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**INTERACTION OF MILK, FAT AND PROTEIN YIELD GENOTYPE WITH
FEEDING LEVEL AND INDICATORS OF COW COMFORT**

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by

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Abstract

The objective of this study was to determine the effect of nutritional management and cow comfort indicators on the level of genetic expression for production traits. There were 305 d milk, fat and protein yields available for 970 cows from 11 tie-stall herds in Pennsylvania. All herds were visited monthly for a period of 6 months to measure individual cow feed intake, BCS and BW. Feed samples were collected on each visit and analyzed for dry matter percentage, crude protein (CP) percentage and calculated net energy of lactation (NE_L). Sire predicted transmitting ability (PTA) was available for all 970 cows, while 881 cows were genotyped and received an Igenity Score (IS) for milk, fat, and protein yield. Two-trait animal models and regression of yield on sire PTA for milk, fat and protein production were used to detect the presence of genotype by environment (GxE) interactions. Environments were defined according to feeding levels of dry matter, dietary composition, and cow comfort measures taken from the facilities. These included stall size (SS), hock lesion score (HLS) and udder hygiene score (HygS) to measure stall management. Response to selection was lower in environments where levels of feed refusals, percentage of CP, and calculated NE_L concentration in the ration were low when compared to environments that fed at high levels for these variables. Animal models showed that large animals are more affected by low levels of feeding of dry matter, CP percentage, NE_L concentration, and high HLS.

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CHAPTER 1

LITERATURE REVIEW

Genotype x Environment Interactions

The phenotypic performance (P) of an animal is typically considered to be the sum of genotypic (G) and environmental (E) effects ($P = G + E$). As a result, the phenotypic variance (V_P) of a trait is equal to the sum of the genetic (V_G) and environmental (V_E) variance ($V_P = V_G + V_E$), assuming that no covariance exists between genotype and environment (Falconer and Mackay, 1996). It is clear, however, that animals have the ability to adapt to their environment and, therefore, genotypic and environmental effects can interact. Genotype by environment (GxE) interactions occur when environmental stresses have different effects on different genotypes (Falconer and Mackay, 1996).

GxE interactions can have two major effects in dairy systems. The first is a scaling effect, where differences between high and low genetic merit individuals are minimal in low performing environments and substantial in high performing environments (Lynch and Walsh, 1998). This scaling effect results from changes in the relative magnitudes of variances (Berry et al., 2003a). That is to say, in environments that are considered to be more advantageous, more genetic variability is observed. The increase in genetic variability can be interpreted as the animal being able to more completely express genetic potential (Cerón-Muñoz et al., 2004). Also, in environments that are considered non-advantageous, less of the total observed variability is due to genetic variability (Van Vleck, 1963). In other words, a favorable genotype will be limited in expression (phenotype) in a suboptimal environment. The scaling effect will

be largely dependent on the environmental sensitivity of the genotype (Falconer and Mackay, 1996; Fikse et al., 2003). Environmental sensitivity is also referred to as the reaction norm, since it refers to the extent to which the genotype reacts to the environment.

The second type of effect that arises from GxE interactions in a dairy system is the re-ranking of genotypes across different environments. In this situation, the difference is not simply a difference in the magnitude of variances across environments, but rather a shift in which genotype is favorable in the new environment. Re-ranking is a larger concern to dairy breeders than the scaling effect because re-ranking can result in poor genetic selection decisions (Mohammad et al., 1982; Horan et al., 2005). Specifically, bulls may be re-ranked as a result of poor daughter performance in suboptimal environments, rather than overall low genetic potential (Lynch and Walsh, 1998).

Genetic variability is what allows selection programs to be effective, as large differences allow favorable genotypes to be identified and selectively improved. The main breeding goal for dairy cattle has traditionally been to increase milk yield. This goal is logical since milk production directly impacts the income of the dairy farmer. Selection for milk yield, however, has negatively affected overall health and fertility traits (Goddard, 1998; Dechow et al., 2004a; van der Waaij, 2004). The extent to which the selection for one trait results in the selection for the other is measured as the genetic correlation.

Genetic correlations between traits can arise from either pleiotropy or physical linkage between genes. Pleiotropy is the phenomenon where one gene influences multiple phenotypic traits (Falconer and Mackay, 1996). If one phenotypic trait

controlled by that gene is more strongly expressed in a given environment, the genetic correlation between traits will change when environments are changed. Genetic linkage refers to two genes being in close proximity to one another on the same chromosome. This typically results in the genes staying together through meiosis, and being inherited together. Genetic correlations between traits may also change if the genotype is altered through selection, as genes with favorable effects on both traits quickly move toward fixation and genes that may be favorable for one trait but unfavorable for a second trait remain segregating (Lynch and Walsh, 1998).

Often, traits compete for a limited number of resources. For example, a cow has limited intake capacity, and must partition those resources between lactation, growth, maintenance, and reproduction. The increase in milk yield at the expense of reproductive performance in recent years indicates that selection has favored animals that prioritize lactation. If resources are restricted more than usual, the competition between traits will increase. So, the least amount of competition between traits occurs when resources are most abundant, and the genetic correlations between traits will be different depending on the level of trait competition (van der Waaij, 2004)

It has been reported that when the correlation of a trait's expression in two different environments is higher than 0.70, breeding programs in each environment could increase genetic gain by changing their breeding goals to one joint breeding goal. Doing so will improve performance in both environments simultaneously (Horan et al., 2005).

Typically, estimated genetic correlations across environments are used to detect GxE interactions by estimating the degree of re-ranking between those two environments (Banos et al., 1990; Lynch and Walsh, 1998; Weigel et al., 1999; Zwald et al., 2001;

Cerón-Muñoz et al., 2004; Beerda et al., 2007). This technique operates under the assumption that different genotypes should be ranked identically when the environmental effect is equal to zero. So, a genetic correlation of less than one between identical traits in different environments indicates that the environment is affecting the expression of the genotype (phenotype) and indicates a GxE interaction (Hayes et al., 2003; Zwald et al., 2003b; Cerón-Muñoz et al., 2004).

Using this method, the characterization of GxE interactions depends on the identification and characterization of advantageous and non-advantageous environments. Therefore, it is important to know which environmental factors result in higher performance. It is also important to know if sires selected based on progeny performance in better managed herds produce offspring well suited to perform in advantageous environments, but which are unable to withstand challenging conditions that may be found in poorer management situations (Legates and Verlinden, 1956).

In addition to genetic correlation, heritability is useful for analyzing GxE interaction. Heritability is a measure of the amount of phenotypic variation in a population that can be attributed to genetic variability. Heritability analyses aim to estimate to what extent genetic factors contribute to the overall phenotypic variation in the population. High heritability estimates indicate that most of the phenotypic variation in the population is due to differences in genotype. A low heritability indicates that there are other factors besides genotype that are affecting the phenotypic variation, namely environment.

Environments have traditionally been defined by country, region, and herd phenotypic performance. Variables reported to be associated with GxE interaction, as

evidenced by increased heritability and genetic variance across environments, include the within herd milk yield standard deviation, average peak milk yield, temperature, and rainfall (Dong and Mao, 1990; Veerkamp, 1998; Cromie et al., 1998; Zwald et al., 2001). High standard deviations in milk yield indicate that genotypes are able to be fully expressed, and are indicative of a good production environment. Herds with high phenotypic variability in milk yield have been reported to have higher heritability for milk yield (0.33) than herds with low yield variability (0.28) (Cerón-Muñoz et al., 2004; Banos et al., 2005). Typically, herds with high peak milk yields show increased heritabilities (Dong and Mao, 1990) and genetic variance of milk yield (Fikse et al., 2003) compared to herds with low peak milk yields. Rainfall and temperature are also associated with decreases in milk production as measures of possible heat stress and high humidity. High levels of average yearly rainfall and high maximum monthly temperatures have been reported to result in decreased heritability estimates (Zwald et al., 2003b).

Environmental interactions are growing increasingly important since many breeding programs are international (Mulder et al., 2005). Currently, the International Bull Evaluation Service calculates sire evaluations using the multiple-trait across country evaluation procedure. This system relies on political boundaries since the input data comes from national evaluations from the participating countries (Zwald et al., 2003b). It is possible, however, that herds close to each other geographically, but across a border, may be more similar in production environment than herds far apart within the same country (Weigel et al., 1999).

GxE Interaction in Grazing Versus Confinement Systems

One situation where environmental differences are clearly evident is in the importation of North American Holstein genetics to South American countries and Australia/New Zealand. North America features a large proportion of confinement systems, which favor cows that produce the most milk when provided with maximal energy input (Fatehi et al., 2001). In confinement herds, heritabilities for milk production traits range from 0.19 to 0.42 for milk, fat and protein (Batra et al. 1987; Kearney et al., 2004; Hammami et al. 2008). It has been reported that heritabilities for milk yield increase linearly with herd average milk yield (Powell et al., 1983; Van Vleck et al., 1985). This difference, possibly, is the result of a more complete expression of the true genetic potential in the best environment (Powell et al., 1983; Dong and Mao, 1990; Cerón-Muñoz et al., 2004).

South America and Australia/New Zealand feature mainly management intensive rotational grazing herds, where animals that can produce somewhat high levels of milk with limited energy input are favored (Fatehi et al., 2001). The concern is that genetic evaluations of sires with daughters in one environment may not accurately represent daughter performance in the other. Variable daughter performance across environments has significant economic implications for the farmer, as unfavorable GxE interactions lead to unequal gains in selection in the different environments (Raffrenato et al., 2003).

Grazing herds have had heritability estimates for production traits similar to those of confinement herds. Haile-Mariam et al. (2008) reported heritabilities of 0.27, 0.22, and 0.22 for milk, fat, and protein yield, respectively, in Australian grazing herds. Kearney et al. (2004) reported similar, but slightly lower, heritabilities of 0.19, 0.19, and

0.17 for milk, fat, and protein in grazing herds in the US. Boettcher et al. (2003) reported a heritability estimate for milk of 0.31 in grazing herds and 0.37 in Canadian grazing and confinement herds, respectively. Fahey et al. (2007) reported heritability estimates of mature equivalent milk yield ranging from 0.14 to 0.18 in grazing herds and 0.14 to 0.20 in confinement herds, depending on level of production in eleven US states. Heritability estimates for mature equivalent fat and protein were also similar in this study, and ranged between 0.15 and 0.25 for both traits.

While heritability estimates appear to be similar when comparing grazing versus confinement systems, significant interactions of genotype and environment are still evident. Genetic correlations for 305 d milk yield between North America and South American countries have been reported to range from 0.6 to 0.93 (König et al., 2005). In a study where herds were grouped into clusters according to environment and production characteristics such as temperature, peak yield, and persistency, the cluster containing mostly New Zealand herds had a 0.68 genetic correlation with the cluster that contained a majority of North American herds for milk yield (Zwald et al., 2003a). Genetic correlations between North America and Australia for 305 d milk yield of Guerseys have been reported to be 0.87 (Fikse et al., 2003).

GxE interactions have also been demonstrated using regression on sire predicted transmitting abilities (PTA). The regression of milk yields for individual cows on their sire PTA for milk yield was reported to be 0.78 in grazing herds and 0.99 in confinement herds (Kearney et al., 2004), indicating that for every one kg increase in sire genetic merit for milk yield, cows in grazing environments only increased milk production by 0.78 kg. Likewise, regressions of fat and protein yield on sire PTA for fat and protein production

were 0.76 and 0.78 in grazing herds, compared to 0.96 and 0.98 in confinement herds, respectively. Genetic correlations between milk, fat, and protein production were 0.89, 0.88, and 0.91, respectively, between confinement and grazing herds (Kearney et al., 2004). These results indicate that fat is the production trait most affected by GxE interaction, which is in agreement with previous studies (Cromie et al., 1998; Weigel et al., 1999; Kennedy et al., 2003).

Differences in gene expression across environments are important because they can lead to re-ranking of sires in terms of total economic net merit, which includes production, as well as health and productive life traits. A bull with high genetic merit for yield but average for fertility will likely produce more economical daughters than a high fertility and moderate yield sire in a confinement herd; however, it is possible for the economic merit of the sires to re-rank in a seasonal grazing herd because the response to selection for yield will be less and fertility will be extremely important.

Level of concentrate feeding has also been shown to affect genotypic expression. Cromie et al. (1998) reported that heritabilities for milk, fat, and protein were different between high concentrate and low concentrate herds. That study also reported that milk and fat production had heritabilities of 0.43 and 0.38 in high input environments compared to 0.29 and 0.24 in low input environments

Response of Milk Yield to Feeding Level

The primary purpose of livestock is to convert feedstuffs not suited to human consumption into desirable food products. Feed costs represent a large proportion of the

variable cost of milk production, making genetic improvement in feed efficiency economically important (Veerkamp, 1998).

Dry matter intake is the most important factor in an animal's level of production, with genetic correlation between intake and milk production reported between 0.39 and 0.61 depending on stage of lactation (Veerkamp et al., 1999). In addition to milk production, the intake levels are important for maintenance, reproduction and growth. An important aspect of feed intake is the efficiency of energy utilization. Genetic correlations between production and feed efficiency range from 0.71 to 0.95 (Lamb et al., 1977; Korver et al., 1988). Heritabilities for feed efficiency have been reported between 0.40 and 0.63 (Hooven et al. 1968; Lamb et al., 1977; Blake et al., 1984).

Efficiency is also dependent on the genetic ability of the cow to use those inputs for milk production (Blake et al., 1984). Studies have shown that diets with low energy density reduce dry matter intake and overall production as much as 9.6 kg ECM/d (Beerda et al., 2007) when compared with a high energy density ration, mainly due to decreased protein yield. These results are typical, as it has been shown that feeding a low-density ration with low concentrate levels will decrease DMI (Donker et al., 1983; Kennedy et al., 2003). Genetic correlations between efficiency and production, efficiency and body weight, and body weight and production have been reported to be 0.92, -0.17, and 0.28 respectively (Hooven et al., 1968).

Since underfeeding and low genetic ability will both limit milk production, feed efficiency needs to be considered from both an environmental and genetic standpoint. In order to perform genetic analysis of feed efficiency, individual feed intakes need to be measured. Cows in many studies are fed according to milk yield, which forces a high

correlation between yield and feed efficiency (Custodio et al., 1983). Because of this trend, in many cases, perceived differences in efficiency are accounted for by differences in milk-yield (Hickman et al., 1971; Lamb et al., 1977). In studies dealing with this correlated response, energy efficiency showed linear increases when regressed on cow transmitting ability for fat corrected milk (Custodio et al., 1983).

Several studies have evaluated the interaction between feeding level and genotype. Macdonald et al. (2008) evaluated the production traits of animals with a high proportion of North American Holstein-Friesian genes in pastoral systems in New Zealand, and reported that these animals require higher levels of feed than animals selected to excel in pastoral systems. Sehested et al. (2003) reported that eliminating concentrate supplementation in high genetic merit cows in Danish organic dairy herds reduced DMI from 6,226 to 4,770 kg per lactation and reduced milk yield from 6723 to 5090 kg of ECM per lactation over a three year period, while cutting concentrate supplementation in half only slightly depressed intake and milk yield. Veerkamp et al. (1994) reported that no feeding system by genetic line interactions were significant in cows that were fed different levels of concentrate, but regression coefficients of breeding value indicated the presence of GxE interactions for milk and component yields. Cows in Australian grazing herds have also been reported to show limited responses to breeding value change when fed a low level of concentrates, while cows fed a medium amount of concentrates showed an increased response, and cows fed at a high level of concentrates showed the highest responses in milk production (Fulkerson et al., 2008). These results indicate that in low concentrate feeding groups, production is being limited by the environment more than genetic ability for milk yield. Body size has also been considered as a factor influencing

reaction to feeding regime. It has been reported that large and small cows selected to have similar genetic potentials for milk production both performed well at high levels of concentrate feeding, but that small animals actually produced more milk per unit of body weight at low levels of concentrate supplementation than genetically similar large animal (Donker et al., 1983).

Response of Milk Yield to Cow Comfort

There are many factors associated with the comfort level of a cow. One indicator is hock lesion scoring, which measures the damage done to the cow's hocks from lying on hard surfaces (Fulwider et al., 2007). In tie-stall situations, adequate, uniform bedding in each stall is important because the animal does not have the opportunity to choose a lying environment. Bedding and overall comfort is of particular concern when animals are transferred from pasture into a tie-stall situation. Hock lesions may form within 3 to 6 weeks if the stalls are not properly bedded (Tucker et al., 2009). Hock lesions have been shown to negatively impact milk production by decreasing dry matter intake (DMI). Intake losses accumulated over the lactation have been reported to result in 46 kg less intake. This lower intake resulted in a loss of 108 kg of milk over the course of the lactation (Bareille et al., 2003).

Bareille et al. (2003) reported that hock lesions first form at a median of 36 DIM, and recurred at 66 DIM. They also reported that most incidences of hock lesions occur in the first lactation (25.4%), and then decrease in second lactation (15.9%) and third and later lactations (12.4%). This decrease in subsequent lactations is likely due to the fact

that animals with poor performance in first lactation are more likely to be culled, and therefore will not have a second lactation.

Lameness in dairy herds increases culling levels, results in poorer milk yield, poorer reproductive performance, increased labor, and higher treatment costs. Production losses due to lameness could reach 2.8 kg/cow/day during an incidence of clinical lameness. These production losses persist, with an average loss of 1.1 kg/cow/day for the remainder of the lactation (Rajala-Schultz et al., 1999).

Overall, health problems account for 79.5% of all culls in the US and 74.5% of all culling in Pennsylvania. Foot and leg problems account for approximately 4.4% of culls nationally and 5.5% in Pennsylvania (Hadley et al., 2006). It is possible that foot and leg problems are indirectly responsible for a much higher proportion of culls because they negatively impact performance in lactation and reproduction. Locomotion problems decrease DMI, which decreases milk production, limits reproductive performance, and could also lead to injury due to altered gait. Damaged skin from hock lesions also provides an entry point for bacteria and viruses that cause infection. In fact, it has been reported that lameness was more strongly associated with poor reproductive performance than any other disease, including reproductive diseases (Domecq et al., 1997).

Hygiene scoring is another method of measuring cow comfort. Somatic cell count (SCC) increases with udder hygiene score, as pathogens are able to enter the udder during milking (Schreiner et al. 2003). It has been reported that the heritability of SCC increases as days in milk increases (Haile-Mariam et al., 2001; Calus et al., 2006). This increase in heritability through lactation indicates that more of the variation in SCC in early lactation

results from environmental factors. So, a low hygiene score is most important in early lactation.

Body Weight and Body Condition Score

Body size is an important factor to consider because it is related to potential productivity and efficiency of feed utilization. It has been suggested that measures of body size should include measures of skeletal size, body condition and body weight (Hickman et al., 1971). It has been reported that intake capacity (as indicated by body frame size) is positively correlated with a high level of intake (0.81) allowing for higher levels of milk production (Veerkamp et al., 1999). However, larger body size is associated with lower feed efficiency at a given level of production because larger animals have higher maintenance energy requirements. This lower efficiency is reflected in the AIPL (2009) net merit index, which places a negative weight on body size.

Body weight is the most common measure of body size. Heritabilities have been reported between 0.39 and 0.61 (Berry et al., 2002; Berry et al., 2003a; Berry et al., 2003b). Body weight gain and feed consumption heritabilities have been estimated at 0.17 and 0.23, respectively, and the genetic correlation and phenotypic correlations between body weight gain and feed consumption have been estimated at 0.44 and 0.27, respectively (Lee et al., 1992). Heritability estimates for body energy content have been shown to increase with days in milk, with heritability being maximized near the end of lactation (Banos et al., 2005).

Body weight is a difficult trait to measure in commercial production situations, as animal scales are often not available. Therefore, equations that use other body

measurements to estimate body weight are useful. Heinrichs et al. (1992) demonstrated that heart girth was more highly correlated with body weight than wither height, hip width and body length. Heart girth circumference is highly heritable with an estimate of 0.66 (Hickman et al., 1971).

Body condition is a measure of the amount of fat carried on the frame of the animal, as determined by visual observation and palpation. Importantly, body condition score is not correlated with frame size or body weight (Wildman et al., 1982).

Heritability estimates for BCS have been reported between 0.14 and 0.37 (Berry et al., 2002; Dechow et al., 2004a; Dechow et al., 2004b, Lassen and Mark, 2008). Change in body weight over the course of lactation has lower heritability, reported between 0.02 and 0.10 (Berry et al., 2002).

Body condition scores have been reported to impact cow health, reproduction, and feed efficiency at the phenotypic level (Dechow et al., 2004a; Dechow et al. 2004b; Beerda et al., 2007). Increases in genetic merit for milk yield are strongly correlated with increases in feed intake (Veerkamp et al., 1999). However, this extra intake does not fully compensate for the increased energy demands of early lactation in a high producing animal. The result is that the animals mobilize their energy reserves to make up the differential (Van Arendonk et al., 1991).

Negative genetic correlations (-0.39 to -0.46) have been reported between milk yield and loss of body weight in early lactation (Lee et al., 1992; Veerkamp et al., 1999), indicating that animals that mobilize body tissue in early lactation are able to support a higher level of milk production during that period. A similar trend has been reported for body condition score, meaning that a strong ability to mobilize body reserves occurs in

response to selection for high production levels (Veerkamp et al., 1999; Berry et al., 2002). Extended periods of negative energy balance have been reported to negatively impact health and reproduction issues (Beerda et al., 2007; Oikarinen et al., 2008).

Genetic correlations between milk, fat, and protein yield and BCS are negative (Veerkamp et al., 1997; Berry et al., 2002). Body condition during the lactation has a negative phenotypic relationship with yield traits because cows that are more efficient producers direct more nutrients toward milk and less towards body reserves during lactation (Wildman et al., 1982; Veerkamp et al., 1997).

General Summary

There are many factors that may contribute to GxE interactions. Previously, GxE studies have focused on factors associated with international boundaries, regional environmental differences, or differences between grazing and confinement feeding systems. Fine level information, or information related to specific aspects of feeding and cow management would help to explain response to selection in specific management environments and lead to the most appropriate selection strategies.

The objectives of this study were to collect fine level herd data such as feed intake, dietary composition, and cow comfort indicators in order to determine if these factors contribute to GxE interactions, and to estimate the differences in response to selection in environments defined by these variables.

CHAPTER 2

INTERACTION OF MILK, FAT AND PROTEIN YIELD GENOTYPE WITH FEEDING LEVEL AND INDICATORS OF COW COMFORT

2.1 INTRODUCTION

Typically, estimated genetic correlations across environments are used to detect GxE interactions by estimating the degree of sire re-ranking between two environments (Banos et al., 1990; Weigel et al., 1999; Zwald et al., 2001; Cerón-Muñoz et al., 2004; Beerda et al., 2007). A genetic correlation of less than 1 between identical traits in different environments indicates that the environment is affecting the expression of the genotype (phenotype) and indicates a GxE interaction (Hayes et al., 2003; Zwald et al., 2003b; Cerón-Muñoz et al., 2004).

The characterization of GxE interactions depends on the identification and characterization of advantageous and non-advantageous environments. Previous GxE studies have focused on national boundaries (Fikse et al., 2003; Zwald et al., 2003a), regional characteristics (Weigel et al., 1999), and overall management characteristics as measured by resulting production traits such as peak milk yield (Fikse et al., 2003).

Considerations of feed characteristics in these studies have generally been limited to differences between grazing and confinement herds. Results of these studies have generally shown that genetic expression of production traits is reduced in grazing environments. High genetic merit animals in grazing environments showed larger responses to high levels of concentrate supplementation and (Kennedy et al., 2003;

Kearney et al., 2004; Fulkerson et al., 2008). It has also been reported that fat yield is the most significantly affected production trait in grazing herds (Weigel et al., 1999).

The objectives of this study were to collect fine level herd data related to feed intake, dietary composition, and indicators of cow comfort, and to determine their interactions with sire PTA and IS.

2.2 MATERIALS AND METHODS

2.2.1 Data Collection

Feed intake, heart girth (**HG**), and body condition score (**BCS**) were recorded in 11 tie-stall herds in Pennsylvania from the fall of 2008 through the spring of 2009. Visits to all herds were conducted in September to record initial BCS and HG measurements, and to determine feeding schedules. Intake measurements began in October for 7 herds that had their cows inside during this month. The remaining 4 herds had their cows out on pasture during October, and their intake measurements began in November.

Individual feed intakes were measured once per month within 7 d of a DHI test date over a period of 6 consecutive months. BCS was assigned to all cows on all visits by a single research technician, and HG was measured for cows that were 0 to 60, 130 to 170, and 280 to 320 days in milk (**DIM**) on the day of each visit, in order to estimate body weights (Heinrichs et al., 1992). Blood samples were also collected from the coccygeal vein of all cows for DNA marker analysis.

The goal of this study was to measure 24 hour feed intake without disrupting the normal feeding routine of the farm. On day 1 of a visit, researchers arrived at the farm for the first AM feeding. The farmers completed all feedings in 30 minutes or less on most of the farms. This short time frame meant that precise measurement of the amount of feed offered to individual cows was not possible.

Eating behavior of the cows was observed for approximately 20 minutes after the completion of the first morning feeding. Cows that were making significant progress towards cleaning their bunks within this timeframe were characterized as having

aggressive (**AG**) feeding behavior. Farmers were instructed not to push feed from one cow to another when feed bunks were empty so that intakes could be accurately measured. Instead, researchers were responsible for moving feed from one cow to another. Moved feed was accounted for by determining the weight of an average shovel-full of feed for that visit, and recording how many shovels of feed were moved to and from each individual cow.

Each herd's general feeding practices (number of feedings per day, whether the herd fed TMR, how dry hay was fed, and whether the herd used a grain top-dress) are reported in Table 1. Ten out of the eleven farms fed a total mixed ration (**TMR**). Those farms either had a feed cart that was equipped with a scale, or a TMR mixer with a scale that unloaded into a feed cart. During feedings, the weight of feed in each cart was recorded and farmers were instructed to deliver TMR as evenly as possible. Each cow was assumed to receive the same amount of feed from the cart, but researchers followed the feed cart to weigh feed from cows that had not begun eating. This was done to make sure that feed was distributed evenly. If it was observed that the amount of feed delivered to a particular cow was much different than the others in the row, the researcher weighed that feed separately, and adjusted the amount offered to the other animals accordingly. This situation of uneven feeding was most common at the end of a row of cows.

In herds that fed hay to all cows, farmers delivered hay evenly, and the amount fed to individual cows was weighed randomly. In herds where hay was fed only to early lactation cows, hay was weighed individually. Herds that fed a grain top-dress used a feed scoop that delivered a known amount of feed. One herd did not feed TMR. That

herd fed corn silage, dry hay from square bales, dry hay from round bales, baleage, high moisture corn, and a grain mix, all separately. Hay was fed evenly to all cows, but hay from cows with a clear deviation was weighed individually. Silage, haylage, and high moisture corn were distributed evenly.

TMR samples were taken monthly and sent to Cumberland Valley Analytical Services, Inc. (Hagerstown, MD) for dry matter and nutrient analysis. If hay was fed in addition to TMR, a sample of each type of hay fed was analyzed once for each farm. If the type of hay changed during the course of the trial, then a new sample was taken and analyzed. Top-dressed grain mixes were also analyzed once for each farm, with the exception of one farm that changed grain mix during the trial period, for which each mix was analyzed. In the herd that fed components in place of TMR, baleage, high moisture corn and corn silage were sampled 3 times, hays were sampled twice, and supplements were sampled once. Results of the analysis were used to determine ration compositions for dry matter (**DM**), crude protein content, and energy density.

On day 2 of each visit, refusals were weighed individually on a portable scale, allowing direct comparison of refusal weights across farms. TMR and hay refusals were weighed separately. In cases where water bowls had overflowed overnight, researchers recorded the condition of the feed as either wet or very wet, since most of the refusal weight in those cases was moisture. Dry matter refusals (**DMR**) were calculated using the DM percentage of the feed obtained from nutrient analysis. Dry matter intake (**DMI**) for each animal was determined by subtracting DMR from the total weight of DM offered.

Test day milk, fat, and protein yield were obtained for all cows through September of 2009. Additionally, all previous lactation test-day records were obtained for cows in the trial and from herd-mates that were not in the herd during the trial, but were contemporaries during earlier lactations. Four percent fat corrected milk (**FCM**) was calculated using test-day milk and fat yields (NRC, 2001).

Records from cows born in 2000 or later and from cows in their seventh lactation or less were retained. Test-day records beyond 500 DIM were removed. The number of records and cows in each herd is shown in Table 2, and the averages for each variable by herd are presented in Table 3.

Cow comfort indicators were recorded once for each animal in each herd by a single research technician. Stall size (**SS**) was measured in cm². Udder hygiene score (**HygS**) was assigned by visual appraisal on a scale of 1 (clean) to 4 (dirty) (Ruegg et al., 2002). Hock lesion score (**HLS**) was assigned on a scale of 1 (mild) to 3 (severe) according to a system designed by James Nocek for Cornell Extension (FARM, 2009). In order to determine whether cows were at ease around people, a temperament scoring system was derived to determine cow reactions to voice and touch. A research technician stepped into the stall on the side where the cow was typically milked, spoke to the cow, and placed his hand on the cow's rump. The score (**TS**) was assigned on a scale from 1 to 4, with 1 corresponding to no response or casual turning of the head, and 4 representing cows that were extremely nervous, kicking, and attempting to avoid contact.

The final data set included intake data and test day records from 970 cows. A total of 3999 DMI records remained after edits. Historical records for an additional 739 animals were included in animal models in order to place past production in context with

herd-mates in an effort to avoid selection bias. The addition of these records brought the total number of animals to 1709, with 36,472 test-day records.

2.2.2 Data Analysis

Records for all traits were initially analyzed with a test-day model and results were then used to derive 305 d records for each trait. Daily milk, fat yield, protein yield, FCM, DMI, crude protein intake (**CPI**), and net energy for lactation intake (**NE_LI**) from 5 to 305 DIM were summed to generate standardized 305 d records, and the average of daily BW and BCS from 5 to 305 DIM was determined.

Sire predicted transmitting abilities (**PTA**) for milk (**PTAM**), fat (**PTAF**), and protein (**PTAP**) were available for all 970 cows in the trial through the Animal Improvement Programs Laboratory (AIPL, 2009). DNA was successfully extracted (QIAGEN, 2006) from blood for 881 cows, which were then genotyped by IGENITY[®] (2009). Cows were assigned an Igenity Score (**IS**) for milk (**ISM**), fat (**ISF**), and protein (**ISP**) where 1 is equivalent to the lowest and 10 is equivalent to the highest genetic potential for yield.

In order to identify factors resulting in GxE interactions, herds were assigned to high and low groups according to several measures of nutritional management, indicators of cow comfort, average cow BW, and BCS (Table 4). Nutritional factors used to stratify the herds included DMR at the end of the 24-h feeding period averaged across all cows and test days, average percentage of crude protein in the diet (**CP**) across test days, average energy density of the ration expressed as the net energy for lactation (**NE_L**) per kilogram of dry matter offered across test days, percentage of cows in the herd that ate

aggressively (AG), amount of dry hay fed separate from the TMR to cows averaged across all cows and test days (**HAY**), the proportion of cows with wet feed refusals (**WET**) and intakes of dry matter, crude protein and NE_L. Additionally, BW and BCS were averaged across all cows and test days. Cow comfort indicators were SS, measured in cm², HLS averaged across all cows, HygS averaged across all cows, and TS averaged across all cows.

The herds were split so that the high and low management groups contained an approximately equal number of records and each group had either 5 or 6 herds represented. Herds were separated into the high or low group based on the numerical value of the trait, regardless of whether the optimal value is high or low.

Milk, fat and protein yield records were first analyzed by regression on sire PTA or IS within the high and low group levels described in Table 4, followed by multiple trait animal models where yield in high and low groups were considered different traits. Regression models were also evaluated where records from all herds were analyzed simultaneously, with interactions of sire PTA or IS with the herd's average for each management factor included.

Single Factor Regressions

Milk, fat, and protein yield were regressed on their respective sire PTA and IS using ASREML (Gilmour et al., 2006) for records that were initiated or in progress during the study. Milk yield, fat yield or protein yield in high and low environments were treated as separate traits and regressed on either sire PTA or IS with the following model:

$$y_{ijkl} = Lact_{ij} + \beta_i GEN + PE_{ik} + HYS_{il} + \varepsilon_{ijkl}$$

Where y = 305-d milk, fat, or protein yield in herd environment i (i =high or low herd environment described in Table 4); $Lact$ = the fixed effect of lactation j for trait i , β = the fixed coefficient of regression of 305 d production for trait i on PTA or IS; GEN = sire PTA or IS for milk, fat, or protein yield; PE = the random permanent environment effect of cow k for trait i ; HYS = the fixed effect of herd year season l for trait i , and ε = random error. Statistical differences of regression coefficients in high or low environments were determined according to the method of Paternoster et al. (1998).

Multiple Trait Animal Models

Data were analyzed using animal models to estimate genetic standard deviations, heritabilities, and genetic correlations between FCM yield in alternate environments (Table 4). FCM was used in the animal models because it was assumed that analysis of a single yield trait would be sufficient to demonstrate the effect of management levels on genetic response and FCM is included in the DMI prediction equations used by NRC (2001). In contrast to the regression models, FCM from all prior lactations and from previous contemporaries were included in the analysis because second and later lactation cows remaining in the herd represented a selected group of cows. This makes the assumption that general herd management practices have remained relatively constant across lactations, which may not be true in all instances.

Two-trait models contained FCM in high and low environments treated as separate traits. Four-trait models contained FCM in high and low environments treated as separate

traits and either BW or BCS in high and low environments treated as separate traits.

Records were analyzed with the following model:

$$y_{ijkl} = Lact_{ij} + Animal_{ik} + PE_{ik} + HYS_{il} + \varepsilon_{ijkl}$$

Where y = 305-d FCM in high and low herd environment (two-trait models) or 305-d FCM plus BW or BCS in high and low herd environment (four-trait models); Lact = fixed effect of lactation j for trait i; Animal = random effect of animal k for trait i; PE_k = random permanent environmental effect of cow k for trait i; HYS = fixed effect of herd-year-season of calving l for trait i; and ε = random error.

Multi-variable regression models

Interactions of genotype with feeding management and cow comfort indicators were lastly evaluated with a series of multiple-variable regression models. The purpose of this final series of analyses was to more clearly estimate the effect of management factors on yield after accounting for other known herd management effects. The feeding management and cow comfort indicator herd averages used to group herds into the high and low management environments described in Table 4 were interacted with sire PTA or IS. 305 d milk, fat, and protein yield were analyzed with the following univariate model:

$$y_{ijk} = Lact_i + PE_j + HYS_k + \beta GEN + \sum_{x=1}^n \beta_x (GEN * FE) + \varepsilon_{ijk}$$

Where y = 305 d milk, fat, or protein yield; Lact = the fixed effect of lactation i; PE = the random effect of permanent environment for cow j; HYS = the random effect of herd-year-season of calving k; β = the coefficient of regression of 305 d yield of milk, fat or protein on PTA or IS; GEN = sire PTA or IS; β_x = the coefficient of regression of 305 d yield of milk, fat or protein on the interaction between GEN and FE; FE = herd average

DMR, CP, NE_L, Wet, Ag, Hay, SS, HygS, HLS, and TS; and ε = random error. FE was not included independently of GEN*FE because all cows within a HYS had the same FE, which also necessitated treating HYS as a random effect.

Initially, interactions for all of the nutritional and cow comfort indicators were included. The most insignificant FE term was sequentially removed from the model using a backwards elimination procedure until only interaction terms that approached significance ($p < 0.10$) remained.

Results for the multi-variable regression models were expressed as the difference of predicted means (Gilmour et al., 2006) for milk, fat, and protein yield between PTA levels 0 kg and 500 kg for milk, and 0 and 25 kg for fat and protein yield, or between IS levels of 1 and 2 for all production traits. For each of the sire PTA or IS levels, herd management factors were set to the lowest 10% and highest 10% of herd averages in the trial, while setting the other management factors in the model equal to the average values across all herds. Significance of the differences between yield at high and low levels of herd management were determined using a 2-tailed T-test at a 0.10 significance level.

2.3 RESULTS AND DISCUSSION

2.3.1 Production Variables

Test-day and 305 d standardized record averages and test-day nutritional parameters broken down by herd are reported in Table 3. The average standardized 305 d DMI was 6,329.3 kg across herds and ranged from 5,659.6 kg (herd 7) to 7,596.5 kg (herd 1). The average 305 d standardized FCM yield was 9,559.5 kg. The lowest yielding herd had 8,051.6 kg FCM (herd 7) while highest yielding herd had 11,917.9 kg FCM (herd 1). Since DMI is directly related to FCM production, it is in line with expectations that the herds would rank similarly for these two variables. This trend is an indication that 305 d DMI measurements were taken with at least a moderate degree of accuracy.

2.3.2 Feeding Levels

Average DMR, CP percent of the diet, and NE_L concentration of the diet were considered the primary indicators of feeding management for this study instead of intake levels. There is a part-whole relationship between genetic potential for yield and intake level because of a positive genetic correlation between yield and intake (Veerkamp, 1998; Toshniwal et al., 2008). Herds with higher yield may have higher intake because their cows are genetically inclined to eat more, rather than a management decision to feed cows at a higher level. Average DMR and diet nutrient content are therefore more direct indicators of feeding management independent of cow genotype.

Additionally, DMR is more directly comparable across farms because the same scale was used to measure DMR for all farms, but not the amount of feed delivered. Scales on feed carts could not be calibrated across farms, making it difficult to directly compare DMI results across herds, but intake comparisons among herd-mates are expected to be accurate. The average daily DMR across herds was 1.40 kg and varied between 0.61 and 2.35 kg. Average DMR was strongly associated with the proportion of cows that had no feed refusals, which ranged from 0 % of cows in herd 4 to 26 % of cows in herd 10, and averaged 11 % across all herds. Ranking herds by the percentage of cows with no refusals yielded an identical (but opposite) result to ranking by level of DMR. Since these variables gave identical results, only DMR was considered.

Levels of inclusion in the diet of CP and NE_L were derived from nutrient analysis and can also be directly compared across herds. Ruminally degradable and undegradable protein fractions were not considered separately to simplify analysis. CP averaged 16.6 % across herds, and ranged from 14.4 to 18.1 %. The herd that averaged 14.4 % CP (herd 11) had lower CP percentage in the TMR at each successive sampling date. Broderick et al. (2003) reported that animals fed a ration with 15.1 % CP showed significantly reduced FCM production compared with animals fed at 16.7 % CP, indicating that the low CP level in this herd could have been a major factor in this herd having one of the lower 305 d FCM production estimates. NE_L , calculated according to the OARDC equation ($NE_L = 0.0245 * TDN - .12$), averaged 1.651 Mcal/kg, with a range of 1.581 to 1.701 Mcal/kg between herds.

2.3.3 Single Factor Regressions

Coefficients of regression of daughter performance on sire PTA and IS are reported in Tables 5 and 6, respectively. The expectation of the coefficient for PTA regressions is 1 if there is no GxE interaction (Lynch and Walsh, 1998). IS results are more difficult to directly interpret in terms of GxE interactions, because the scale is from 1 to 10, as opposed to PTA which is in units of production. Regression coefficients for IS give information on the value, in terms of production, of a one point increase in IS. In this case, if the response is significantly higher in one of the groups, there is an indication that GxE interactions may be present.

Regression coefficients for PTAM, PTAF, and PTAP when herds were split by DMR were near 1 in herds with a high level of refusals, indicating that response to selection did not deviate from expectation. In herds a low level of refusals and a high proportion of cows with no residual feed, however, regression coefficients were 0.45, 0.34, and 0.34 for PTAM, PTAF, and PTAP, respectively, and were significantly different from the high DMR herds for PTAM and PTAP. These results give evidence that underfeeding is limiting the production of animals in the low herds. Low regression coefficients indicate that sire re-ranking is likely in these herds (Weigel 1999).

Regressions of fat yield on ISF when separated by DMR were in agreement with PTAM regressions, where a 1-point increase in ISF corresponded to 4.43 kg more fat in the high group, as opposed to only 0.16 kg in the low group. However, the same was not true of regression of milk yield on ISM. A higher milk production response (163.8 kg per point of ISM) was observed in herds fed to a low level of DMR, compared to herds fed a high level of DMR (114.6 kg per point of ISM), but differences were not significant. ISP

regression coefficients were also not significantly different in the high or low groups (1.38 kg vs. 2.26 kg in the high and low groups, respectively). Higher intake of dry matter and CP were also associated with a higher response to ISF, but not for ISM and ISP which were in the opposite direction but not significant.

Concentration of NE_L in the ration significantly affected protein production in the PTAP model. Herds that fed a more energy dense ration produced more protein. The trends for the PTAM and PTAF models were in the same direction, but were not significant. Higher NE_L was also associated with higher milk, fat, and protein production in the IS models, but results were not significant.

The WET variable was included in the analysis because it is possible that overflowing water cups could reduce feed quality and palatability. PTA regression coefficients indicated that herds with a higher proportion of wet refusals had values closer to 1 for all production traits. However, there was a significantly larger response in milk production in herds with a higher proportion of wet refusals according to the ISM regression. Herds with a high proportion of wet refusals also tend to be high producing herds. This may indicate that wet refusals result from more drinking activity in these herds to support higher levels of milk production.

Splitting herds by BW significantly affected milk and protein in the PTA models and fat production in the IS models. Herds with heavier cows generally exhibited higher levels of response to sire PTA and IS. High body weight could be associated with high production because larger animals have more intake capacity, and can support a higher plane of milk production (Blake and Custodio, 1984). The results of splitting herds by

BW and DMR are the same because, even though the herds ranked differently for those variables, the high and low groups contained the same herds.

Regression coefficients were higher in herds with higher HLS for both milk and protein in the PTA models, and higher in herds with high TS for fat in the IS model. These results were surprising, since high scores for these variables were considered less favorable. However, these results may reflect that animals producing at a high level experience more discomfort than a low producing animal, which may lead to more shifting in the stall, resulting in hock lesions, and a higher temperament score.

Overall, IS models found more significant differences in fat production, whereas the PTA models tended to have significant results for milk and protein. The more significant results for fat yield with IS could indicate that ISF were more accurate due to DGAT1. A lysine to alanine substitution at the centromeric end of chromosome 14, in the DGAT1 gene has been shown to significantly impact milk, protein, and especially fat production (Spelman et al., 2002). The IS score is generated in part from analysis of the DGAT1 gene, so it is unsurprising that IS models are sensitive to differences in fat production.

2.3.4 Animal Models

Four-trait animal models were used to determine the effects of nutritional management, body conformation, and cow comfort indicators on FCM production (Table 7). Genetic standard deviation and heritability estimates were compared among the high and low groups. High heritability estimates indicate that environmental factors are contributing a relatively small percentage of the observed phenotypic variation. The

group with a higher genetic standard deviation and higher heritability is considered to be the environment that allows greater expression of genetic potential for FCM. Standard errors for genetic standard deviation estimates were high, and none of the differences between groups were outside the range of the standard errors. However, the differences in genetic standard deviation for most separation criteria were in the direction of PTA and IS regression results, with higher genetic standard deviations in herds with high DMR, DMI, CPI, CP, NE_{LI}, NE_L, BW, BCS, SS, HLS, TS, and low HygS.

Heritability estimates for FCM yield in this study ranged from 0.12 to 0.46 with an average heritability of 0.26 across analyses. These values are consistent with previous literature, where heritability of FCM has been reported to be between 0.26 and 0.30 when multiple lactations are included (Seykora and McDaniel, 1983). Heritabilities were similar between high and low groups for a majority of the variables. However, there were substantially larger heritability estimates for FCM in herds that fed at high levels of CP, had drier refusals, fed more hay, had higher BCS, higher HLS, and low TS.

Genetic correlations between FCM in high and low environments are also reported in Table 7. Genetic correlations significantly less than 1 typically indicate the presence of a GxE interaction (Hayes et al., 2003; Zwald et al., 2003b; Cerón-Muñoz et al., 2004). Values in this study were associated with large standard errors, and the range often approached 1. However, AG, HygS, and TS were associated with the lowest genetic correlations. The number of animals in the high and low groups is very low compared to previous studies, which may have resulted in inaccurate values.

Body Weight and Body Condition Score

The average standardized 305 d BW for animals in this study was 655.6 kg. BCS averaged 3.18 across herds. BCS varied widely across herds, with herd averages ranging from 2.85 to 3.54. Four-trait animal models were used to estimate genetic correlations of FCM yield with BW and BCS (Table 8). Correlations between milk yield and live weight have been previously reported to be slightly negative, ranging from -0.9 to -0.14 (Veerkamp and Brotherstone, 1997; Toshniwal et al., 2008). Correlations in the current study were similar to values previously reported in the groups associated with high levels of DMR (-0.01), DMI(-0.22), CPI (-0.06), CP (0.02) and NE_LI (-0.10), and low HLS (0.00). However, correlations are more negative than previously reported in groups with low levels of DMR (-0.80), DMI (-0.49), CPI (-0.56), CP (-0.56), NE_LI (-0.45), and high HLS (-0.66). The differences between these groups indicate that large animals were more affected by low levels of DMR, CP and NE_L, as well as more affected by hock damage.

Genetic correlations between FCM and BCS were also strongly negative (Table 8) and showed similar results as the BW analysis, with more negative correlations associated with unfavorable levels of DMR, DMI, CPI, CP, NE_LI, and HLS. This result suggests that cows genetically inclined to direct nutrients toward increasing BCS and BW were particularly affected by low levels of nutrition, as defined by those variables.

2.3.5 Multiple Regressions

A limitation of the two and four-trait models is that in some cases it forced herds to be separated into two groups based on continuous variables. Because of this, the

difference between the lowest herd in the high group and the highest herd in the low group was often minimal. Separation of herds into more groups was not considered practical because of the limited number of animals in this trial. Separating herds into high and low groups according to just one management variable is also problematic, since observed results may stem from a different underlying characteristic that the herds shared. Multiple regression models were used to evaluate this possibility. Individual management effects were evaluated by setting all other values to the overall mean for that factor, and then generating predicted production values when that single variable was varied between a value that fell into the bottom 10 % and top 10 % of herd averages (Table 9). Predictions were generated for 305 d milk, fat, and protein production at low and high values of PTA (Table 10) and IS (Table 11). All variables considered in the single factor regressions (except intake variables) were included in the initial multiple regression models. Variables were then removed by a backwards elimination procedure based on a two-tailed T-test until all terms had an associated p-value less than 0.10. Removing insignificant terms allows the best predictors of production to be identified and quantified.

BW was not included in the final models since higher feeding levels are expected to result in higher BW, indicating that DMR and BW have a part-whole relationship as evidenced by the identical ranking of herds (Table 4). This study focuses on the management effect (feeding, comfort) rather than the outcome of that management (BW). So, BW was not included in the model to give a clearer indication of the feeding level effect.

Significantly different production responses were predicted between high and low levels of PTAM, PTAF and PTAP when levels of DMR were increased (Table 10). Increasing PTAM from 0 to 500 kg resulted in a change in predicted production of 603.1 kg at the 90th percentile of refusals, and a change in predicted production of 81.4 kg at the 10th percentile of refusals. This difference suggests that feeding to a higher level of refusals allows animals to more fully express their genetic potential for milk production than animals that were fed to a low level of refusals. These results are in agreement with previous studies that have also reported a difference in milk response among high and low genetic merit animals fed at different energy levels (Fulkerson et al., 2008; Beerda et al., 2007)

There are two different situations that could result in low refusal rates. The first possibility is that cows are not offered enough feed to support their particular level of production. In this case, production would be limited, since cows could not increase their intake to meet their energy requirements. The second possibility is that animals are offered lots of feed, but eat a high proportion of it in order to support higher levels of milk production. Since herds in this study with low levels of DMR tended to also have low levels of 305 d FCM production and have a high proportion of cows with 0 % DMR, it is likely that these animals were not fed adequately, which limited milk production.

Crude protein level in the diet tended ($p < 0.10$) to affect predictions of milk and fat production at different levels of PTA. High levels of CP in the diet corresponded to an increase in 584.0 kg of milk when PTAM increased from 0 to 500 kg, compared with an increase of only 270.5 kg at low levels of CP. Fat production response was predicted to be 24.1 and 6.5 kg when PTAF was increased from 0 to 25 kg at high and low levels of

CP respectively. These results agree with those reported by Olmos and Broderick (2006) where 3.5 % FCM production increased linearly over 5 feeding levels of CP ranging from 13.5 to 19.4 %, although diet was not a significant effect ($P = 0.17$). Fat yield (kg/d) and composition (%) also increased linearly over the 5 CP levels and were both significantly affected by diet ($P < 0.05$). Also, as in the current study, protein production was not affected by CP level.

Broderick (2003) reported that CP concentration in the diet affected milk, fat, and protein production, although protein production was only different at the lowest level of CP (15.4 %) and did not differ between CP concentrations of 16.7 % and 18.4 %. CP levels in the current study fell mostly in this upper range, so it is unsurprising that dietary CP concentration in the diet did not significantly predict protein production.

In the PTAP model, HLS significantly affected predicted protein production ($P = 0.052$). Increasing PTAP from 0 to 25 kg resulted in an increase in predicted production of 34.8 kg at the 90th percentile of HLS, and 12.9 kg at the 10th percentile of HLS. These results are opposite to those reported by Bareille et al. (2003), which showed that high HLS (more damage) is associated with losses in milk production, due to reduced DMI. Cows in the Bareille study were housed in a free-stall facility with pasture access in spring and summer months. Since mobility is important for maintaining high levels of DMI, high HLS may be associated with animals that are too lame to successfully compete at the feed bunk.

IS multiple regression models typically had more significant terms, and the only predictive variable shared between the two models was CP. DMR was not a significant

variable despite the fact that it was the most significant variable affecting production in the PTA models.

CP concentration in the diet significantly affected the response to selection for milk yield in this study. However, results were opposite to those found in the PTAM model. In the ISM model, higher CP levels in the diet were associated with a response to selection that was 100.7 kg lower than the response at the low CP levels when ISM was increased by 1. However, in this model, CP level was the least significant of 5 significant variables, with a p-value of 0.070.

A one-point increase in ISM, ISF, and ISP corresponded to increases of 205.1, 5.6, and 5.5 kg of milk, fat, and protein, respectively between high and low levels of NE_L density in the ration. These results are similar to the expected differences published by IGENITY[®] (2009), where production differences between IS scores 1 and 2 for milk, fat, and protein are reported to be 203.6, 6.4, and 4.0 kg, respectively. In situations where NE_L is fed at a low level in this study, predicted production was actually lower as IS increased. Animals eating a ration with low energy density may not be able to increase their intake enough to meet lactation energy requirements, causing production to suffer (Veerkamp and Brotherstone, 1997).

SS was a significant factor in the predicted production responses to selection for ISM and ISP. Contrary to expectations, smaller stalls were associated with higher responses to selection than larger stalls. Large stalls were actually associated with a decrease in milk and protein production when ISM and ISP score increased. However, stall comfort was not considered and could have varied significantly from SS in these herds.

Predictions were significantly different for high and low levels of ISM, ISF, and ISP with different levels of HygS. Animals with a low HygS (cleaner udder) were predicted to produce 241.5, 2.5, and 5.6 kg more milk, fat, and protein, respectively than cows with a higher HygS (dirtier udder). This result could be due to a mastitis effect, as high HygS has been shown to be associated with the increased presence of major and minor mastitis pathogens (Scheiner and Ruegg, 2003). Sub-clinical mastitis has been reported to decrease DMI and result in the loss of approximately 160 kg of milk throughout the course of lactation (Bareille et al., 2003), while clinical mastitis has been shown to negatively affect lactation performance, in addition to being a major reason for culling (Hadley et al., 2006; Feliciano et al., 1989). Moreover, cows in a clean environment may be more comfortable than cows in a dirtier environment.

Animals with high TS were predicted to produce significantly more milk and protein when ISM and ISP were increased. High scores for this variable indicate more agitated behavior. However, a high score in this variable may reflect discomfort associated with high levels of production.

2.4 CONCLUSIONS

Results of this study suggest that nutritional management factors affecting nutrient intake are associated with GxE interactions. In particular, cows in herds with low dry matter refusals appeared unable to fully express their production potential according to single and multiple factor regressions. This result is likely due to herds with low levels of overall refusals having a high proportion of animals with no refusals at the end of a 24-hour feeding cycle. In tie-stall situations where the goal is feeding to a low level of refusals, extra care should be taken to ensure that most animals are not left with empty bunks. Selection response also tended to be less optimal in environments with lower levels of protein and energy density in the ration, according to multiple factor regression models. Lower levels of intake of dry matter, crude protein, and energy, and poor hock lesions score appeared to limit genetic potential for yield more severely in large cows than in small cows according to animal models. Cow comfort factors may play a part in GxE interactions, but additional measures and a larger sample size is likely needed in order to quantify their impact.

2.5 Future Research Implications

Collecting intake data on commercial dairy farms led to many challenges associated with accuracy and consistency. All farms had different management systems in terms of times and frequency of feeding. This variation made scheduling visits a challenge. Cows were also able to push feed between stalls, which likely led to individual intakes being somewhat inaccurate. Placing dividers in the bunks between the animals would have reduced this variation, but the number of farms in the trial would have made it very difficult to install the equipment, and it would have interfered with the normal feeding routine of the farmer. Due to the amount of labor involved in data collection, it would be infeasible to add more farms without adding technicians. More technicians in the trial means that more time could have been spent on each farm, but then variation between technicians would have to be considered. Using fewer farms may have allowed for more precise measurements, but the variation in the ensuing genetic analysis would be greater with less animals.

APPENDIX 1: Data Tables

Table 1. Summary of general herd feeding practices

Herd	TMR	n TMR feedings	Dry hay	Grain Top Dress ¹
1	Yes	5	Fed separately from TMR to all cows	No
2	Yes	4	None	No
3	Yes	2	Fed separately from TMR to fresh cows	Yes / Varied
4	Yes	4	Fed separately from TMR to all cows	Yes / Varied
5	No	0	Fed to all cows	Yes / Varied
6	Yes	2	None	No
7	Yes	3	None	No
8	Yes	2	Fed as part of TMR to all cows	No
9	Yes	2	Fed separately from TMR to all cows	Yes / Varied
10	Yes	2	Fed separately from TMR to all cows	Yes / Even
11	Yes	2	Fed separately from TMR to all cows	No

Table 2. Number of test day observations and records of dry matter intake (DMI), body weight (BW), body condition score (BCS), and cow comfort indicators (CC) for each herd

Herd	1	2	3	4	5	6	7	8	9	10	11	Total
n cows ¹	90	111	111	41	61	178	64	47	86	108	69	970
n cows ²	154	172	208	67	126	310	121	91	161	189	110	1,705
n Records ³	3,570	4,085	4,262	1,439	2,439	6,713	2,536	1,468	2,997	4,095	2,868	36,472
n DMI	391	537	427	158	265	639	275	201	327	459	320	3,999
n BW	190	268	273	79	157	416	136	101	164	246	165	2,195
n BCS	455	625	592	180	312	926	324	236	431	547	370	4,998
n CC ⁴	75	100	102	30	46	140	54	32	60	84	57	780

¹ Does not include animals with only historical records

² Includes all cows, including those with historical records

³ Includes historical records

⁴ Stall size, hock lesion score, hygiene score, and temperament score

Table 3. 305 d standardized lactation averages of dry matter intake (DMI), fat corrected milk (FCM), milk yield (MY), fat yield (FY), protein yield (PY), body weight (BW), and body condition score (BCS), and test day averages for dry matter refusals (DMR), dietary crude protein (CP), and energy density of the ration (NE_L) by herd

Herd	1	2	3	4	5	6	7	8	9	10	11	Average
DMI, kg	7,596.5	5,844.3	6,098.3	6,135.9	6,119.8	6,186.4	5,659.6	6,500.5	6,484.5	6,273.1	6,723.7	6,329.3
FCM, kg	11,917.9	9,880.1	9,929.7	8,927.3	8,078.2	9,271.8	8,051.6	9,071.8	10,622.5	10,524.1	8,879.3	9,559.5
MY, kg	11,580.9	10,241.8	10,118.2	9,813.2	8,345.0	10,174.1	9,383.2	9,324.5	9,324.5	11,280.9	8,865.9	9,859.3
FY, kg	394.2	378.5	388.6	372.1	317.6	347.1	313.0	353.3	430.4	420.5	358.5	370.3
PY, kg	335.5	322.5	307.6	304.3	250.8	301.7	278.1	286.8	330.8	339.0	262.2	301.8
BW, kg	660.2	650.7	705.0	669.4	627.5	671.5	628.7	664.1	678.5	633.5	623.0	655.7
BCS	3.04	3.31	3.49	3.24	2.85	3.04	3.07	3.54	3.34	3.1	2.98	3.18
DMR ¹ , kg	1.54	1.20	1.68	2.35	1.10	1.62	1.28	1.52	1.50	0.97	0.61	1.40
CP ¹ , %	16.4	16.6	16.0	15.6	18.1	16.0	16.9	16.9	17.2	17.9	14.4	16.55
NE _L ¹ , Mcal/kg	1.672	1.616	1.701	1.671	1.581	1.659	1.661	1.613	1.683	1.676	1.625	1.651

¹ Test Day Records

Table 4. Summary of herds included in high (H) and low (L) groups for each management indicator

Herd	1	2	3	4	5	6	7	8	9	10	11
Trait ¹	Nutritional Management Factors ²										
DMR, kg	H	L	H	H	L	H	L	H	H	L	L
DMI, kg	H	L	L	L	L	H	L	H	H	H	H
CPI, kg	H	L	L	L	H	L	L	H	H	H	L
CP, %	L	L	L	L	H	L	H	H	H	H	L
NE _L I, Mcal	H	L	L	L	L	L	L	H	H	H	H
NE _L , MCal/kg	H	L	H	L	L	H	H	L	H	L	H
WET, %	H	H	H	L	H	H	L	H	L	L	L
AG, %	L	L	H	H	H	H	L	H	L	L	H
HAY, kg	L	L	L	L	H	L	L	H	H	H	H
	Body Composition										
BW, kg	H	L	H	H	L	H	L	H	H	L	L
BCS	L	H	H	H	L	L	L	H	H	L	L
	Cow Comfort Indicators										
SS, cm ²	H	H	L	H	L	L	L	L	H	L	H
HLS	H	L	H	H	L	L	L	L	H	H	L
HygS	L	L	H	L	H	H	H	L	L	L	H
TS	H	H	L	L	H	H	L	L	H	L	L

¹DMR = Dry matter refusals; DMI = Dry matter intake; CPI = Crude protein intake; CP = Dietary crude protein inclusion rate; NE_LI = Net energy for lactation intake; NE_L = Energy density of the ration; WET = Percentage of cows with wet feed refusals; AG = Percentage of cows that exhibited aggressive eating behavior; HAY = Average amount of hay offered to cows; BW = Body weight; BCS = Body condition score; SS = Area of the stalls; HLS = Hock lesion score; HygS = Udder hygiene score; TS = Temperament score

Table 5. Coefficients of regression of 305 d milk, fat, and protein on sire predicted transmitting ability of milk (PTAM), fat (PTAF), and protein (PTAP) in high (H) and low (L) management groups with standard errors generated using single factor regression models

Trait ¹	Group	PTAM	SE	PTAF	SE	PTAP	SE
Nutritional Management Factors							
DMR, kg	H	1.03*	0.20	0.87	0.19	1.23*	0.21
	L	0.45*	0.21	0.34	0.21	0.34*	0.20
DMI, kg	H	0.56	0.19	0.60	0.20	0.68	0.20
	L	1.04	0.22	0.58	0.20	1.07	0.22
CPI, kg	H	0.97	0.24	0.85	0.25	0.90	0.24
	L	0.72	0.19	0.63	0.18	0.90	0.19
CP, %	H	1.04	0.23	0.76	0.24	0.85	0.24
	L	0.72	0.19	0.63	0.18	0.89	0.19
NE _L I, Mcal	H	0.53	0.24	0.70	0.26	0.61	0.24
	L	0.97	0.19	0.71	0.17	1.05	0.19
NE _L , Mcal/kg	H	1.10	0.25	0.87	0.24	1.33*	0.24
	L	0.63	0.18	0.55	0.17	0.58*	0.19
WET, %	H	0.87	0.19	0.76	0.18	0.97	0.19
	L	0.56	0.23	0.44	0.24	0.61	0.23
AG, %	H	0.77	0.18	0.73	0.18	0.96	0.19
	L	0.70	0.24	0.55	0.23	0.66	0.24
HAY, kg	H	0.61	0.20	0.69	0.24	0.62	0.21
	L	0.95	0.20	0.66	0.18	1.03	0.20
Body Conformation Factors							
BW, kg	H	1.03*	0.20	0.87	0.19	1.23*	0.21
	L	0.45*	0.21	0.34	0.21	0.34*	0.20
BCS	H	1.04	0.22	0.87	0.22	1.37*	0.22
	L	0.53	0.20	0.43	0.19	0.52*	0.20
Cow Comfort Indicators							
SS, cm ²	H	0.75	0.23	0.51	0.23	0.76	0.22
	L	0.85	0.19	0.76	0.18	0.99	0.20
HLS	H	1.30*	0.24	1.00	0.23	1.43*	0.23
	L	0.61*	0.18	0.55	0.17	0.60*	0.19
HygS	H	0.64	0.21	0.63	0.19	0.74	0.21
	L	0.90	0.21	0.70	0.21	0.97	0.20
TS	H	0.77	0.20	0.59	0.19	0.72	0.20
	L	0.62	0.21	0.64	0.22	0.95	0.22

¹ DMR = Dry matter refusals; DMI = Dry matter intake; CPI = Crude protein intake; CP = Dietary crude protein inclusion rate; NE_LI = Net energy for lactation intake; NE_L = Energy density of the ration; WET = Percentage of cows with wet feed refusals; AG = Percentage of cows that exhibited aggressive eating behavior; HAY = Average amount of hay offered to cows; BW = Body weight; BCS = Body condition score; SS = Area of the stalls; HLS = Hock lesion score; HygS = Udder hygiene score; TS = Temperament score

* High and low groups are different at $p < 0.05$ (Paternoster et al., 1998)

Table 6. Coefficients of regression of 305 d milk, fat, and protein on IGENITY® score for milk (ISM), fat (ISF), and protein (ISP) in high (H) and low (L) management groups with standard errors generated using single factor regression models

Trait ¹	Group	ISM	SE	ISF	SE	ISP	SE
Nutritional Management Factors							
DMR, kg	H	114.6	39.2	4.43*	1.39	1.38	0.85
	L	163.8	41.2	0.16*	0.88	2.26	0.88
DMI, kg	H	111.9	38.2	3.68*	1.03	1.59	0.85
	L	184.0	41.2	0.57*	1.13	2.04	0.89
CPI, kg	H	138.6	42.8	4.49*	1.15	1.36	0.98
	L	135.5	37.9	0.78*	1.03	1.97	0.79
CP, %	H	180.1	51.6	2.63	1.36	2.15	1.11
	L	116.5	34.0	2.50	0.95	1.51	0.74
NE _L I, Mcal	H	140.1	43.2	3.64	1.16	1.63	0.98
	L	135.6	38.1	1.46	1.04	1.83	0.79
NE _L , Mcal/kg	H	147.6	40.4	3.75	1.01	2.11	0.88
	L	133.2	39.4	1.58	1.17	1.48	0.86
WET, %	H	192.2*	33.0	1.35	0.91	2.43	0.75
	L	64.4*	43.2	3.71	1.15	1.19	0.92
AG, %	H	108.0	41.0	3.81	1.07	1.52	0.83
	L	168.1	39.9	1.76	1.10	1.98	0.92
HAY, kg	H	119.6	47.0	3.40	1.30	1.22	1.02
	L	146.8	35.5	2.01	0.97	1.99	0.77
Body Conformation Factors							
BW, kg	H	114.6	39.2	4.29*	1.06	1.38	0.85
	L	163.8	41.2	0.20*	1.12	2.26	0.88
BCS	H	123.9	42.9	2.80	1.29	1.16	0.94
	L	148.6	38.0	2.39	0.97	2.32	0.82
Cow Comfort Indicators							
SS, cm ²	H	179.2	37.6	2.80	1.14	2.05	0.88
	L	104.0	41.1	2.42	1.07	1.55	0.85
HLS	H	147.6	40.4	3.49	1.04	2.11	0.88
	L	133.2	39.4	1.58	1.17	1.48	0.86
HygS	H	120.6	45.1	1.93	1.16	1.80	0.91
	L	151.2	36.3	3.07	1.06	1.76	0.83
TS	H	121.5	37.2	3.97*	1.08	1.42	0.84
	L	172.0	42.8	0.84*	1.09	2.15	0.91

¹ DMR = Dry matter refusals; DMI = Dry matter intake; CPI = Crude protein intake; CP = Dietary crude protein inclusion rate; NE_LI = Net energy for lactation intake; NE_L = Energy density of the ration; WET = Percentage of cows with wet feed refusals; AG = Percentage of cows that exhibited aggressive eating behavior; HAY = Average amount of hay offered to cows; BW = Body weight; BCS = Body condition score; SS = Area of the stalls; HLS = Hock lesion score; HygS = Udder hygiene score; TS = Temperament score

* High and low groups are different at p < 0.05 (Paternoster et al., 1998)

Table 7. Genetic standard deviations (σ_a), heritability estimates (h^2), and genetic correlations (r_g) of FCM in high (H) and low (L) management groups, generated using animal models

Trait ¹	Group	σ_a	SE	h^2	SE	r_g	SE
Nutritional Management Factors							
DMR, kg	H	2801.4	532.1	0.26	0.05	0.61	0.29
	L	2527.4	545.0	0.22	0.07		
DMI, kg	H	2863.9	554.6	0.25	0.06	0.75	0.29
	L	2464.3	523.8	0.21	0.07		
CPI, kg	H	2812.1	600.3	0.32	0.07	0.48	0.29
	L	2626.4	508.2	0.20	0.06		
CP, %	H	2758.6	597.5	0.37	0.07	0.66	0.28
	L	2665.0	503.0	0.16	0.05		
NE _L I, Mcal	H	2807.0	601.2	0.33	0.07	0.70	0.28
	L	2626.0	497.6	0.17	0.05		
NE _L , MCal/kg	H	2836.4	504.1	0.23	0.01	0.95	B ²
	L	2470.4	511.2	0.25	0.01		
WET, %	H	2657.8	496.6	0.14	0.05	0.55	0.27
	L	2772.0	613.3	0.43	0.07		
AG, %	H	2540.5	500.1	0.22	0.06	0.39	0.29
	L	2888.3	594.9	0.31	0.07		
HAY, kg	H	2651.0	581.5	0.38	0.07	0.76	0.26
	L	2724.5	510.6	0.16	0.05		
Body Conformation Factors							
BW, kg	H	2837.1	558.7	0.28	0.06	0.60	0.29
	L	2525.9	529.7	0.22	0.07		
BCS	H	2756.4	530.3	0.46	0.02	0.89	B ²
	L	2667.4	489.6	0.09	0.00		
Cow Comfort Indicators							
SS, cm ²	H	2820.5	613.7	0.34	0.07	0.47	0.26
	L	2629.4	494.1	0.18	0.05		
HLS	H	2733.3	580.1	0.39	0.07	0.46	0.30
	L	2641.4	504.6	0.14	0.05		
HygS	H	2659.9	406.8	0.12	0.00	0.27	0.31
	L	2788.7	571.1	0.33	0.06		
TS	H	2864.6	559.6	0.23	0.06	0.15	0.25
	L	2512.0	531.8	0.41	0.07		

¹ DMR = Dry matter refusals; DMI = Dry matter intake; CPI = Crude protein intake; CP = Dietary crude protein inclusion rate; NE_LI = Net energy for lactation intake; NE_L = Energy density of the ration; WET = Percentage of cows with wet feed refusals; AG = Percentage of cows that exhibited aggressive eating behavior; HAY = Average amount of hay offered to cows; BW = Body weight; BCS = Body condition score; SS = Area of the stalls; HLS = Hock lesion score; HygS = Udder hygiene score; TS = Temperament score

² Model restrained to remain positive definite and standard errors not available

Table 8. Genetic correlations (r) between FCM and BW, and FCM and BCS in high (H) and low (L) management groups, generated using animal models

Trait ¹	Group	r _{FCM,BW}	SE _{FCM,BW}	r _{FCM,BCS}	SE _{FCM,BCS}
Nutritional Management Factors					
DMR, kg	H	-0.01	0.15	-0.21	0.19
	L	-0.80	0.20	-0.63	0.24
DMI, kg	H	-0.22	0.16	-0.18	0.20
	L	-0.49	0.21	-0.45	0.31
CPI, kg	H	-0.06	0.16	0.02	0.23
	L	-0.56	0.18	-0.54	0.23
CP, %	H	0.02	0.16	-0.13	0.20
	L	-0.56	0.18	-0.32	0.27
NE _L I, Mcal	H	-0.10	0.16	-0.16	0.19
	L	-0.45	0.20	-0.35	0.29
NE _L , Mcal/kg	H	-0.34	B ²	-0.36	0.20
	L	-0.26	B ²	-0.16	0.28
WET, %	H	-0.50	0.20	-0.33	0.30
	L	0.06	0.16	-0.31	0.19
AG, %	H	-0.17	0.20	-0.38	0.30
	L	-0.24	0.15	-0.25	0.18
HAY, kg	H	-0.09	0.16	-0.13	0.20
	L	-0.49	0.19	-0.38	0.26
Body Conformation Factors					
BW, kg	H	-0.01	0.15	-0.21	0.19
	L	-0.80	0.20	-0.63	0.24
BCS	H	-0.23	B ²	-0.31	B ²
	L	-0.36	B ²	-0.07	B ²
Cow Comfort Indicators					
SS, cm ²	H	-0.38	0.16	-0.45	0.18
	L	-0.16	0.17	-0.15	0.25
HLS	H	-0.66	0.19	-0.38	0.29
	L	0.00	0.14	-0.23	0.19
HygS	H	-0.22	0.14	-0.23	0.17
	L	-0.17	0.21	-0.53	0.41
TS	H	-0.14	0.15	-0.43	0.18
	L	-0.35	0.17	-0.39	0.23

¹ DMR = Dry matter refusals; DMI = Dry matter intake; CPI = Crude protein intake; CP = Dietary crude protein inclusion rate; NE_LI = Net energy for lactation intake; NE_L = Energy density of the ration; WET = Percentage of cows with wet feed refusals; AG = Percentage of cows that exhibited aggressive eating behavior; HAY = Average amount of hay offered to cows; BW = Body weight; BCS = Body condition score; SS = Area of the stalls; HLS = Hock lesion score; HygS = Udder hygiene score; TS = Temperament score

² Model restrained to remain positive definite and standard errors not available

Table 9. Top 10%, bottom 10%, and mean values used in multiple factor regression prediction models

Trait ¹	10%	Mean	90%
Nutritional Management Factors			
DMR, kg	0.973	1.384	1.681
CP, %	15.591	16.510	17.907
NEL, Mcal/kg	1.613	1.654	1.701
WET, %	0	-	1
AG, %	0	0.265	1
HAY, kg	0	4.308	9.600
Body Conformation Factors			
BW, kg	555.8	668.3	786.3
BCS	2.25	3.15	4.25
Cow Comfort Indicators			
SS, cm ²	3264	3448	3744
HLS	1.783	2.056	2.320
HygS	1.256	1.696	2.067
TS	1.588	1.733	1.864

¹ DMR = Dry matter refusals; CP = Dietary crude protein inclusion rate; NE_L = Energy density of the ration; WET = Percentage of cows with wet feed refusals; AG = Percentage of cows that exhibited aggressive eating behavior; HAY = Average amount of hay offered to cows; BW = Body weight; BCS = Body condition score; SS = Area of the stalls; HLS = Hock lesion score; HygS = Udder hygiene score; TS = Temperament score

Table 10. Differences in predicted milk, fat, and protein yield at high (500 kg) and low (0 kg) values of sire predicted transmitting ability for milk (PTAM), and high (25 kg) and low (0 kg) values of sire predicted transmitting ability for fat (PTAF), and protein (PTAP) at high and low management levels

Trait ¹	Level	PTAM	SED	P	PTAF	SED	P	PTAP	SED	P
DMR, kg	1.68	603.1	96.0		19.6	4.5		34.6	4.8	
	0.97	81.4	110.7		5.0	6.0		1.6	6.0	
	Diff ²	521.7	139.0	0.001	14.6	7.4	0.054	33.0	7.1	0.001
CP, %	17.91	584.0	135.4		24.1	6.7				
	15.59	270.5	100.6		6.5	5.6				
	Diff	313.6	178.1	0.085	17.6	9.8	0.078			
HLS	2.32							34.8	7.5	
	1.78							12.9	5.9	
	Diff							21.9	11.0	0.052

¹ DMR = Dry matter refusals; CP = Dietary crude protein inclusion rate; HLS = Hock lesion score

² Diff = Difference in response to selection at different management levels

Table 11. Differences in predicted milk, fat, and protein yield at high (IS = 2) and low (IS = 1) values of IGENITY[®] score for milk (ISM), fat (ISF) and protein (ISP), at high and low management levels

Trait ¹	Group	ISM	SED	P	ISF	SED	P	ISP	SED	P
CP, %	17.91	-29.4	37.5							
	15.59	71.4	30.2							
	Diff ²	-100.7	54.5	0.070						
NE _L , Mcal/kg	1.70	142.1	29.9		4.8	1.1		3.6	0.8	
	1.61	-63.0	25.8		-0.8	1.0		-2.0	0.7	
	Diff	205.1	38.9	<0.001	5.6	1.5	0.001	5.5	1.1	<0.001
SS, cm ²	3744	-99.5	41.8					-2.0	0.9	
	3264	112.8	31.0					2.2	0.7	
	Diff	-212.3	60.6	0.001				-4.2	1.2	0.001
HygS	2.07	-156.5	37.6		-2.0	1.0		-3.1	0.8	
	1.26	254.3	45.1		6.2	1.1		5.0	0.9	
	Diff	-410.9	72.4	<0.001	-8.2	1.5	<0.001	-8.0	1.4	<0.001
TS	1.86	85.7	25.2					1.9	0.6	
	1.59	-28.7	26.3					-0.9	0.7	
	Diff	114.5	32.7	0.001				2.8	0.8	0.001

¹ CP = Dietary crude protein inclusion rate; NE_L = Energy density of the ration; SS = Area of the stalls; HygS = Udder hygiene score; TS = Temperament score

² Diff = Difference in response to selection at different management levels

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