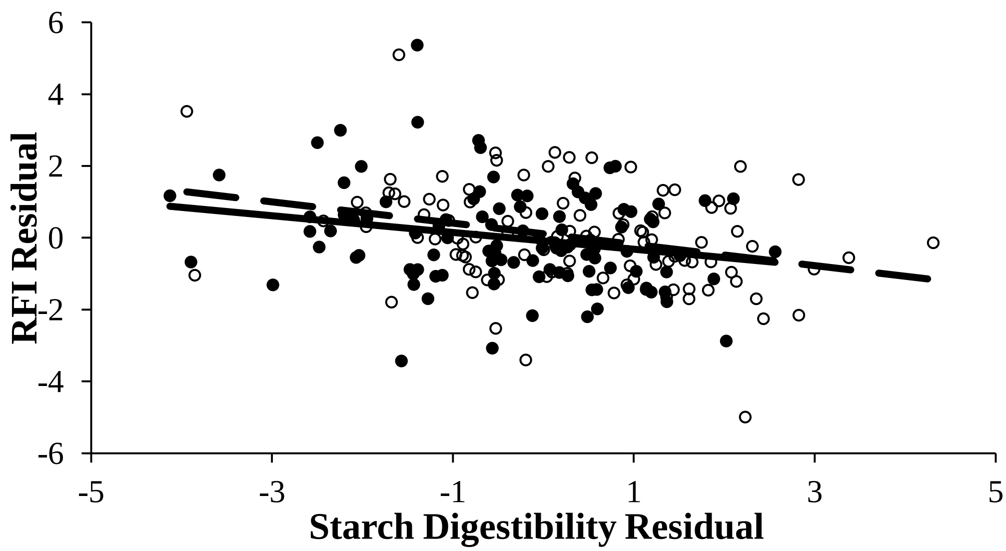

Figure 3.1b. Residuals for RFI vs. residuals for starch digestibility when cows were fed high (HS) and low (LS) starch diets after both variables were regressed on cohort, experiment, and parity. Each point represents an individual cow when fed each diet. Performance for HS diets is indicated by ○ and performance for LS diets is indicated by ●. The dashed line indicates the linear regression for HS (y = -0.30x + 0.11; R^2 = 0.10) and the solid line indicates the linear regression for LS diets (y = -0.23x - 0.08; R^2 = 0.05). Slopes of the regressions for both diets were significant (P<0.05).

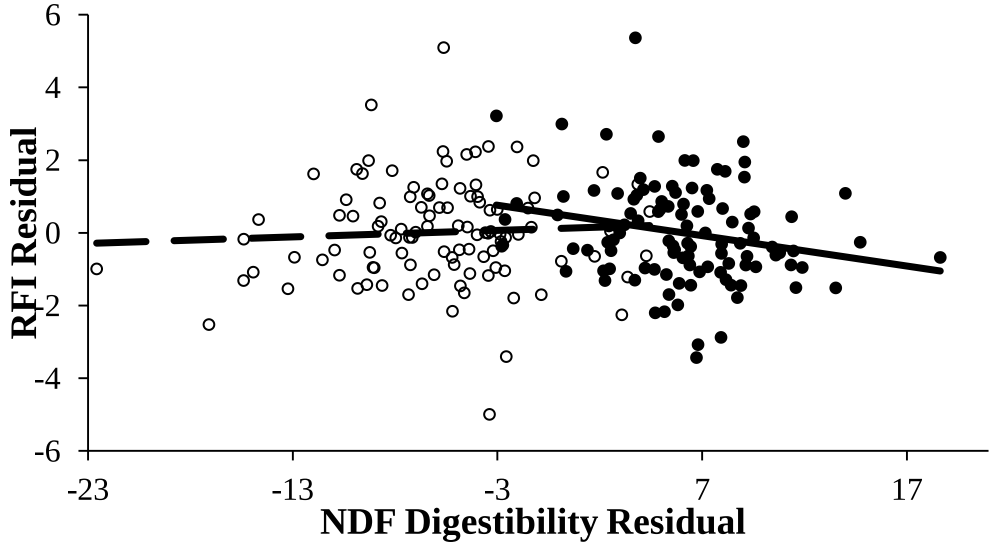

Figure 3.1c. Residuals for RFI vs. residuals for NDF digestibility when cows were fed high (HS) and low (LS) starch diets after both variables were regressed on cohort, experiment, and parity. Each point represents an individual cow when fed each diet. Performance for HS diets is indicated by ○ and performance for LS diets is indicated by ●. The dashed line indicates the linear regression for HS (y = 0.02x + 0.12; R^2 = 0.00) and the solid line indicates the linear regression for LS diets (y = -0.08 x + 0.50; R^2 = 0.05). Slope of the regression for LS diet was significant (*P*<0.05).

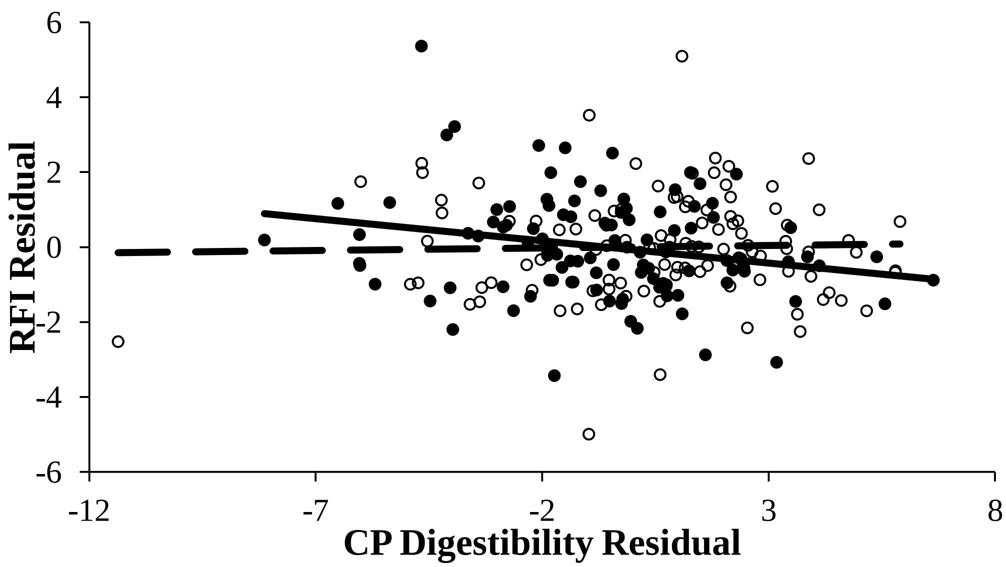

Figure 3.1d. Residuals for RFI vs. residuals for CP digestibility when cows were fed high (HS) and low (LS) starch diets after both variables were regressed on cohort, experiment, and parity. Each point represents an individual cow when fed each diet. Performance for HS diets is indicated by ○ and performance for LS diets is indicated by ●. The dashed line indicates the linear regression for HS (y = 0.01x + 0.01; R^2 = 0.00) and the solid line indicates the linear regression for LS diets (y = -0.12 x - 0.07; R^2 = 0.05). Slope of the regression for LS diet was significant (*P*<0.05).

Multiple of Maintenance

Multiple of maintenance based on intake was negatively related to digestibilities of DM (r=-0.47; P<0.01), starch (r=-0.25; P=0.01), and NDF (r=-0.43; P<0.01) when cows were fed LS diets (Figure 3.2). In contrast, when cows were fed HS diets, MM_I was not related to DM or NDF digestibilities (P>0.2), but correlated negatively with starch digestibility (r=-0.35; P<0.01). As MM_I increased, digestibility of NDF and DM decreased 4% and 2.8% per MM (P<0.05) for LS diets, respectively, but depression in DM and NDF digestibilities associated with MM_I was not significant for the HS diets. As MM_I increased, digestibility of starch decreased 1.2% and 0.8% per MM_I (P<0.05) when cows were fed HS and LS diets, respectively. Multiple of maintenance based on requirements was not related to digestibility of starch when cows were fed HS and LS diets (P>0.05; data not shown), but correlated negatively with NDF and DM digestibilities (r=-0.31 and r=-0.33; P<0.01; data not shown) for LS diets, with NDF and DM digestibilities decreasing 1.97 and 1.32% (P<0.01; data not shown) per unit increase in MM_R, respectively. Multiple of maintenance based on intake was positively associated with RFI when cows were fed HS (r=0.49; P<0.01) and LS diets (r=0.52; P<0.01), but MM_R was not related to RFI for either diet (P>0.30; Figure 3.3). For HS and LS diets, LRFI cows ate at a lower MM_I than HRFI cows (4.0 vs. 4.5 and 3.7 vs. 4.2, respectively; P<0.05; Table 3.3), but MM_R was similar among HRFI, MRFI, and LRFI cows (P>0.05).

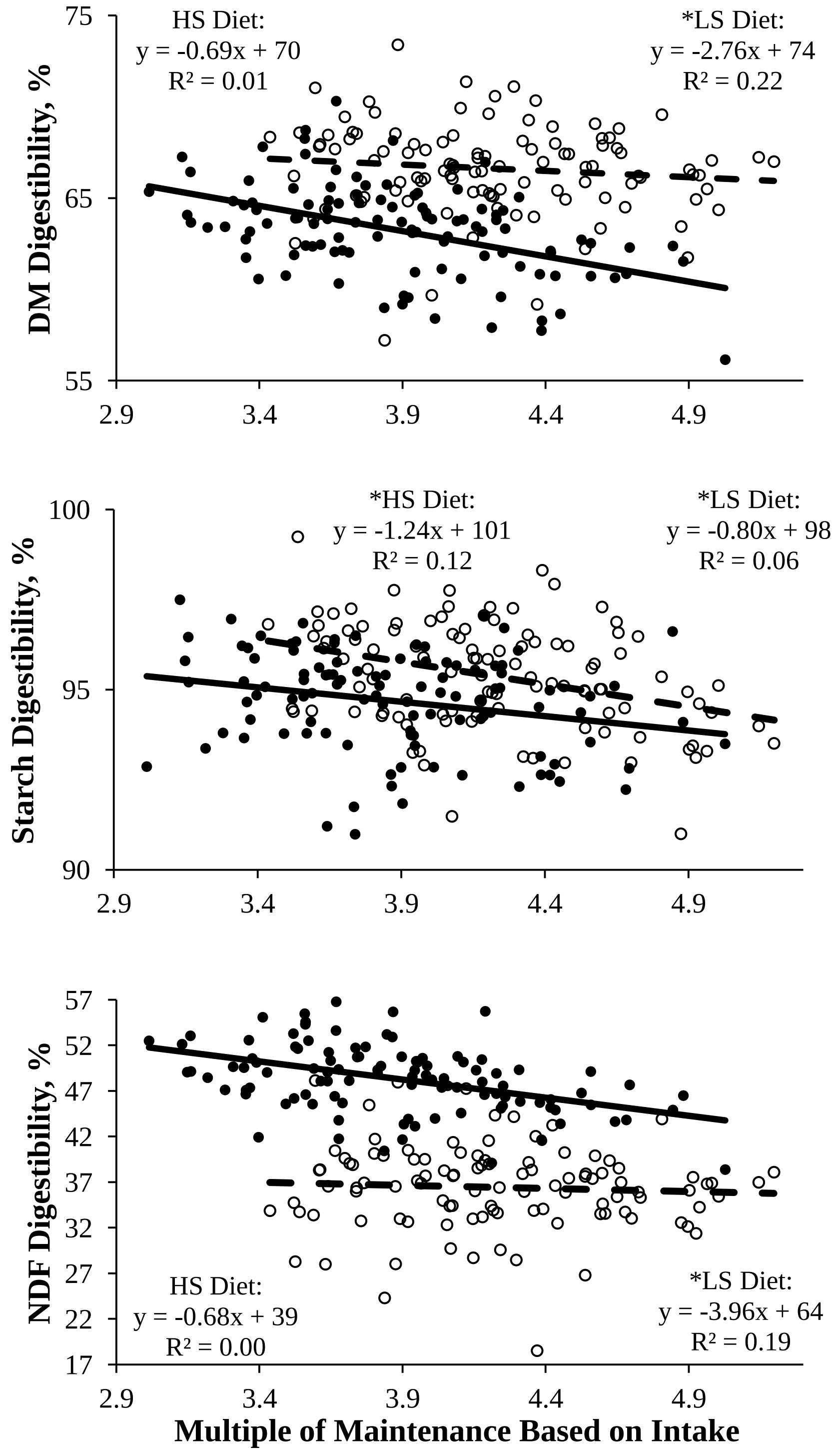

Figure 3.2. Digestibility of DM, starch, and NDF vs. multiple of maintenance determined from actual DMI for cows (n=107) fed high (HS) and low (LS) starch diets. Performance for HS diets is indicated by ○ and performance for LS diets is indicated by ●. The dashed line indicates the linear regression for HS and the solid line indicates the linear regression for LS. * Indicates slope is significant (*P*<0.05).

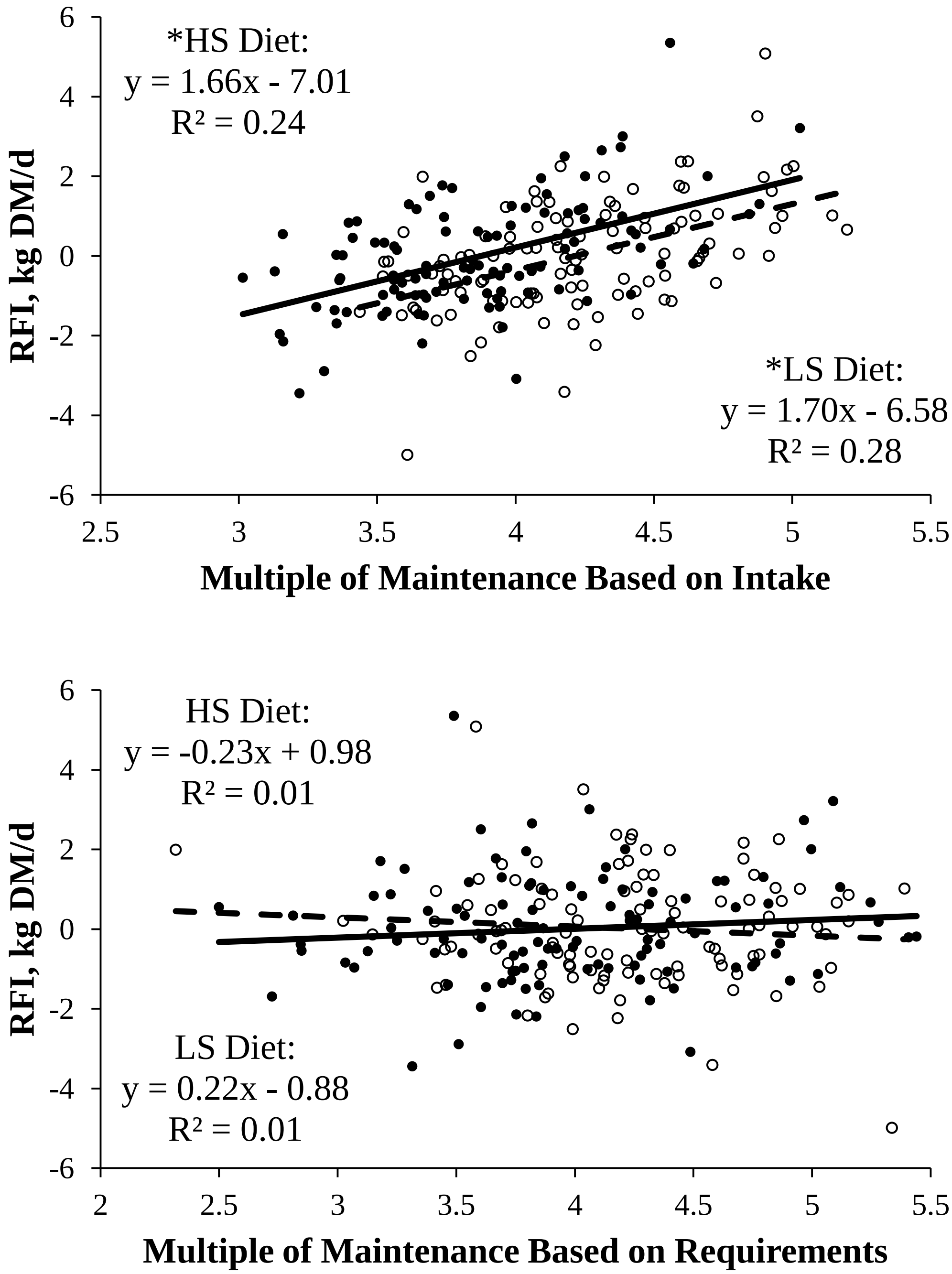

Figure 3.3. Relationship between RFI and multiple of maintenance based on requirements and multiple of maintenance based on intake for cows (n=107) fed high (HS) and low (LS) starch diets. Performance for HS is indicated by ○ and performance for LS is indicated by ●. The dashed line indicates the linear regression for HS and the solid line indicates the linear regression for LS.

* Indicates slope is significant (*P*<0.05).

Digestibility Depression and RFI

Because RFI was related to MM_I (Figure 3.3) and MM_I was related to digestibility (Figure 3.2), digestibilities were modeled as a function of efficiency grouping and MM_I as a covariate (Table 3.4). For LS diets, MM_I was significant for NDF and DM digestibilities ($P<0.01$), but not digestibilities of starch or CP. The effect of efficiency grouping was not significant for nutrient digestibilities for either diet. The relationship between DM digestibility and MM_I by RFI group for HS and LS diets is illustrated in Figure 3.4. For HS diets, DM digestibility decreased 0.39 and 1.34% ($P>0.05$) for each increase in MM_I for LRFI and HRFI cows, respectively. For LS diets, DM digestibility decreased 1.08% ($P>0.05$) and 2.75% ($P<0.05$) for each increase in MM_I for LRFI and HRFI cows, respectively. We applied 95% confidence intervals for the mean response of HRFI and LRFI cows and observed substantial overlap between the two groups for both diets (Figure 3.4), further supporting results from Table 3.4 that suggest that these groups of cows did not differ in their ability to digest feed independent of MM_I for both diets.

Repeatability of Digestibility

Repeatability of digestibilities of DM, starch, and NDF are shown in Figure 3.5. Digestibility of DM was repeatable across HS and LS (r=0.28; $P<0.01$). Starch digestibility when cows were fed LS diets was also correlated with starch digestibility when cows were fed HS diets (r=0.31; $P<0.01$). Digestibilities of NDF (r=0.23; $P=0.02$) and CP (r=0.22; $P=0.02$; data not shown) were less repeatable across HS and LS.

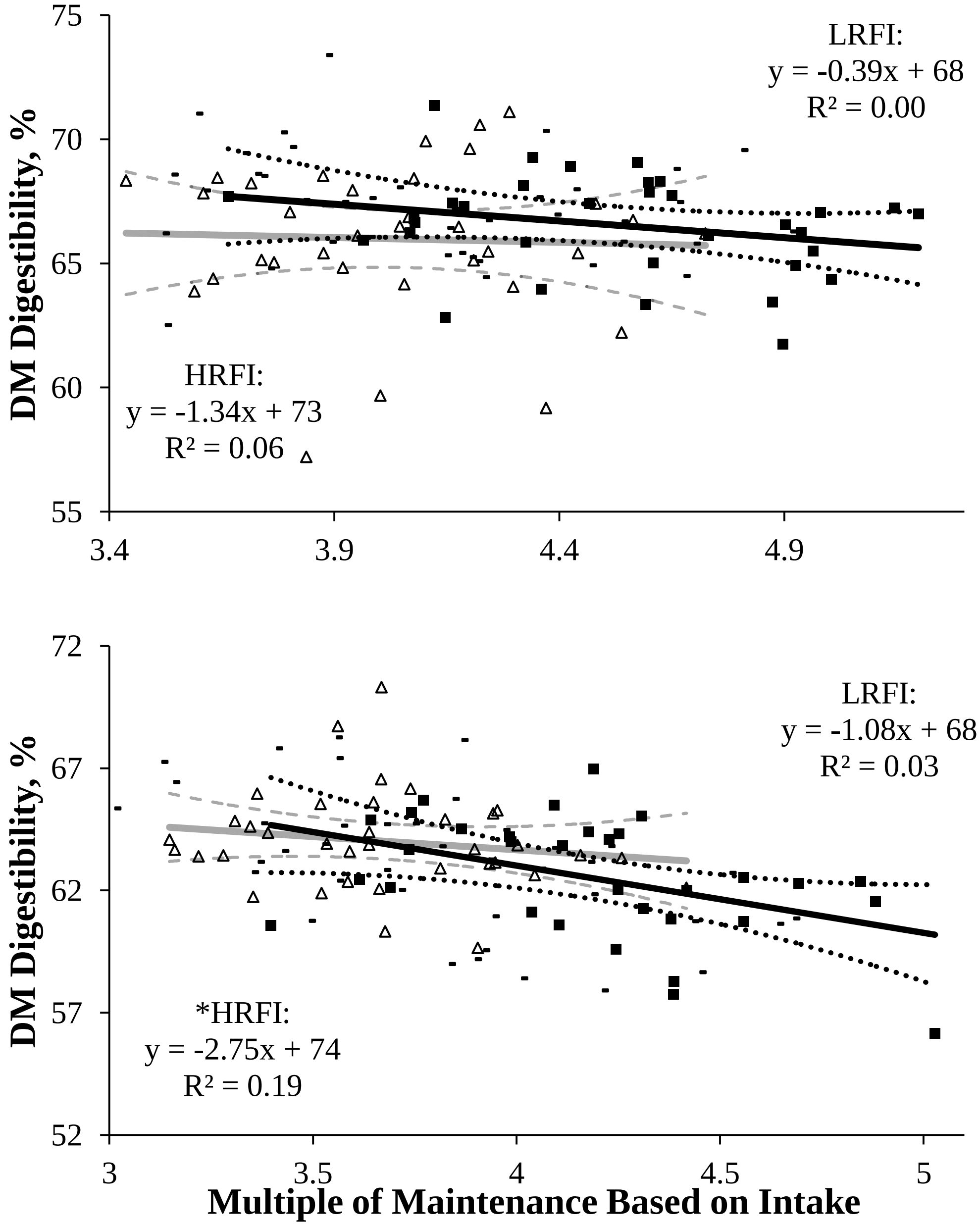

Figure 3.4. DM Digestibility vs. multiple of maintenance determined from actual DMI from cows (n=107) fed high (HS) and low (LS) starch diets. The top panel shows performance when cows were fed HS diets; the bottom panel shows performance when cows were fed LS diets. Cows that were classified as high RFI (HRFI; >0.5 SD of the cohort mean) are indicated by ■; cows that were classified as low RFI (LRFI; <0.5 SD of the cohort mean) are indicated by △; cows that were classified as medium RFI (MRFI; ±0.5 SD of the cohort mean) are indicated by ▬. The solid dark line is the regression for HRFI cows and the solid light line is the regression for LRFI cows. The black dotted lines show the 95% confidence limits for the regression of HRFI; the grey dashed lines show the 95% confidence limits for the regression of LRFI.

* Indicates slope is significant (*P*<0.05).

Table 3.4. Digestibility of cows (n=107) fed high and low starch diets by RFI grouping using feed intake as a multiple of maintenance (MM_I) as a covariate.

	High Starch Diet					Low Starch Diet				
	RFI Group[1] (Mean ± SE)			P-value[2]		RFI Group (Mean ± SE)			P-value	
Item[3]	HRFI	MRFI	LRFI	RFI Group	MM_I	HRFI	MRFI	LRFI	RFI Group	MM_I
n	33	40	34			32	39	36		
Digestibility, %										
Starch	95.4 ± 0.48	95.3 ± 0.29	95.7 ± 0.41	0.51	0.11	94.7 ± 0.38	94.6 ± 0.25	95.0 ± 0.34	0.82	0.18
NDF	38.8 ± 1.57	36.9 ± 0.95	36.8 ± 1.37	0.11	1.00	49.2 ± 0.98	47.8 ± 0.65	49.7 ± 0.87	0.28	<0.01
DM	67.7 ± 0.84	66.9 ± 0.50	66.5 ± 0.71	0.16	0.70	63.7 ± 0.61	63.0 ± 0.40	64.1 ± 0.54	0.44	<0.01
CP	66.5 ± 0.96	66.4 ± 0.57	66.2 ± 0.82	0.24	0.38	64.5 ± 0.73	64.8 ± 0.48	65.7 ± 0.64	0.68	0.43

[1]HRFI = high RFI cows (>0.5 SD), MRFI = medium RFI cows (±0.5 SD), LRFI = low RFI cows (<-0.5 SD).
[2]P-values associated with the effects of RFI grouping (HRFI, MRFI, or LRFI) and multiple of maintenance based on feed intake (MM_I).
[3]Means within a row and diet with different superscripts are significantly different ($P<0.05$).

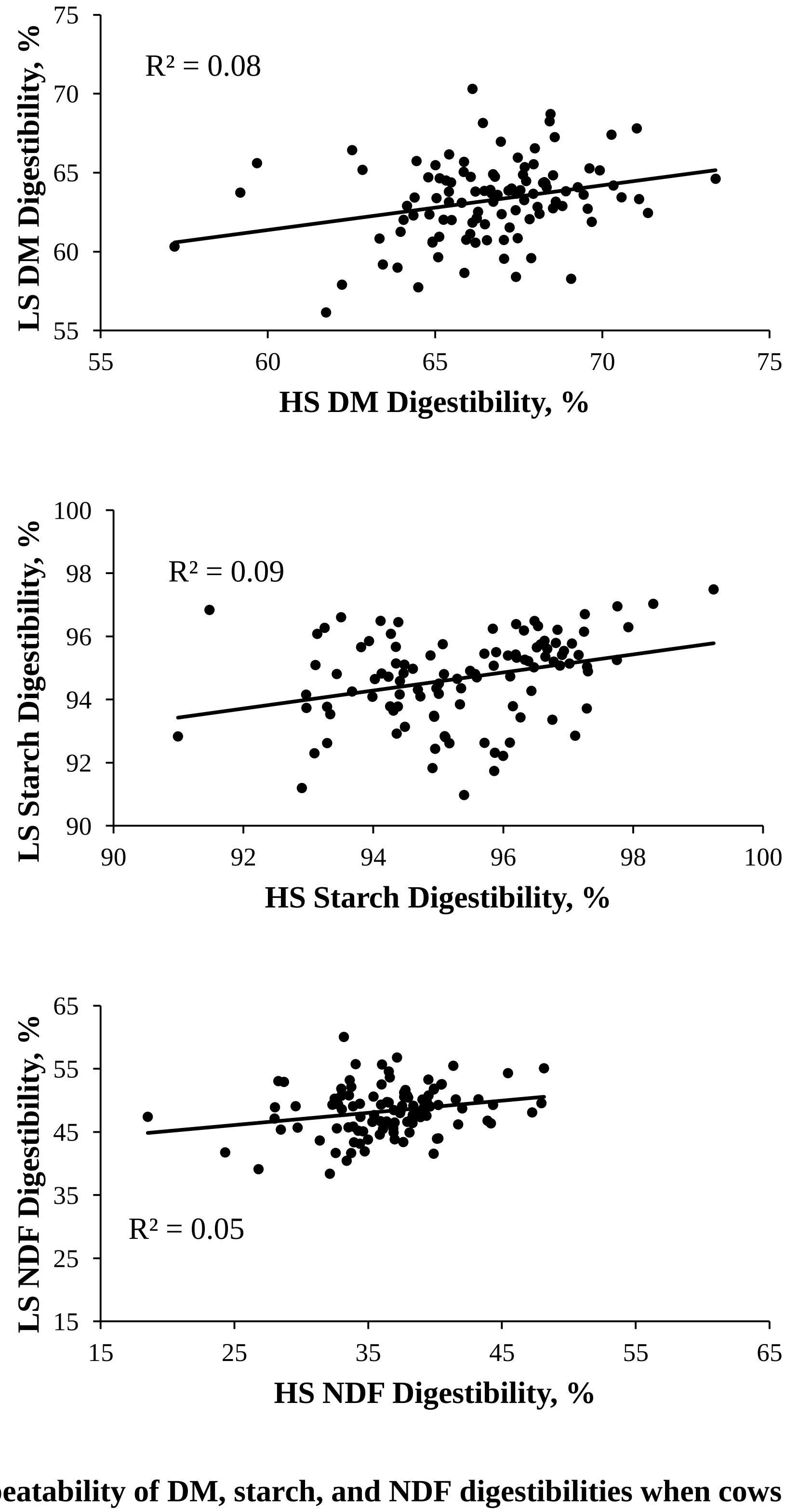

Figure 3.5. Repeatability of DM, starch, and NDF digestibilities when cows (n=107) were fed high (HS) and low (LS) diets. Each point indicates an individual cow and her performance when she was fed each diet.

DISCUSSION

Digestibility of DM correlated negatively with RFI and accounted for 9% of the variation in RFI when cows were fed LS diets but not HS diets. Digestibility of DM also correlated negatively with MM_I and MM_R. Cows with low RFI ate at a lower MM_I than cows with high RFI for both diets, and these decreases in DMI could have led to improved digestibility by these cows, as predicted by NRC (2001) and by our data (see Figures. 3.2 and 3.4). Digestibility of DM was not significantly different between HRFI and LRFI cows after differences in multiple of maintenance were considered (Figure 3.4). However, because DM digestibility and the interaction of DM digestibility and diet were significant in the model used to estimate DMI (Appendix E), digestibility may still be important to determining RFI.

The NRC (2001) assumes a digestibility discount of ~4% for each increase in intake as a multiple of maintenance. This is similar to what we observed for DM digestibility of LS diets (~3%) but not HS diets (0.7%). Furthermore, the NRC (2001) suggests that the digestibility of diets that are more digestible at 1X maintenance intake are depressed more than the digestibility of diets that are less digestible at 1X maintenance. Based on this idea, we would have expected to see greater digestibility depression per increase in intake as a multiple of maintenance for the HS diet than the LS diet because corn grain contains more TDN at one multiple of maintenance (89%) than ingredients that replaced it for the formulation of LS diets [soybean hulls (67%), whole cottonseed (77%), and corn and legume silages (69% and 57%, respectively)]; however, this was not the case for our experiment.

Mixed results are reported for the relationship between RFI and digestibility. To our knowledge, only one other study in dairy cattle examined differences in digestibility between groups of cows classified as high or low RFI (Rius et al., 2012). In their study, Rius and coworkers (2012) assessed digestibility using total collection methods for 16 early lactation cows previously measured for RFI as 8-month old heifers. Digestibility of DM and organic matter tended to be greater for cows previously classified as low RFI as calves (Rius et al., 2012). These results suggest that cows with low RFI have greater digestive efficiency, which would correlate to the relationship we observed between RFI and digestibility for low starch diets; however, Rius et al. (2012) did not measure RFI during the time that digestibility was assessed. Lawrence et al. (2011) did not observe significant differences in digestibility of DM for high, medium, and low RFI beef heifers pre- or postpartum (n=73 and 24, respectively). Additionally, Richardson et al. (2004) reported no significant relationship between RFI and DM digestibility for beef steers (n=33) fed an 85% concentrate diet. In contrast, Richardson et al. (1996) fed beef cattle a diet that contained 70% pelleted hay and 30% concentrate, and observed that low RFI cattle tended to have greater DM digestibility than high RFI cattle. Furthermore, Nkrumah et al. (2006) determined that finishing steers with low RFI had greater DM and CP digestibilities (75 vs. 71% and 75 vs. 70%, respectively) than high RFI steers (n=27), and that RFI tended to be negatively associated with both DM and CP digestibilities (r=-0.3). For pigs selected divergently for RFI, both DM and N digestibilities for low RFI pigs were greater than that of high RFI pigs (Harris et al., 2012). In broilers selected for high and low digestive efficiency (n=864), chickens of the high digestive efficiency line had significantly lower RFI than chickens of the low digestive efficiency line, confirming that chickens with improved digestive ability were in fact more feed efficient (Mignon-Grasteau et al., 2004). Similar to results reported by Richardson et al. (1996) and Nkrumah et al. (2006), we observed that low RFI cows had greater DM digestibility than high RFI cows for LS diets. Richardson and Herd (2004) estimated that digestibility accounted for 10% of the variation in RFI for beef cattle fed an 85% concentrate diet (estimated starch concentration ~28%), which is similar to what we observed for DM digestibility when cows were fed LS diets; however DM digestibility accounted for none of the variation in RFI when cows were fed HS diets, suggesting that this relationship may be dependent on the type of diet that is fed. That DM digestibility and the interaction of DM digestibility and diet were significant in the model used to estimate DMI lends support to the hypothesis that digestibility might be somewhat important to determining RFI.

With the exception of starch, the relationships we observed between RFI and nutrient digestibilities were stronger for LS than HS diets. We hypothesize that this difference is partially due to differences in MM_I among HRFI and LRFI cows (4.20 vs. 3.67) for LS diets. Intake as a multiple of maintenance correlated positively to RFI for both diets, indicating that cows with high RFI ate at a higher MM_I. Digestibilities of NDF and DM were significantly depressed as MM_I increased for LS but not HS diets. That digestibility depression associated with greater levels of intake was more pronounced for LS diets is consistent with the stronger relationships observed between RFI and digestibilities for these diets. Greater intake by the high RFI cows likely increased rate of passage, which could depress digestibility for both diets (NRC, 2001). The greater digestibility depression for LS diets could be related to the smaller particle size of soybean hulls compared to other NDF sources, and greater feed intake could have reduced their ruminal retention time, enabling a greater proportion to travel out of the GI tract undigested (Firkins, 1997). This hypothesis might account for the reduction in both NDF and DM digestibilities that were observed as MM_I increased for LS diets.

Variation among HS and LS diets for the relationships between RFI and nutrient digestibilities could be reflective of true differences between animals for digestive efficiency and the ability of some animals to utilize certain types of feed more efficiently than others. In their study of broilers selected for high or low digestive efficiency, Rougière et al. (2009) observed that digestive efficiency of the most efficient birds was not influenced by the type of diet fed. In contrast, the least efficient birds experienced improvements in digestive efficiency when presented with a diet that promoted increased gut retention time (Rougière et al., 2009). The authors hypothesized that the low digestive efficiency birds required the stimulation by the diet offered to improve digestive efficiency, through increasing gizzard mass, whereas the high efficiency birds had already achieved superior digestive efficiency independent of diet type (Rougière et al., 2009). For our study, feeding LS diets resulted in greater differences in digestibility among high and low RFI cows which might have resulted from low RFI cows having an increased capacity to digest high fiber, low starch diets than high RFI cows. Low RFI cows had greater apparent DietNE$_L$ than HRFI cows for both diets, indicating that these cows had a superior ability to extract net energy from their feed. For LS diets, differences in digestibility observed among HRFI and LRFI cows could have accounted for up to 33% of the differences in apparent DietNE$_L$. This suggests that differences in digestive efficiency may partially explain why some animals have a superior ability extract net energy from their feed. Residual feed intake is essentially a measure of how efficiently cows convert gross energy into net energy (Figure 1.1), though there are errors associated with determining RFI, such as the estimation of NE for maintenance which is assumed to be 0.08 x MBW for every cow. Because digestibility may account for a large portion of the between-animal differences for apparent DietNE$_L$, it may also account for large differences in RFI.

The greater DM digestibility that we observed for LRFI cows compared with HRFI cows for LS diets (64.2 vs. 62.4%) could have resulted from differences in feed intake. The LRFI cows ate 3 kg/d less and at a lower MM_I than HRFI cows (3.67 vs. 4.20). Each unit increase in MM_I resulted in a ~3% reduction in DM digestibility for LS diets, which is similar to NRC predictions and accounts for most of the difference in DM digestibility (84%) observed between HRFI and LRFI cows. Because of this relationship, adjusting for differences in intake were expected to have a large impact on the digestibility differences we observed between HRFI and LRFI cows fed LS diets. Apparent differences in DM digestibility between HRFI and LRFI cows became insignificant after adjusting for differences in MM_I for LS diets. Intake as a multiple of maintenance did not cause a significant reduction in DM digestibility when cows were fed HS diets which could explain why significant differences in DM digestibility were not observed between HRFI and LRFI cows fed HS diets, even before differences in MM_I were considered. Because the effect of RFI group was never significant after adjusting for differences in MM_I for either diet, LRFI cows might not have had truly greater digestive efficiency than HRFI cows when fed high or low starch diets. Thus, it is unlikely that digestibility directly influenced RFI status; however, cows with low RFI ate less, probably because of a superior ability to convert digested energy into net energy, and consequently had the additional energetic advantage of being able to digest their feed more efficiently due to a slower rate of passage.

CONCLUSION

We conclude that digestibility accounts for 9% of the variation in RFI for mid-lactation cows fed low starch diets, but no variation in RFI when cows were fed high starch diets. Furthermore for low starch diets, digestibility may have accounted for 33% of the differences among high and low RFI cows for apparent diet energy density, as determined by observed cow performance. Apparent diet energy density and RFI are similar measurements of efficiency because both quantify an animal's ability to convert gross energy into net energy. However, because high RFI cows ate at a higher multiple of maintenance, digestibility depression related to increases in feed intake might have accounted for most of the differences in DM digestibility when cows were fed low starch diets. Because of reduced feed intake, low RFI cows have the additional advantage of increased digestive efficiency. However, low RFI cows may in fact eat less because of a greater ability to digest their feed. From our data, we cannot determine if cows with low RFI eat less because of superior digestive efficiency or if they have superior digestive efficiency because they eat less.

APPENDIX

Table B.1. **Least square means of performance and efficiency for cows fed high and low starch diets (n=107) by digestive efficiency group[1].**

	High Starch Diet					Low Starch Diet				
	Digestive Efficiency Group			P-value[2]		Digestive Efficiency Group			P-value	
Item[3,4]	High	Mid	Low	Linear	Quadratic	High	Mid	Low	Linear	Quadratic
Number of Animals	32	43	32			33	41	33		
Intake and Performance										
DMI, kg/d	25.7	26.5	26.4	0.46	0.53	23.6^{c}	25.7^{b}	27.5^{ab}	<0.01	0.89
MM_R	4.16	4.24	4.22	0.63	0.58	3.76^{b}	4.00^{ab}	4.27^{a}	<0.01	0.93
MM_I	4.07	4.31	4.24	0.13	0.07	3.70^{b}	3.85^{b}	4.16^{a}	<0.01	0.31
MilkE, Mcal/d	29.4	30.6	29.9	0.71	0.73	26.5^{b}	30.1^{a}	31.7^{a}	<0.01	0.34
ΔBodyE, Mcal/d	4.32	3.19	4.11	0.83	0.17	1.72	1.89	2.89	0.10	0.46
MBW, kg0.75	134	130	132	0.59	0.26	128	133	132	0.10	0.16
Estimated DietNE_L, Mcal/kg	1.74	1.68	1.70	0.46	0.30	1.63	1.67	1.64	0.77	0.27
Efficiency										
Milk:feed	1.65	1.67	1.64	0.84	0.46	1.62	1.69	1.66	0.36	0.13
Gross Efficiency, %	31.4	30.6	30.9	0.65	0.50	28.3	29.6	29.7	0.15	0.41
RFI, kg DM/d	-0.25	0.29	-0.25	0.60	0.15	-0.30^{b}	-0.34^{b}	0.76^{a}	<0.01	0.04
Digestibility, %										
Starch	96.3^{a}	95.3^{b}	94.7^{b}	<0.01	0.54	95.1^{a}	94.9^{a}	93.9^{b}	<0.01	0.17
NDF	40.7^{a}	36.5^{b}	31.4^{c}	<0.01	0.53	52.4^{a}	48.5^{b}	44.2^{c}	<0.01	0.63
DM	69.4^{a}	66.8^{b}	63.9^{c}	<0.01	0.58	66.2^{a}	63.4^{b}	60.3^{c}	<0.01	0.48
CP	68.6^{a}	66.1^{b}	63.6^{c}	<0.01	0.93	67.7^{a}	64.8^{b}	62.3^{c}	<0.01	0.66

[1]Digestive efficiency groups High (>0.5 SD of the cohort mean DM digestibility), Mid (±0.5 SD of the cohort mean DM digestibility), and Low (<0.5 SD of the cohort mean DM digestibility).
[2]P-value associated with linear and quadratic contrasts for digestive efficiency group.
[3]MM_R = multiple of maintenance based on requirements; MM_I = multiple of maintenance based on feed intake; MilkE = milk energy output; ΔBodyE = change in body energy; MBW = metabolic BW; Estimated Diet NE_L = apparent net energy concentration of the diet, calculated by:[(MilkE + 0.08 x MBW + ΔBodyE) / DMI]; RFI = residual feed intake.
[4]Means within a diet with different superscripts are significantly different (P<0.05).

Table B.2. Type three sums of squares for the DMI prediction model used to determine RFI using DM digestibility and the interaction of DM digestibility and diet as covariates.

Source[1]	DF	Type III SS	Mean Square	F-Value	Pr > F
MilkE	1	392	392	192	<0.01
MBW	1	131	131	64.0	<0.01
ΔBodyE	1	2.44	2.44	1.19	0.28
Parity	1	70.0	70.0	34.2	<0.01
Experiment	3	19.6	6.54	3.20	0.02
Cohort (Experiment)	4	36.4	9.10	4.45	<0.01
Diet (Experiment x Cohort)	8	63.4	7.92	3.87	<0.01
DM Digestibility	1	8.81	8.81	4.31	0.04
DM Digestibility x Diet	1	9.34	9.34	4.57	0.03

[1]MilkE = milk energy output; MBW = metabolic BW; ΔBodyE = body energy change; parity = primiparous or multiparous; experiment = 1, 2, 3, or 4; cohort = groups of cows that ate the same diet at the same time; diet = high or low starch.

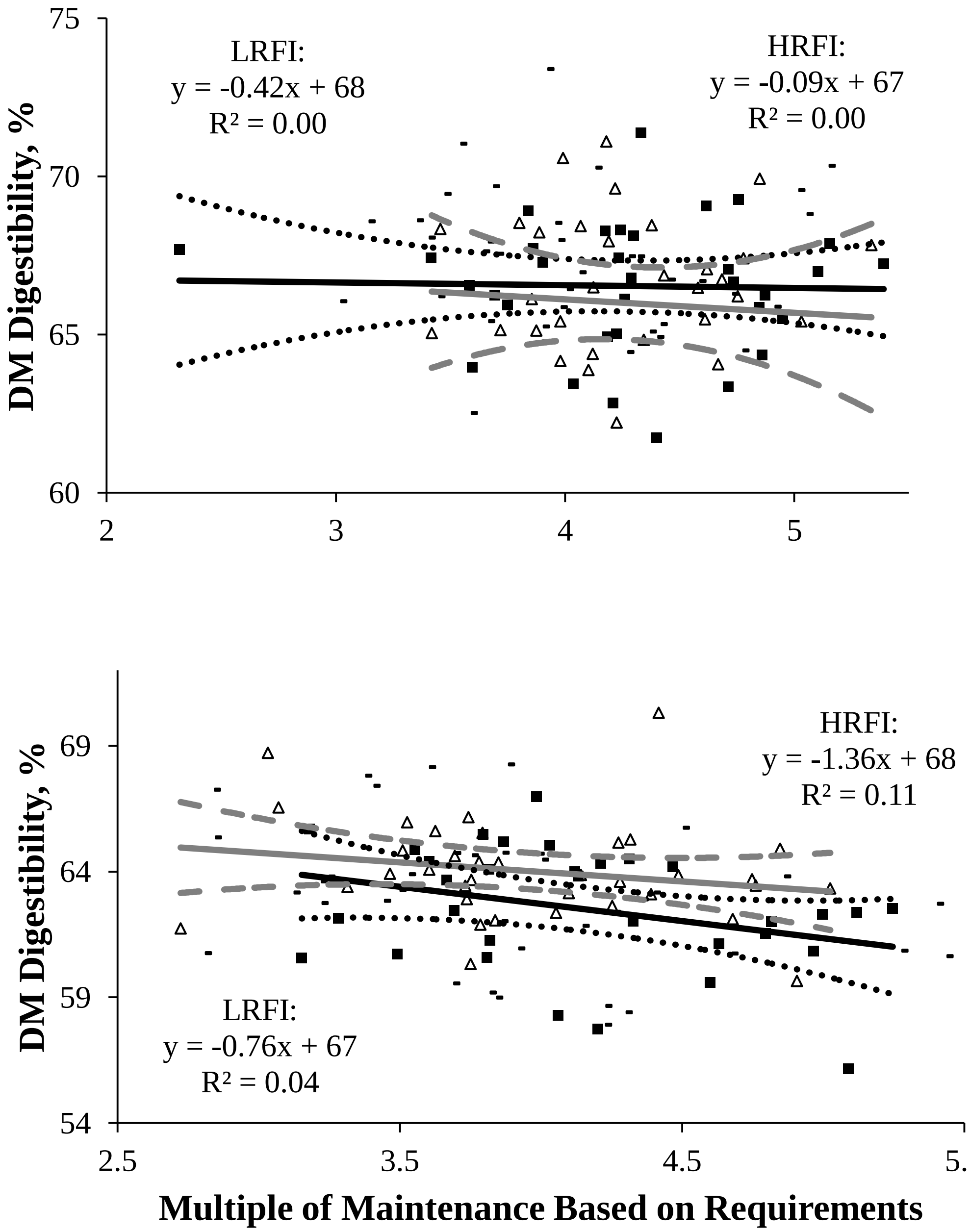

Figure B.1. DM Digestibility vs. multiple of maintenance determined from requirements for cows (n=107) fed high (HS) and low (LS) diets. The top panel shows performance when cows were fed HS diets; the bottom panel shows performance when cows were fed LS diets. Cows that were classified as high RFI (HRFI; >0.5 SD of the cohort mean) are indicated by ■; cows that were classified as low RFI (LRFI; <0.5 SD of the cohort mean) are indicated by Δ; cows that were classified as medium RFI (MRFI; ±0.5 SD of the cohort mean) are indicated by ▬. The solid dark line is the regression for HRFI cows and the solid light line is the regression for LRFI cows. The black dotted lines show the 95% confidence limits for the regression of HRFI; the grey dashed lines show the 95% confidence limits for the regression of LRFI.

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CHAPTER 4

RELATIONSHIP BETWEEN BLOOD METABOLITES AND RESIDUAL FEED INTAKE IN LACTATING HOLSTEIN COWS FED HIGH AND LOW STARCH DIETS

ABSTRACT

Residual feed intake (RFI) is an alternative tool used to quantify efficiency in livestock production and is the difference between what an animal consumes and what it is predicted to consume based on production and maintenance requirements. The objective of this study was to determine if some commonly measured plasma metabolites are correlated with RFI in mid-lactation cows fed high (~30%; HI) and low (~14%; LO) starch diets. Data from two cross-over experiments (n=32 and n=20) with 28-d treatment periods were used for this analysis. Individual DMI and milk yield were recorded daily, milk was sampled at 4 consecutive milkings per wk and analyzed for components, and BW was recorded 3 times per wk. Samples of blood were collected every 15 h during the last 5 d of each period for both experiments and composited. Additional samples were collected 1 h before and 3 h after feeding on day 21 of each period in experiment 2. Samples were analyzed for concentrations of insulin, NEFA, urea nitrogen (BUN), and glucose. Individual DMI was modeled as a function of milk energy output, metabolic BW, and body energy change plus the fixed effects of parity, experiment, cohort nested within experiment, and diet nested within cohort and experiment; the residual term was used to define RFI. Cows gained more energy as body tissue (4.6 vs. 2.0 Mcal/d; $P<0.01$) and plasma insulin concentration was 20% greater when fed HI diets. Plasma NEFA concentration tended to be negatively associated with RFI (r=-0.26; $P<0.10$) when cows were fed LO diets but not HI diets. Concentrations of insulin, BUN, and glucose were not related to RFI when cows

were fed either diet. Furthermore, we did not observe any strong relationships between pre- and post-feeding plasma metabolite concentrations and RFI. We conclude that RFI is not strongly related to plasma concentrations of insulin, NEFA, BUN, or glucose and that they are not indicative of a cow's RFI status.

INTRODUCTION

Residual feed intake (RFI) is an alternative measure of energetic efficiency and is the difference between what a cow consumes and what she is predicted to consume based on performance and maintenance requirements (Koch et al., 1963). Cows with low RFI consume less than contemporaries for the same level of production and are therefore more efficient than those with high RFI. Residual feed intake allows for identification of energetically efficient animals, which are those that convert gross energy into net energy more efficiently by reducing heat, gas, urine, or fecal losses. Because some animals eat less than others to yield the same amount of product, there are likely differences in biological mechanisms that enable them to do so. Richardson and Herd (2004) predicted that sources of variation for RFI in beef cattle include: feeding pattern (2%), body composition (5%), protein turnover and tissue metabolism (37%), heat increment of feeding (9%), digestive efficiency (10%), physical activity (10%), and other unknown metabolic processes (27%). Some (Richardson et al., 2004; Kelly et al., 2010a; Kelly et al., 2010b; Lawrence et al., 2012) have determined relationships between RFI and plasma metabolites in beef cattle, which could provide insight as to which metabolic mechanisms differ among efficient and inefficient animals. The objective of this study was to determine if some commonly measured plasma metabolites are correlated with RFI in mid-lactation cows fed high and low starch diets.

MATERIALS AND METHODS

Cows, Experimental Design, and Diets

Experimental procedures were approved by the Institutional Animal Care and Use Committee of Michigan State University. Data from two separate cross-over experiments were used to determine the relationship between RFI and plasma metabolites across high and low starch diets. Lactating Holstein cows were fed diets that differed in starch concentration in experiments 1 (n=32; 50% primiparous) and 2 (n=20; 55% primiparous). Mean DIM and BW for all cows (mean ± SD) was 115 ± 26 d and 659 ± 78 kg at experiment start, respectively, and mean milk yield was 45 ± 9 kg/d. For both experiments, the two experimental periods lasted 28 d, and cows were blocked based on milk yield and parity and randomly assigned to treatment sequence. All cows were housed in individual tie stalls and milked twice daily (0300 and 1430 h). Cows were fed high (HI) or low (LO) starch diets that were markedly different in starch concentration (~30 vs. 14%; Table 4.1). Diets were adjusted for changes in forage DM concentration twice weekly.

Table 4.1. Ingredient and nutrient composition of high (HI) and low (LO) starch diets fed during each experiment[1,2].

	Experiment 1		Experiment 2	
	HI	LO	HI	LO
Ingredient, % of DM				
Corn silage	23.7	24.2	23.5	20.9
Legume silage	11.1	22.6	20.6	18.4
Wheat straw	3.79	1.94	4.82	--
Soybean hulls	--	10.6	--	32.1
Cottonseed, whole	7.45	9.07	--	9.22
Corn, ground	13.1	--	30.8	7.18
Corn, high moisture	21.5	11.0	--	--
Soybean meal	15.9	14.6	17.2	9.08
Fat supplement[3]	--	2.51	--	--
Vitamin & mineral[4]	2.02	2.05	2.08	2.08
Limestone	0.75	0.76	0.52	--
Sodium bicarbonate	0.75	0.76	0.51	0.51
Dicalcium phosphate	--	--	--	0.51
Nutrient, % of DM				
DM	55.8	51.7	49.5	52.2
NDF	25.1	32.8	27.6	44.2
Starch	32.5	16.1	28.2	11.8
CP	17	18.3	16.9	15.2
Ash	5.4	6.8	6.1	6.5
Ether Extract	3.24	5.61	2.3	3.41
NE^L, Mcal/kg[5]	1.8	1.75	1.72	1.62
GE (calculated), Mcal/kg[6]	4.26	4.34	4.19	4.21

[1]Diets were fed to lactating cows in experiments 1 (n=32) and 2 (n=20).
[2]Nutrient composition was determined from feed ingredients sampled during the last 5 d of each 28-d experimental period.
[3]Fat supplement was palmitic acid enriched.
[4]Vitamin and mineral mix contained 34.1% dry ground shell corn, 25.6% white salt, 21.8% calcium carbonate, 9.1% Biofos, 3.9% magnesium oxide, 2% soybean oil, and < 1% of each of the following: manganese sulfate, zinc sulfate, ferrous sulfate, copper sulfate, iodine, cobalt carbonate, vitamin E, vitamin A, vitamin D, and selenium.
[5]Mean apparent net energy concentration of diets, based on average cow performance. For each diet, $DietNE_L$ = the average of (MilkE + 0.08 x MBW + ΔBodyE) / DMI for all cows on the diet.
[6]Gross energy concentration, calculated from nutrient profile of individual feed ingredients, with sugar and organic acid content of feeds being estimated from Spartan Dairy Ration Evaluator (version 3.0; Michigan State University, East Lansing, MI): 4.20 kcal/g carbohydrate, 5.65 kcal/g crude protein, 9.50 kcal/g fatty acid estimated from ether extract, 3.95 kcal/g sugar (Merrill and Watt, 1973).

Sample Collection and Analysis

Cows were fed once daily at 1000 h (experiment 2) or 1200 h (experiment 1) for >110% of expected intake, and orts were removed and weighed daily. Milk yield was recorded at each milking, and milk samples were obtained from 4 consecutive milkings per wk. Milk samples were analyzed for fat, protein, lactose, somatic cell count, and milk urea nitrogen (MUN) with infrared spectroscopy by Michigan DHIA (East Lansing). Body weight for each cow was recorded 3 times per wk immediately after the morning milking. Body condition score (BCS) was determined on a 5-point scale, where 1=thin and 5=fat, as described by Wildman et al. (1982). During the last 5 d of experimental periods, samples of feed ingredients were obtained to determine the nutrient profile of the diets. Samples were composited to obtain one sample per period, dried in a forced air oven (135°C for > 72 h), and ground through a Wiley mill (1-mm screen; Arthur H. Thomas Co., Philadelphia, PA).

Samples of feed were analyzed for CP, starch, NDF, ether extract, and ash. Crude protein was determined according to Hach et al. (1987). Starch was analyzed by an enzymatic method after gelatinization with sodium hydroxide (Karkalas, 1985); glucose concentration was determined via glucose oxidase method (Glucose kit #510; Sigma Chemical Co., St. Louis, MO), and absorbance was measured with a micro-plate reader (SpectraMax 190; Molecular Devices Corp., Sunnyvale, CA). Neutral detergent fiber was determined according to Mertens (2002). Ether extract was determined using a modified Soxhlet apparatus (AOAC, 1990) and ash was determined after 5 h combustion at 500°C. Concentrations of all nutrients are expressed as a percent of diet DM.

Samples of blood were collected every 15 h during the last 5 d of each period to obtain samples that collectively represented every 3 h of a 24-h period (2400, 0230, 0600, 0900, 1200, 1500, 1800, 2100 h). Additional blood samples were collected 1 h before and 3 h after feeding on day 21 of each period in experiment 2. Blood was sampled via coccygeal venipuncture into 3 evacuated tubes (6 mL each), two containing potassium EDTA and one containing potassium oxalate with sodium fluoride as a glycolytic inhibitor. Immediately after collection, samples were centrifuged at 2,000 x g for 15 min, and plasma was separated and stored at -20°C.

Plasma samples collected every 15 h were composited to obtain 1 sample per cow per period and were analyzed for concentrations of NEFA, insulin, urea nitrogen (BUN) and glucose. Concentration of plasma NEFA was determined by an enzymatic colorimetric method (NEFA-HR (2) kit; Wako Chemicals, Richmond, VA). Insulin concentration was determined by an ELISA (Bovine Insulin ELISA; Mercodia, Uppsala, Sweden), and BUN was determined by an enzymatic colorimetric procedure (Enzymatic Urea Nitrogen, Procedure #2050; Stanbio Laboratory, Boerne, TX). Plasma glucose concentration was analyzed using a glucose oxidase method that combined 10 μL of plasma with 250 μL of AB solution (Sigma Chemical Co.), and absorbance was measured with a micro-plate reader (SpectraMax 190; Molecular Devices Corp., Sunnyvale, CA). Samples were analyzed in duplicate; if CV between duplicates was >5% then samples were reanalyzed until a CV <5% between two analyses was achieved.

Calculations and Statistical Analysis

Milk energy output (MilkE; Mcal/d) for a cow was estimated from the following equation (NRC, 2001; from Equation 2-15):

$$\text{MilkE} = 9.29 \times \text{fat (kg)} + 5.63 \times \text{protein (kg)} + 3.95 \times \text{lactose (kg)},$$

where yields of fat, protein, and lactose were based on the average output of a cow during a 28-d period. Metabolic BW for a cow (MBW; $kg^{0.75}$) was estimated as $BW^{0.75}$, where BW was the mean BW for the cow during a period. Daily BW change (ΔBW; kg/d) was calculated for each cow within a period by linear regression. Energy used for body tissue gain (ΔBodyE; Mcal/d) was calculated by an equation derived from NRC (2001; Table 2-5):

$$\Delta BodyE = (2.88+1.036 \text{ x } BCS) \text{ x } \Delta BW,$$

where BCS is the average BCS for a cow during a 28-d period.

Data from both experiments were used to determine individual RFI. Dry matter intake for an individual cow during each 28-d period was regressed as a function of major energy sinks using GLM Procedure in SAS (v. 9.3; SAS Institute, Cary, NC). A cohort was a group of animals that consumed the same diet at the same time and animals were always compared to others within the same cohort. To define RFI, DMI was modeled as follows: $DMI_i = \beta_0 + \beta_1 \text{ x } MilkE_i + \beta_2 \text{ x } MBW_i + \beta_3 \text{ x } \Delta BodyE_i + Parity + Experiment + Cohort(Experiment) + Diet(Cohort \text{ x } Experiment) + \varepsilon_i$, where DMI_i was the observed DMI, $MilkE_i$ was the observed milk energy output, MBW_i was the average $BW^{0.75}$, and $\Delta BodyE_i$ was the predicted change in body energy, based on measured BW and BCS, for ith cow. Parity (1 or 2+), experiment (1, 2, 3, or 4), cohort nested within experiment, and diet nested within cohort and experiment were fixed effects. The error term in the model was used to determine RFI.

Performance responses to HI and LO diets were analyzed using the MIXED Procedure in SAS, with fixed effects of experiment, diet, period, parity, all two-, three-, and four-way interactions of fixed effects, and the random effect of cow nested within experiment. A similar model, without the effect of experiment, was utilized to analyze the effect of diet on pre- and post-prandial metabolites. Pearson correlations were determined using the CORR Procedure. Main effects and correlations were considered significant at $P<0.05$ and trends were defined as $P<0.10$. Interactions were considered significant at $P<0.10$ and tendencies at $P<0.15$.

RESULTS AND DISCUSSION

We did not observe any strong relationships between RFI and plasma metabolites when cows were fed HI and LO diets. Additionally, metabolite concentrations before and after feeding, as well as the change in metabolite concentration in response to feeding were not significantly related to RFI. Conflicting results for relationships between plasma metabolites and RFI are reported in the literature. Others have examined these relationships in growing or finishing beef cattle that were fed a variety of different diets. Plasma metabolite concentrations are influenced by diet type and animal physiological state; thus conflicting results are likely a consequence of the different conditions under which animals were studied. That we fed high and low starch diets to lactating cows likely influences how our results compare to those reported for growing or finishing beef cattle. Additionally, when RFI is determined for beef cattle, the energy composition of BW gain is not considered, which may impact the relationships observed in those studies. To determine RFI for our experiment, we quantified the energy content of milk produced, the energy required for maintenance, and the energy required for apparent body tissue gain; our calculation of body tissue gain was adjusted for BCS in an attempt to accurately reflect the energy content of gain. Furthermore, we accounted for diurnal variation in plasma metabolite concentration by compositing samples that represented every 3 h of a 24-h period. In contrast, those that have examined the relationship between RFI and plasma metabolites in beef cattle have not accounted for diurnal variation in metabolite concentration. In these studies, samples were obtained at the same time of day on multiple occasions evenly spaced throughout the RFI test period (Kelly et al., 2010a; Kelly et al., 2010b; Lawrence et al., 2011; Lawrence et al., 2012) or before weaning and at the beginning and end of the RFI test period (Richardson et al., 2004). These differences in sampling technique likely also contribute to inconsistency of results among studies.

Table 4.2. Pearson correlations of DMI and RFI with plasma metabolites for cows fed high and low starch diets.

	High Starch Diet		Low Starch Diet	
Item[1]	DMI, kg/d	RFI, kg/d	DMI, kg/d	RFI, kg/d
Plasma metabolites[2]				
Insulin, µg/L	0.02	0.06	-0.28*	0.07
NEFA, mEq/L	0.01	-0.15	-0.09	-0.26†
BUN, mg/dL	0.27†	0.03	0.23†	-0.01
Glucose, mg/dL	0.02	0.01	-0.35*	-0.22
Pre-feeding plasma metabolites[3]				
Insulin, µg/L	0.12	0.03	-0.18	-0.10
NEFA, mEq/L	-0.13	0.06	0.29	-0.16
BUN, mg/dL	0.04	0.33	-0.07	-0.11
Glucose, mg/dL	-0.09	-0.04	-0.31	0.04
Post-feeding plasma metabolites[3]				
Insulin, µg/L	0.23	-0.27	0.12	0.15
NEFA, mEq/L	0.16	0.40†	0.41†	-0.26
BUN, mg/dL	0.10	0.41†	-0.03	-0.08
Glucose, mg/dL	0.46*	0.17	0.08	0.01
Change in response to feeding[4]				
Insulin, µg/L	0.19	-0.34	0.32	0.25
NEFA, mEq/L	0.20	0.03	-0.19	0.09
BUN, mg/dL	0.10	0.06	0.05	0.03
Glucose, mg/dL	0.44†	0.17	0.30	-0.02

[1]RFI = residual feed intake; BUN = blood urea nitrogen.
[2]Data from experiment 1 and experiment 2 (n=50).
[3]Data from experiment 2 only (n=20).
[4]Change = difference between post-feeding concentration and pre-feeding concentration.
* indicates $P \leq 0.05$; † indicates $P \leq 0.10$.

Plasma Metabolites and RFI

Insulin. We observed no relationship between RFI and plasma insulin when cows were fed HI and LO diets (Table 4.2), which is consistent with results observed for growing beef heifers (Kelly et al., 2010a; Lawrence et al., 2012). In contrast, Kelly et al. (2010b) and Richardson et al. (2004) observed positive relationships (r=0.23 and r=0.43, respectively) between RFI and plasma insulin concentration for finishing beef heifers and steers, respectively. Insulin stimulates lipogenesis and some (Richardson et al., 2004; Kelly et al., 2010a) report that high RFI cattle are fatter than low RFI cattle. The finishing cattle observed by Richardson et al. (2004) and Kelly et al. (2010b) had greater a greater degree of fatness, which might have been a result of increased insulin secretion. However, composition of BW gain in beef cattle is not considered in the calculation of RFI. Since gain per unit of feed intake is greater for lean tissue than fat, it might be expected that high RFI cattle would be fatter than those with low RFI if composition is not considered. If composition of gain was considered on an energetic basis, perhaps no differences would exist among high and low RFI cattle for degree of fatness and RFI and insulin would not be correlated.

The change in insulin concentration in response to feeding was not significantly related to RFI for either diet. There were also no relationships between RFI and either pre- or post-prandial concentrations of insulin. It might be expected that the greater DMI of high RFI cows would result in greater post-feeding insulin concentrations, but this was not the case, and pre- and post-feeding insulin concentration was not related to DMI for our study. It has been shown that animals with high and low RFI have different feeding patterns and meal sizes (Montanholi et al., 2010; Williams et al., 2011; Green et al., 2013). Differences in initial meal size and meal frequency may have impacted the results we observed for plasma insulin concentration, with a greater initial meal size resulting in a greater increase in plasma insulin post-feeding.

Glucose. Similar to results reported by others for beef cattle (Richardson et al., 2004; Kelly et al., 2010a; Kelly et al., 2010b; Lawrence et al., 2011), we did not observe any significant relationship between RFI and plasma glucose concentration (Table 4.2). Pre- and post-prandial plasma glucose concentrations, as well as plasma glucose concentration change in response to feeding, were not related to RFI for HI or LO diets, suggesting that these cows did not differ in the ability to maintain blood glucose concentration after feeding occurred.

NEFA. Plasma NEFA tended to be related to RFI (r=-0.26; $P<0.10$) when cows were fed LO diets, but not HI diets (r=-0.15; $P>0.10$), indicating that plasma NEFA concentration increased as RFI decreased for LO diets (Table 4.2). Similar to our results, low RFI beef heifers tended to have greater plasma NEFA concentrations (Lawrence et al., 2012). However, others either did not observe a significant relationship (Kelly et al., 2010a; Lawrence et al., 2011) or observed a positive relationship between RFI and plasma NEFA (Kelly et al., 2010b).

Plasma NEFA concentration before feeding was not related to RFI for HI or LO diets (Table 4.2), thus cows probably did not differ in adipose utilization before feeding. Post-prandial NEFA concentration tended to be positively related to RFI (r=0.40; $P<0.10$), for the HI diet but not the LO diet, indicating that the low efficiency (high RFI) cows had greater NEFA after feeding. This in contrast to the relationship observed for RFI and mean NEFA concentration, which suggested that low RFI cows tended to have higher mean plasma NEFA concentration. These results suggest that the relationship between plasma NEFA and RFI may depend on when the blood sample is collected relative to feeding. Post-feeding NEFA concentration may be more dependent on eating rate than on total meal size in sheep (Bowden, 1971), and high and low RFI dairy heifers and cows are shown to differ in eating patterns and eating rate (Williams et al., 2011; Connor et al., 2013; Green et al., 2013), which may have impacted our results. However, the change in plasma NEFA in response to feeding was not correlated with RFI for either diet (P>0.10).

Blood urea nitrogen. Blood urea nitrogen was highly correlated with MUN (r=0.84; P<0.01; data not shown), and both MUN and BUN may be reflective of nitrogen efficiency (Broderick and Clayton, 1997); however, MUN and BUN may also be influenced by dietary factors, such as CP intake (Wattiaux and Karg, 2004), and thus neither are perfect indicators of protein efficiency. Blood urea nitrogen was not associated with RFI for either diet (Table 4.2). Similar to our results, others (Richardson et al., 2004; Kelly et al.,2010a; Lawrence et al., 2012) did not observe significant relationships between BUN and RFI for finishing steers and growing beef heifers. These results suggest that high RFI cattle do not differ from low RFI cattle in their efficiency of nitrogen use. In contrast, for finishing (Kelly et al., 2010b) and gestating beef heifers (Lawrence et al., 2011), RFI was positively related to BUN (r=0.4 and r=0.2, respectively). Since dietary CP intake influences MUN (Wattiaux and Karg, 2004), which is highly correlated with BUN (Broderick and Clayton, 1997), it is reasonable that diet differences may result in contrasting relationships between BUN and RFI since high RFI animals eat more than low RFI animals.

The change in BUN in response to feeding was not related to RFI for either diet. Post-prandial BUN concentration tended to be positively related to RFI (r=0.41; P<0.10) when cows were fed HI diets, but not LO diets, which might have been the result of greater DMI by high RFI cows, since MUN is correlated positively to DMI (Wattiaux and Karg, 2004).

Responses to High and Low Starch Diets

Animal production responses to HI and LO diets are reported in Table 4.3. There was a significant diet by experiment interaction for DMI (*P*=0.02), with DMI being significantly greater for the HI diet in experiment 1, but similar between HI and LO diets for experiment 2. Milk energy output and MBW were similar between HI and LO diets. Energy gain as body tissue was greater for HI diets (4.6 vs. 2.0 Mcal/d; *P*<0.01). However, there was a trend for a diet by experiment interaction for ΔBodyE (*P*=0.15), with ΔBodyE being significantly greater for the HI diet in experiment 1. Cows partitioned more energy to body gain (9.5 vs. 3.9%; *P*<0.01) and less to milk (68 vs. 72 %; *P*<0.01) when fed HI diets (data not shown). This shift in partitioning that occurred when cows were fed HI diets is consistent with results reported by Van Knegsel et al. (2007), who fed glucogenic and lipogenic diets to cows 2-9 wk postpartum. In that study, the lipogenic diet was 10% starch and 40% NDF, and the glucogenic diet was 27% starch and 32% NDF (Van Knegsel et al., 2007). Cows consuming the lipogenic diet partitioned less energy into body tissue and more energy into milk production (Van Knegsel et al., 2007).

Table 4.3. Least square means for performance and plasma metabolites for cows fed high (HI) and low (LO) starch diets.

	Diet			P-value[1,2]			
Intake and Performance[3]	HI	LO	SEM	Diet	Exp	Diet x Exp	Diet x Period
DMI	26.5	26.1	0.28	0.30	0.45	0.02	0.28
MilkE, Mcal/d	31.3	31.6	0.51	0.63	<0.01	0.81	0.92
MBW, $kg^{0.75}$	131	131	1.23	0.78	0.37	0.93	0.33
ΔBodyE, Mcal/d	4.56	1.98	0.46	<0.01	0.89	0.15	0.75
Plasma Metabolites[4]							
Insulin, µg/L	1.11	0.89	0.04	<0.01	0.02	0.89	0.32
NEFA, mEq/L	90.8	128.6	3.71	<0.01	0.02	0.91	0.95
BUN, mg/dL	15.8	16.8	0.39	0.08	<0.01	<0.01	0.01
Glucose, mg/dL	64.4	64.1	0.55	0.73	0.42	0.13	0.61
Pre-Feeding Metabolites[5]							
Insulin, µg/L	0.48	0.49	0.06	0.90	--	--	0.70
NEFA, mEq/L	129	182	16.7	0.03	--	--	0.03
BUN, mg/dL	14.9	11.9	0.54	<0.01	--	--	<0.01
Glucose, mg/dL	65.2	65.6	0.77	0.77	--	--	0.84
Post-Feeding Metabolites							
Insulin, µg/L	0.89	0.65	0.07	0.02	--	--	0.22
NEFA, mEq/L	80.8	117	5.47	<0.01	--	--	0.36
BUN, mg/dL	16.4	14.0	0.56	<0.01	--	--	0.18
Glucose, mg/dL	61.0	62.6	1.07	0.30	--	--	0.96
Change[6]							
Insulin, µg/L	0.42	0.16	0.06	<0.01	--	--	0.10
NEFA, mEq/L	-48.6	-65.0	14.0	0.42	--	--	0.02
BUN, mg/dL	1.54	2.04	0.35	0.32	--	--	0.01
Glucose, mg/dL	-4.29	-3.01	1.21	0.46	--	--	0.93

[1]P-value associated with fixed effects of diet and experiment (exp), their interaction, and interaction of diet and period.
[2]For pre- and post-feeding plasma samples, data is from experiment 2 only (n=20) so there was no effect of experiment.
[3]MilkE = milk energy output; MBW = metabolic BW; ΔBodyE = body energy change.
[4]Plasma analysis based on samples taken every 15 h for 5 days and composited for both experiments (n=50); BUN = blood urea nitrogen.
[5]Plasma metabolite concentration 1 h before and 3 h after feeding for experiment 2 cows (n=20).
[6]Change = difference between post-feeding concentration and pre-feeding concentration.

Consistent with the changes in partitioning observed, plasma insulin was 20% greater when cows were fed HI diets (*P*<0.01; Table 4.3). This response was likely the result of increased production of propionate from ruminal starch digestion and subsequent up regulation of gluconeogenesis, followed by insulin secretion (Allen et al., 2009). The change in plasma insulin concentration in response to feeding was 39% greater (*P*<0.01) for the HI diet in experiment 2, which is consistent with the idea that HI diets probably increased production of glucose precursors in the rumen. Plasma NEFA was 29% (*P*<0.01) lower when cows were fed HI diets, likely due to reduction of lipolysis by insulin (Allen et al., 2009) or the addition of supplemental fat in the LO diet for experiment 1 (Allen, 2000). Glucose concentration was similar between HI and LO diets (~64 mg/dL; *P*=0.74) and was not different before or after feeding in experiment 2. These results were expected because insulin and glucagon work antagonistically to maintain blood glucose levels. There was a significant diet by experiment interaction for BUN (*P*<0.01), with cows in experiment 1 having significantly greater concentrations for the LO diet and cows in experiment 2 having significantly greater concentrations for the HI diet. When compared with the HI diet, the LO diet was greater in CP content in experiment 1; however, in experiment 2 the LO diet contained a lower concentration of CP than the HI diet. These differences may have caused the diet by experiment interaction for BUN. Blood urea nitrogen was greater for the HI diet before and after feeding in experiment 2 likely because the HI diet in that experiment contained a greater concentration of CP than the LO diet, and CP intake is positively related to MUN (Wattiaux and Karg, 2004), which is strongly related to BUN (Broderick and Clayton, 1997).

CONCLUSION

Energy partitioning was altered by feeding high and low starch diets and this change in partitioning is supported by higher plasma insulin concentration but lower NEFA concentration for high starch diets. Concentrations of plasma insulin, glucose, and BUN for mid-lactation cows fed high and low starch diets were not correlated with RFI and are thus not indicative of a cow's RFI status. There are likely mechanisms other than those that might be associated with basic carbohydrate metabolism that contribute more variation in RFI, such as heat production.

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CHAPTER 5

DISCUSSION

Residual feed intake (RFI) is a tool that allows for the identification of energetically efficient animals, independent of level of production. Its independence of production level, and thus the dilution of maintenance, makes it an attractive tool to assess feed efficiency for many reasons. Its independence of production level enables identification of efficient animals without reliance on the dilution of maintenance alone, which may allow for more rapid advances in feed efficiency in combination with the dilution of maintenance. Furthermore, low RFI cows may be economically valuable because they eat less than expected for a given level of production when compared to cohorts and thus daily feed costs for these animals are lower. Residual feed intake is also heritable (h^2=0.15; Tempelman et al., 2013), and it has potential to be incorporated into selection indices. Because RFI is independent of production, when incorporated into selection indices, it will enable selection for energetic efficiency without altering milk production traits. Selection pressure could be applied to improve feed efficiency without placing more emphasis on milk production than is desirable. Using genomics as a tool to identify efficient animals is a possibility (Karisa et al., 2013), and would expedite genetic progress toward more efficient animals. However, RFI must be repeatable if it is to be used to effectively improve feed efficiency of future generations that may be subjected to different diets and environmental conditions. Additionally, understanding why some animals are more efficient than others might lead to new approaches in selecting and modifying dairy cattle to improve efficiency.

Repeatability of Residual Feed Intake

Residual feed intake was reasonably repeatable across diets that differed markedly in starch and fiber content and that caused significant shifts in energy partitioning, milk production, or both in all four experiments, as reported in Chapter 2. Most cows that were efficient on one diet were also efficient on the other diet relative to others in their cohort. These results suggest that selection for RFI will yield future generations of cows that will likely still be efficient even if fed diets that are more economically or environmentally favorable during those times. That RFI is a robust assessment of energetic efficiency and is repeatable across diets makes it a good tool to identify and select for more efficient cows. However, it is still of interest to examine the repeatability of RFI across diets differing in forage:conentrate ratio. Although high and low starch diets for this study were markedly different in starch and fiber content, they had similar forage:concentrate ratios. In the future more or less forage may be fed to lactating dairy cows; thus, it is imperative that RFI also be repeatable across diets differing in forage content.

Repeatability of RFI may vary with stage of maturity at the time of assessment. In growing animals, repeatability may be influenced by between-animal variation in the composition of body gain since efficiencies of protein and adipose gain are different (Moe, 1981). The inability to accurately quantify changes in body composition adds further complication. In beef cattle, RFI measured across two consecutive growing periods where heifers were fed the same diet in both periods (Durunna et al., 2012) was less repeatable (r=0.52) than our observation across diets. Archer and Pitchford (1996) examined repeatability of weekly RFI estimates for mice from 3 to 18 weeks of age and observed higher repeatability across weekly estimates as animals aged. Because the efficiencies of protein and fat gain differ, changes in the type of body tissue gain (fat or protein) for each animal over time may have contributed to the low repeatability of growing animals in both studies. Macdonald et al. (2014) determined RFI for females as growing heifers and subsequently as first lactation cows; they concluded that divergence for RFI was greater for heifers when compared with RFI predictions for cows. Other metabolic processes that function throughout various periods of life may vary in efficiency such that the most efficient animals at a young age might not retain their RFI status at maturity.

Physiological state may also influence efficiency because metabolic processes that support different functions may change over time. Throughout lactation, dairy cows undergo physiological changes; the beginning of lactation is associated with tissue mobilization to support the high energy demand for lactation, but mid- to late-lactation cows are able to consume enough energy to support milk production and replenish body tissue utilized during early lactation. These dramatic changes might influence the repeatability of RFI because of the previously mentioned issues associated with the composition of body gain. Prendiville et al. (2011) assessed RFI during 6 periods of a full lactation cycle and determined that measurements around 150 DIM and 230 DIM were most highly correlated (r~0.5) with RFI determined for all 6 periods. Connor and coworkers (2013) determined that measurements for RFI through 53 DIM accounted for 81% of the variation of RFI measured through 90 DIM and that repeatability of weekly RFI estimates through 90 DIM was 0.47. These results suggests that RFI may be at least somewhat repeatable across different stages of lactation. Although the ideal period during a lactation cycle when RFI should be measured has not been determined, it seems reasonable that periods during which tissue gain or loss is minimal might yield the most accurate and repeatable estimates of RFI.

For beef cattle, others have also reported moderate repeatability (r=0.6) of RFI across different types of diets (Kelly et al., 2010), which is similar what we observed (r=0.72). That the repeatability of RFI across high and low starch diets was not perfect lends support to the hypothesis that genotype by environment interactions exist and that environment may impact an animal's RFI status, although some differences may also be due to measurement error.

Sources of Variation in Residual Feed Intake

The flow of energy through a cow is depicted in Figure 1.1. Essentially, RFI facilitates the identification of animals that convert consumed energy (GE) into net energy (NE) more efficiently. Cows with low RFI are more efficient because they lose less energy in feces, gas, urine, or heat associated with feeding. Metabolic processes that contribute to the production of these energy losses are of interest and variation in these processes among animals likely explain some variation in RFI.

We investigated the relationship between digestibility and RFI in Chapter 3. Our results indicate that digestibility may not account for a significant portion of the variation in RFI for lactating cows fed high and low starch diets. Cows with low RFI consume less feed than those with high RFI and, consequently, eat at a lower multiple of maintenance. Increased feed intake as a multiple of maintenance is accompanied by a depression in digestibility (NRC, 2001). The negative association between DM digestibility and intake as a multiple of maintenance confirms that this depression in digestibility occurred for both diets in our study. After adjusting for these differences in intake, we observed no differences in digestive efficiency among cows with high, medium, and low RFI, which suggests that digestibility might not directly influence a cow's RFI status. Cows that have high RFI eat more probably because they convert DE to ME or ME to NE less efficiently than cows with low RFI. However, since digestibility could have accounted for 33% of the differences in apparent DietNE$_L$ among high and low RFI cows fed low starch diets, it is likely still important to feed efficiency. Cows with low RFI may actually eat less because they can digest their feed better than cows with high RFI. From our data, we are unable to determine cause and effect.

Digestive efficiency did not account for a large portion of the variation in RFI, which means that processes involved in converting DE to NE may be more influential to a cow's RFI status. Cattle with low RFI have reduced methane production (Hegarty et al., 2007), but this likely accounts for a small portion of the differences in RFI. High and low RFI cattle differ in the amount of heat produced, either as part of the heat increment of feeding or maintenance (Basarab et al., 2003; Montanholi et al., 2010). Some cows probably have a lower maintenance requirement per unit of metabolic BW than others. Differences in mechanisms associated with protein turnover (Richardson and Herd, 2004) and mitochondrial function have been studied in high and low efficiency beef cattle (Kolath et al., 2006; Kelly et al., 2011). Other mechanisms associated with oxidative stress may also be relevant to differences in maintenance requirement (Bottje and Carstens, 2009).

We examined relationships between RFI and blood metabolites and hormones associated with nutrient partitioning (insulin and NEFA), basic carbohydrate metabolism (glucose and insulin), and nitrogen efficiency (BUN). We did not observe strong relationships between metabolites and RFI when cows were fed either diet. Furthermore, because there were no significant differences among high, medium, and low RFI cows for pre- and post-feeding metabolite concentrations or the change in their concentrations in response to feeding, cows with high or low RFI probably do not differ in their metabolic responses to feeding. There were only 20 cows utilized for the analysis of pre- and post-prandial metabolites, which limited our ability to detect statistical differences. An assessment of feeding behavior may have provided further insight, since high and low RFI cattle have been reported to exhibit different feeding patterns

(Montanholi et al., 2010; Green et al., 2013). We also did not observe a significant relationship between energy partitioning to body tissue or milk and RFI, which suggests that selection for RFI will not bias toward cows with a greater propensity to mobilize tissue to support lactation or those that gain more BW than is desirable. Our results for energy partitioning are consistent with our observations for plasma metabolites, which also did not suggest differences in partitioning among high and low RFI cows.

In addition to possible differences in efficiencies of processes related to maintenance requirement and the conversion of DE to NE, cows may differ in the efficiency of converting ME to milk and ME to body tissue. These efficiencies are assumed to be the same and similar among cows (NRC, 2001); however, this is probably not be the case. If some cows convert ME to milk energy more efficiently, it would be of interest to identify these animals for selection purposes.

Implications

Our results provide evidence that RFI is a robust tool that, if implemented in selection indices, could result in efficient dairy cows independent of the type of diet consumed. Profitability , as indicated by IOFC, was not associated with RFI probably because RFI is mostly independent of the dilution of maintenance, which is important to determining overall profitability. Although cows with low RFI did not have significantly greater income over feed cost than high RFI cows, low RFI cows consume less feed per day to produce the same value of product and cost less to feed each day per unit of product value produced. This can be advantageous especially during times when feed supply is limited. Because digestibility does not appear to have a large impact on determining and animal's RFI status, efforts may be focused on other processes that may better explain why some cows consume less feed than contemporaries to produce a similar amount and value of product.

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