Selecting for Feed Efficiency in Pigs and its Effect on Growth Performance, Nutrient Digestibility and Carcass Characteristics

By

Laura Beens

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Department of Animal Science

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ABSTRACT

With a higher demand for protein and a limited supply of feed, the ideal animal with low inputs costs and high-quality output is sought after. This is termed feed efficiency (FE) and it measures the animal's ability to turn feed into an edible product with the least amount of resources including environmental impacts. Feed accounts for about 60 - 70% of the total cost of production and with the cost of feed at a steady increase, it would be profitable to improve the pig's efficiency. The goals for researchers are to find methods to produce more food with less input and environmental impacts while ensuring animal welfare. Genetic selection programs have focused on selecting FE traits such as feed conversion ratio (FCR) and residual feed intake (RFI). Improving FE can be difficult to estimate due to its variation from animal to animal as well as the many biological factors involved. The impact of individual biological factors on FE is important to evaluate in research to help predict selection for FE outcomes including negative outcomes. Our study was conducted to determine the effect of selecting for feed efficiency using estimated breeding value (EBV) for FCR on digestibility, growth performance, and carcass characteristics of two Large White lines. High feed efficient (HFE) pigs consumed less feed ($P < 0.05$), had thinner fat depth ($P < 0.05$,) and had greater loin depth ($P < 0.05$) than low feed efficient (LFE) pigs. In addition, HFE pigs had a significantly higher apparent total tract digestibility (ATTD) of calcium ($P = 0.05$) and a tendency for a higher ATTD for crude protein ($P = 0.06$), and phosphorous ($P = 0.10$) compared to LFE pigs. In conclusion, pigs can be selected for high feed efficiency and as a result, will consume less feed and produce leaner carcass without affecting growth performance (ADG). It is possible that the feed intake and nutrient digestibility can explain part of the animal-to-animal variation. However, the underlying biological mechanisms as well as any negative effects of selecting for FE requires investigation.

Keywords: Feed efficiency, Feed conversion ratio, Apparent total tract digestibility, Growth performance, Carcass characteristics

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LIST OF ABBREVIATIONS

AA	Amino acids
ADFI	Average daily feed intake
ADG	Average daily growth
ADF	Acid detergent fiber
ATTD	Apparent total tract digestibility
BF	Back fat
BW	Body weight
CF	Crude fiber
CM	Castrated males
CT	Computed tomography
CP	Crude protein
DDGS	Distillers dried grains with solubles
DE	Digestible energy
DF	Dietary fiber
EBV	Estimated breeding value
EBV_FCR	Estimated breeding value for feed conversion ratio
ICM	Immunocastrated
FCR	Feed conversion ratio
FE	Feed efficiency
FI	Feed intake
GE	Gross energy

GIT	Gastrointestinal tract
HFE	High feed efficiency
HI	Heat increment
HP	Heat production
IF	Intact females
KG	Kilogram
LD	Loin depth
LFE	Low feed efficiency
ME	Metabolizable energy
NDF	Neutral detergent fiber
NE	Net energy
NIRS	Near infrared spectroscopy
PD_{max}	Maximum protein deposition
PRRSV	Porcine reproductive and respiratory syndrome virus
RFI	Residual feed intake
RFID	Radio frequency identification

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CHAPTER 1: GENERAL INTRODUCTION

In pig breeding, one of the main objectives is to create the most efficient pig. The importance of this has intensified over the years as resources have become limited and competition grows due to the increase in human population. In pork production, feed costs and the ability of the pig to utilize feed towards growth largely effects profitability of operations. Feed accounts for about 60-70% of the total cost of production (McCormack et al, 2017; Yang et al., 2017) and with the cost of feed at a steady increase, it would be profitable to improve the pig's efficiency. Feed efficiency (FE) can be described as the pig's ability to turn feed into a edible product. efficiency (FE). Over the years, FE has gained its popularity and improvements have been made through nutrition and genetics (Knap and Wang, 2012). Genetic factors can determine the FE of an animal, and this has resulted in genetic selection programs for improving FE. Over the last 35 years, FCR has decreased from 3.0-3.6 to 2.6-2.2. Due to selection breeding for lean carcasses (Knap and Wang, 2012; Gaillard et al., 2020).

Selection for FE traits have also shown positive effects with growth performance, and carcass characteristics (Gilbert et al., 2017). However, the underlying biological mechanism that cause the animal-to-animal variation is inconclusive. Biological processes are those involved in nutrient digestion, absorption, metabolism and tissue accretion. In cattle, the main biological factors that contribute to RFI are activity, feed intake patterns and behaviour, stress, digestibility, protein turnover and tissue metabolism (Herd and Arthur, 2009). With pigs, it has been partly quantified (Barea et al., 2010; Boddicker et al., 2011; Smith et al., 2011; Young et al., 2011; Harris et al., 2012). Disparities in heat production and maintenance energy utilization were found by both Barea et al. (2010) and Boddicker et al. (2011) to be contributing to FE differences. Feed intake patterns may be another biological factor with higher FE pigs eating faster, spending less time at

the feeder but overall consuming less feed compared lower FE pigs (Young et al., 2011). Finally, nutritional digestibility differences may be another biological component determining FE, with high FE pigs having a greater digestibility for some nutrients (Harris et al., 2012; Vigors et al., 2016; Mauch et al., 2018). With all these facts combined, there is still areas for further research. External factors such as management practices, diet composition, and diseases can also cause variations in the FE. FE is a complex trait with many factors that control it making it difficult to predict the effects of selection (Cruzen et al., 2013). Understanding the underlying biological processes is valuable to improve the accuracy of selecting for FE and to identify biomarkers to be used as early predictors of FE (Gilbert et al., 2017). In this review, how these factors influence the FE will be discussed. Furthermore, FE differences and their association with digestibility will be reviewed.

CHAPTER 2: LITERATURE REVIEW

2.1 Feed efficiency in swine

Feed efficiency (FE) is defined in the simplest of terms as the pig's ability to turn feed into pork product. FE is measured as body weight gain (Kg) per unit of feed (Kg) consumed (Patience et al., 2015). The definition seems simple but expressing and measuring FE is often difficult and misunderstood. Common terms used to quantify FE are feed conversion ratio (FCR) and residual feed intake (RFI). The former is calculated as feed intake over body weight gain (Hoque et al., 2007) and the latter is calculated as the difference of actual feed intake and the predicted nutrient requirement for the animal (Koch et al., 1963). Both terms express FE, however, each are used in different situations depending on the knowledge being sought and how the information will be used to make decisions (Patience et al., 2015). FCR is the main measure of FE in production farms (Gondrett et al., 2017) however many selection studies have used RFI as a measure of FE (Gilbert et al., 2017).

2.2 Biological basis of feed efficiency

To comprehend FE, we need to understand the biological basis of how pigs interact with feed to achieve a growth rate and produce an edible product. Nutrients are acquired from the diet that is consumed by the pig and nutrients enter the stomachwhere it is digested with stomach acid and enzymes. After the stomach, the digesta enters the small intestine where further digestion occurs with pancreatic and bile juices. As the digesta travels the small intestine, microvilli located on the villi increase surface area for nutrients to be absorbed into the blood stream (Mosenthin, 1998). Nutrients not absorbed are lost in the feces which is considered inefficiency, and nutrient digestibility can be measured from the feces. The nutrients absorbed in the small intestine are then

metabolized for growth. Each body tissue requires different nutrients for growth at their own nutrient efficiency (Patience, 2012). Muscle growth requires a combination of essential and nonessential AAs and are limited to the supply of essential AAs. Even with no muscle, growth protein turnover occurs, which is the continuous break down and rebuilding of proteins (Hewitt et al., 2020). Muscle growth requires a higher rate of protein deposition than protein breakdown, and both processes require energy and a steady supply of AA (Cantalapiedra-Hajar et al., 2018). Fat deposition can either result when excess nutrients are consumed far above the protein deposition capacity or one or more essential AA is lacking or limiting protein deposition (Gaillard et al., 2020). The amount of energy required to produce the same Kg of fat compared to muscle tissue is approximately four times thus fat deposit reduces FE (Gaillard et al., 2020). The ratio of lean-to-fat deposit is important for FE and will be discussed further on.

Each pig has its own nutritional requirements which depend on body weight (BW), health status, genetics, and gender (Remus et al., 2021). Energy and nutrients consumed are primarily used for maintenance requirements first, then lean accretion, and any excess is used for lipid accretion (Patience et al., 2015). Maintenance requirements are the biological process of the body that sustains everyday life and results in no gain nor loss of tissue and include basal metabolic rate, thermoregulation, protein turnover, physical activity, and other coping functions (Patience, 2012). Most maintenance costs are inevitable; however, they can be decreased by minimizing stress caused by the environment or disease (Patience, 2012). Nevertheless, with a 70 kg pig, about 34% of the metabolizable energy is used towards maintenance requirements (Patience, 2012) which is a sizable proportion of the energy intake. Meeting the nutrient requirements of the pig is important to prevent oversupply or undersupply of nutrients and energy. An excessive supply of nutrients will increase fat deposits, nutrients excretion and overall lower FE (Gaillard et al., 2020). A lack

of nutrients will reduce lean tissue growth and thus FE. There are several non-genetic factors that inhibit the pig's nutrient intake and utilization and as a result affects FE (Patience, et al., 2015). Due to the complexity of the biological basis of FE, it is often misunderstood and requires further research to better understand the factors involved.

2.3 Factors affecting feed efficiency

2.3.1 Genetics

Since genetics plays a role in determining the animal's maintenance requirements, feed intake and nutrient utilization (Gaillard et al., 2020), genetic selection for high feed efficiency (HFE) has paved the way to pigs that are more efficient at converting feed into BW compared to their counterparts (Boddicker et al., 2011). Both growth rate and feed intake can be different between breeds. Piétrain sired males have a lower growth rate (ADG -87.8 g/d) than Duroc-sired males (Edwards et al., 2006) whereas Creole pigs had a lower growth rate (ADG – 219 g/d) than Large White pigs (Renaudeau et al., 2005). Daily voluntary feed intake has been found to be different among Peitrain breed (1659 g/d), Large White breed (1746 g/d) and Meishan (1622 g/d) breed (Quiniou et al., 1999).

Selecting for improved FE through genetics has become a popular topic in the industry to benefit production and economical goals. Most efforts at improving efficiency through genetics has been through increasing carcass leanness (Knap and Wang, 2012). This is considered an indirect selection technique and has been remarkably successful over many decades (Knap and Wang, 2012). With advances in technology like electronic feeding systems, precision feeding, tracking individual feed intake has become effortless and improving FE through selection based on RFI or FCR has advanced animal's efficiency further (Gaillard et al., 2020). One method to

genetically improve FE is by using estimated breeding values (EBV) which is the genetic value of an animal (Verschuren et al., 2020; Van der Peet-Schwering et al., 2021). Selection for FE has been accomplished within studies over several generations of Yorkshire pigs (Cai et al., 2008) and Large White pigs (Gilbert et al., 2007). Both divergent selection experiments for FE (RFI) have resulted in high and low FE pigs providing evidence that genetics controls FE (Gilbert et al., 2017).

However, selection based on carcass leanness, and reduced feed intake focuses reallocation of dietary nutrients towards lean and fat tissue growth (Martinsen et al., 2015). Martinsen et al. (2015) introduced a new concept of measuring FE as lean meat and fat efficiency. Both lean meat and fat efficiency describes how much feed is required to produce 1 kg of each (Martinsen et al., 2016). The genetic variance was estimated for both efficiency for lean meat deposition and fat deposition in Norwegian Landrace and Duroc boars suggesting that pigs can be selected based on their potential to deposit lean meat efficiency (Martinsen et al., 2015).

2.3.2 Gender

Differences between genders have been seen with FE, growth performance and carcass characteristics. It is well known that the most efficient gender is entire males, then castrated males and then females (Patience et al., 2015). Entire males or intact males are known for their faster growth rates and deposit less fat than castrates or females, primarily ascribed to the hormone testosterone (Needham et al., 2017). A castrated male loses its source of testosterone elucidating the reason they have slower growth rates and deposit more fat compared to intact males (Needham et al., 2017). However, intact males are at risk for producing undesirable meat products with boar taint. Between physically castrated males and boars of Large White pigs, a higher feed intake was seen with the boars (Quiniou et al., 1999) whereas castrated males had a higher ADFI compared to gilts (Renaudeau et al., 2006). This concept of using the entire male's growth rate without boar

tainted meat has led to the use of immunocastration (Dunshea, 2012). Morales et al. (2011) compared immunocastrated (IMC), surgically castrated males (CM) and intact females (IF) in Large White lines for growth rate and carcass composition. IMC and CM grew at a faster rate than IF, and IMC was the most efficient. IMC had less backfat depth and more lean percentage compared to CM. The presence of testosterone stimulates growth in the animal and given that males have higher levels of testosterone compared to females, they will exhibit better feed efficiencies.

2.3.3 Diet

FE can be influenced by the overall ingredient quality, diet composition, nutrient availability, and feed processing type of the diet (Tokach et al., 2012). The quality of each ingredient determines nutrient availability and composition. For example, low-quality protein can be deficient in essential amino acids (AA) (de Lange et al., 2012). High-quality protein is vital in growing pigs as it will increase whole-body protein deposition and influence skeletal muscle growth (de Lang et al., 2012). Feeds can be underbudgeted and expensive ingredients can be limited or opted for lower quality ingredients, reducing growth and thus FE (Patience, 2012).

The composition of the diet such as quantity of dietary energy and dietary protein can influence feed intake and thus FE. It is well known in the literature that animals consume feed to meet their energy needs and will maintain constant daily energy intake by compensating feed intake (Li and Patience, 2017). However, this is limited to the physical digestive capacity of the animal (Beulieu et al., 2009). In circumstances when pigs are fed diets that are low in energy that they are not able to compensate with feed intake, it will negatively impact the performance of the pig. Another dietary component in determining feed intake that is also well known in the literature is dietary protein level and AA profile (Harper, 1959). The challenge with dietary protein, is feed

intake is reduced by either a severe lack of limiting AA or an abundance of total protein or some essential AA. (Li and Patience, 2017) Thus, it is important for nutritionists to understand the protein (or AA): energy ratio to maintain feed intake and growth rate in pigs (Li and Patience, 2017).

Some diet components are not readily available, and it is important to ensure availability to maximize nutrient digestibility and utilization. Fiber is a component of the diet that the animals do not easily digest as they lack the digestive enzymes required to digest the complex carbohydrate compounds compared to starch, which is easily digested. The level of starch and fibre in the diet can affect the pig's efficiency of energy utilization (Vershuren et al., 2018). With more fibre in the diet, the animal would be less efficient as the nutrients are less likely available to the animal. With this, diets are usually higher in starch to aid in FE; however, including fibre in the diet has its own benefits, such as improving fecal consistency (Vershuren et al., 2018). Mauch et al. (2018) demonstrated the effect of high fiber diet on low and high FE Yorkshire pigs. The low-energy-high-fiber diet reduced the performance of both lines even though ADFI was increased compared to the high-energy-low-fiber diet (Mauch et al., 2018) Because the energy was not readily available to the pigs, they increased feed intake to compensate for the energy. Thus, regardless of the genetic potential, the bioavailability of the diet can influence FE.

Feed processing (e.g., grinding, pelleting) is a method used by feed mills that can influence feed intake and nutrient utilization through feed form and particle size (Stark, 2012). By reducing the particle size, it increases surface area for enzymes activity which improves nutrient digestibility (Stark, 2012). In addition, pelleting has advantages in the swine industry because it agglomerates ingredients into one bite to reduce feed sorting (Stark, 2012). Presenting feed in the pelleted form, reduces feed intake but improves growth performance (Nyachoti et al., 2004) since feed processing

uses both temperature and humidity to break chemical bonds, and in this way, increase nutrient digestibility (Stark, 2012). Wondra et al. (1995) provided a diet in either meal (at 4 different particle sizes) or pelleted form to finisher pigs and ADG and gain/feed (FCR) was 5% and 7% greater respectively when the diet was in pelleted form. In addition, as particle size decreased (1000 to 400 µm) the gain/feed (FCR) increased by 8%. In a more recent study, a corn-soybean meal diet was provided in a mash form or pellet form at 3 different particle sizes. (Jo et al., 2021). There was no significant difference in BW and average daily gain (ADG) among all dietary treatments however, mash diet had a higher ADFI for the finishing phase. As a result, the pellet diet consistently improved pigs FE throughout the entire experimental period as well as decreasing particle size for part of the experimental period (Jo et al., 2021). Interestingly there was no significant difference with live weight, carcass yield and backfat thickness. Thus, feed processing can influence FE.

2.3.4 Feed intake

Pigs' capacity to freely ingest feed is critical since it controls the amount of nutrients and energy available for optimal growth. Since feed intake is closely associated with growth performance and production efficiency (Nyachoti et al., 2004), it has a vast influence on FE. Growing pigs require nutrients for maintenance and growth and voluntary feed intake is driven by the need to meet these nutrient demands (Nyachoti et al., 2004). Since voluntary feed intake is regulated by many factors including breed, sex, stage of growth, dietary energy concentration, AA balance, feed processing and form, housing conditions and climatic factors (Li and Patience, 2017; Renaudeau et al., 2006) it is highly variable (Albun et al., 2001). As discussed above, the breed and sex of the pig does determine the voluntary feed intake. As for the stage of growth, as the pig increase in BW (age) their maintenance requirements and stomach’s physical capacity increases

and as a result, their daily feed intake. Daily voluntary feed intake increased linearly with BW in Piétrain, Large white and Meishan male pigs however the rate of increase was different for each breed (Quiniou et al., 1999). Between 20 and 60 kg, the increase of voluntary feed intake for 1 kg of BW increase was 0.33, 0.21, and 0.17 MJ KE/kg in Large White, Piétrain and Meishan male pigs respectively (Quiniou et al., 1999). Meal frequency decreased with increased BW (-3.8 meals per day) but meal size increased (+126 g/meal) (Quiniou et al., 1999) and which may be caused by the increased physical capacity of the gastrointestinal tract. Of the stage of growth, the body composition and the type of nutrient deposition can affect the feed behaviour (Quiniou et al., 1999). Meishan and Creole are considered a fattier breed compared to the leaner breeds Piétrain and Large white (Quiniou et al., 1999; Renaudeau et al., 2006). Given their different body compositions they had similar voluntary feed intake however different feed strategies (Quiniou et al., 1999; Reneaudeau et al., 20060). Meishan pigs consumed half the amount of feed per day (7.3 vs 14.4 meals/day) but meal size was double the size (250 vs 125 g/meal) compared to Piétrain pigs (Quiniou et al., 1999) whereas Creole pigs consumed less meals per day (5.9 vs. 8.8 meals/d) but meal size was greater (431 vs 279 g/meal) compared to Large white pigs (Renaudeau et al., 2006).

2.3.5 Disease

Energy required for maintenance costs of the body are one factor that can reduce energy allocated towards growth. As mentioned previously maintenance costs uses about one third of the total dietary energy intake for a 70 kg pig (Patience, 2012) which is a sizable portion. Yet other factors like stress, environmental conditions and diseases can also increase body maintenance costs. When pigs are exposed to pathogens, the metabolic pathways shift priorities to elicit an immune response (Johnson, 2012) which is associated with inflammation (Li and Patience, 2017). An immune response may increase maintenance requirements and nutrients are allocated towards

immune functions rather than growth (Johnson, 2012). For example, protein is the first nutrient to become limiting since it makes up most components of immune response (Patience et al., 2015). Thus, with an immune-challenged animal, less protein will be allocated toward skeletal muscle growth. Energy can also become limiting due to increased heat production (fever) and immune response activation (Patience, et al., 2015). Sick animals also respond with a reduced feed intake, reducing nutrients allocated towards growth (Johnson, 2012). Both reduced feed intake and impaired metabolic pathways affect growth rate in sick animals (Johnson, 2012). Such, it is common to see an animal that is immune compromised with a slower growth rate compared to a healthy animal (Patience et al., 2015). Dunkelberger et al. (2015) evaluated the effect of porcine reproductive and respiratory syndrome virus (PRRSV) in two FE lines and on average, the non-challenged pigs had a 173 g/d greater ADG than the challenged pigs which reduced FE. Helm et al. (2018) also observed lower ADG (17%) with challenged pigs (*Mycoplasma hypopnemoniae* and *Lawsonia intracellularis*) as well as a reduced ADFI (12%) and reduced G:F (FCR) (7%) compared to control pigs. This indicates that diseases can negatively impact FE.

In research there has been some concern if selection for increased FE would lead to increased susceptibility to diseases as HFE pigs are allocating more nutrients towards growth (Dunkelberger et al., 2015). However, pigs selected for low RFI (high FE) were less affected by PRRSV-challenge compared to high RFI (low FE) suggesting that HFE pigs may be more robust compared to LFE pigs (Dunkelberger et al., 2015). In addition, HFE pigs' response was similar to LFE pigs when challenged with a duel respiratory and enteric infection indicating that genetic selecting for increased FE does not disadvantage HFE pigs.

2.3.6 Management practices

Although pigs selected for improved FE may be better prepared for commercial stressors (Colpoys et al., 2019), variation in FE can still occur due to environmental stressors. The barns where the pigs are raised in are considered their environment which has many factors that can influence FE such as sanitation, stocking densities, ventilation, temperature, water quality, number of feeders, flooring conditions and enrichment (Tokach et al., 2012; Averós et al., 2012). Sanitation for instance has an influence on pig performance such that an unsanitary environment can cause a reduction in average daily gain and a reduction in feed intake (Renaudeau, 2009; Sierżant et al., 2019). Poor hygiene conditions have found to cause a systemic inflammatory response indicated by elevated haptoglobin (acute phase protein associated with inflammation) concentrations, white blood cells, and granulocytes of pigs housed in unsanitary environments (Chatelet et al., 2017). This indicates that poor environmental conditions may increase the exposure and susceptibility to potential pathogens and diseases to the pigs. Indeed, pigs have also shown high prevalence of pneumonia and lung lesions when housed in poor hygiene environments (Chatelet et al., 2017). As previously mentioned, disease impairs the animal's feed intake, nutrient utilization, and energy expenditure towards growth (Johnson, 2012). Conversely, a clean environment reduces diseases and encourages feed intake (Tokach et al., 2012).

Another environmental factor influencing growth rate is barn temperature. Temperature changes can determine the quantity of energy allocated towards growth. The body requires energy to maintain basal functions at thermal neutral temperatures, called thermoregulation. The body requires more energy to increase heat production to maintain thermoregulation when the body is below the lower critical temperatures. Therefore, the animal will increase feed intake, but the increase in energy will be reprioritized towards heat production and away from growth (Tokach et al., 2012). In contrast, pigs decrease feed intake when temperatures increase to decrease heat

production. With a difference in 10 °C (23 °C to 33 °C), VFI was reduced by 30 % and subsequently BW gain was 37% lower and FCR was lower (1.50 vs 1.68) (Collin et al., 2001). Overall VFI can decline by 45 g/d per °C (Collin et al., 2001). As a producer, keeping the environmental barn temperatures in optimal zones is ideal to limit energy allocated toward thermoregulation (Tokach et al., 2012). The optimal temperature for maximum BW gain was 15 °C whereas for maximum FE was 23°C, for finishing pigs, thus between 15 and 23 °C is an optimal temperature range for production (Hansen and Bjerg, 2018). Pigs housed below or above critical temperatures decrease FE (Nienaber et al., 1990). Although in some climates it is difficult to avoid extreme temperatures and so seasonal variation exits. In circumstances where heat stress is unavoidable diet strategies can be used to reduce heat production in growing pigs. For example, providing diet with a low dietary protein level (12% CP) and supplementing crystalline AA (lysine, tryptophan and threonine) will decrease heat production in heat-stressed environments and performed similar compared to pigs fed an adequate dietary protein level (16% CP) (Kerr et al., 2003).

Management practices such pen density and handling practices can cause stress if not done properly can cause stress to the pigs. Overstocking pens can affect growth performance (Tokach et al., 2012). Overstocking pens can occur if pig numbers or pen size are not adjusted as they grow in size. Overstocked pens reduce space and time at the feeder for individuals, restrict the pig's movement, cause stress and impair growth, and result in a reduced average daily gain (Wolter et a., 2003). Poor handling practices can also cause stress to the pig. External stress can activate a primary endocrine stress response pathway called hypothalamic-pituitary-adrenocorotical (HPA) axis and it plays a role in metabolism regulation (Colpoys et al., 2019). Colpoys et al. (2019) administered exogenous adrenocorticotropic hormone (ACTH) (hormone released in response to

stress) intramuscularly into low RFI and high RFI gilts and evaluated cortisol and non-esterified fatty acids (NEFA) response. In response to the ACTH challenge, Low RFI (high FE) gilts had less cortisol and NEFA concentrations indicating that genetic selection for FE may result in pigs with less stress responsiveness.

2.4 Nutrient and energy digestibility

Nutrient and energy digestibility is another factor affecting FE. Digestion is the result of the interaction between the feed and the animal (Bastinelli, 2013). Digestibility is dependent on two factors: the digestibility "potential" that is determined by the properties of the feed and the animal's digestive capabilities (species, age, sex, physiological state) (Bastinelli, 2013). It is widely recognized and accepted that a close relationship exists between nutrient and energy digestibility and FE (Patience, 2012). FE is increased by formulating diets that are balanced to the nutrient requirements of the animal and by using different dietary ingredients that are selected based on their nutrient composition and bioavailability for digestibility. FE is dependent on feed bioavailability (Gaillard et al., 2020) and the pig's digestion potential is limited to its enzyme capabilities. Thus, FE decreases when the indigestible portion of feed increases (Gaillard et al., 2020). For example, fibre is a complex carbohydrate, and the pig lacks the digestive enzymes required to digest fibre. High efficient pigs have shown to have higher nutrient digestibility (Harris et al., 2012; Vigors et al., 2016; Mauch et al., 2018). Other studies, however, have not found differences in efficiency of digestibility concluding that digestibility doesn't play a significant role in the variation of FE (Barea et al., 2010; Hewitt et al., 2020).

2.4.1 Factors affecting digestibility

The digestive efficiency of nutrients is determined by the amount of nutrient update in the body to the total dietary intake (Kasper et al., 2020). Nutrient and energy digestibility is affected by diet-specific factors and animal-specific factors. Diet-specific factors include, diet composition, feed intake and feed processing.

The main cause of differences in nutritional digestibility across pigs is diet ingredient composition (Verschuren et al., 2021) notably the presence of DF. DF is more difficult to digest and can reduce the digestibility of other nutrients (Patience, 2012). Between corn-soybean diet and wheat-barley diet, pigs (both gilts and boars) had a significantly higher nutrient digestibility when fed the corn-soybean diet since DF content was lower (Verschuren et al., 2021). In another study, where sugar beet pulp was used as the fiber source, the ATTD of DM, CP and GE decreased as the total dietary fiber content increased. (Zhang et al., 2013).

Feed intake is another factor affecting digestibility. Lowering feed intake can increase nutrient digestibility by decreasing the rate of passage of the digesta through the gastrointestinal tract (De Haer and De Vries, 1993). A higher retention time will increase the enzyme activity time. A reduced feed intake also reduces the amount of nutrients. The pigs' digestive systems become inefficient when there is an adequate supply of nutrients but when challenged with nutrient shortages, the digestive system works more efficiently. This is termed marginal efficiency of retention, and it is at its highest when nutrients are undersupplied (Gaillard et al., 2020). Thus, it is important that nutrients are no oversupplied in the diet but rather adequately meet the nutrient requirements of the pig. Even with the same daily feed intake, the frequency of meals can improve growth performance and nutrient digestibility. Jia et al. (2021) evaluated feeding one time per day, three times per day or five times per day with the total ADFI being the same for all regimens with growing pigs. Apparent total tract digestibility (ATTD) of CP was significantly higher in the three

times and five times per day feeding regimens compared to one time per day (Jia et al., 2021). ADG was significantly improved in pigs fed the three and five times per day feeding regimens (Jia et al., 2021). Another study fed two times and four times per day and reported no nutrient digestibility differences between feeding regimes (Kang et al., 2019) thus further research is required to establish the effect of feeding frequency on nutrient digestibility.

Feed processing is another diet-specific factor affecting nutrient digestibility such as particle size manipulation. By reducing the particle size of feed, it increases the surface area for enzymatic action such it may have a positive effect on nutrient digestibility. Wondra et al., 1995 demonstrated a 5-8% increase in digestibility of DM, nitrogen and gross energy (GE) as particle size decreased (1000-400 µm). However, particle size reduction may increase the passage rate and reduce enzyme activity (Joe et al., 2021; Gao et al., 2020). Gao et al. (2020) saw no differences in activities of amylase, trypsin and chymotrypsin in duodenal fluid related to mean particle sizes (390 and 511 µm) With this, the study reported no effect of mean particle size on ATTD of GE, CP, ether extract, neutral detergent fiber (NDF) and acid detergent fiber (ADF). In agreement, Jo et al. (2021) observed no significant difference in ATTD of dry matter (DM), crude protein (CP) and crude fiber (CF) between particle sizes (600, 750, or 900 µm). Restricted feeding regime was used in both Gao et al. (2020) and Jo et al. (2021) compared to Wondra et al. (1995) which may explain why no differences were seen in nutrient digestibility. Another study with no feed restrictions, showed an ATTD of CP improvement with reduced particle size (Ball et al., 2015). Pelleting also increases nutrient digestibility from the steam condition process which increases starch gelatinization and protein confirmation. (Jo et al., 2021). Jo et al. (2021) observed a higher ATTD for CF and no difference in ATTD for DM and CP when pigs were fed the diet in a pellet form rather than mash form. Whereas Ball et al. (2015) showed an improvement with DM, energy

and ash digestibility with the pelleted diet compared to the mash diet. However, Jo et al. (2021) experiment study involved a restricted feeding method resulting in improved digestibility (DM and CP digestibility were all over 94%) regardless of the diet treatment.

There is also variation in the digestion capability of nutrients between individual pigs fed the same diet (Ouweltjes et al., 2018) which can be explained by animal-specific factors like genetics, sex, and age of the animal. Firstly, the genetics of the pig can alter nutrient digestibility between breeds. Noblet et al. (2013) found that the digestibility of energy is influence by sire which implies that nutrient digestibility is partly dependent on genetics. Barea et al. (2010) evaluated nutrient digestibility differences between Iberian (obese breed) and Landrace X Large White (lean type breed) pigs and reported that ATTD of nitrogen was higher for Landrace X Large White at 30 kg of BW and nitrogen retention and efficiency of nitrogen retention were both higher compared to Iberian pigs. Interestingly, Landrace X Large White had 10% higher villi length and villi-to-crypt ratio than Iberian pigs which may explain the genetic advantage of lean-type breeds in nutrient digestibility (Barea et al. (2010).

In terms of sex, the hormone difference between entire males, castrated males and females may cause differences in nutrient digestibility. Boars fed a wheat-barley diet had a lower ATTD of nutrients expect for crude fat and ash compared to gilts with no change in feed intake between sexes which is not expected since boars are more efficient than females. Although boars had lower FCR and RFI values so there may be differences in the postabsorptive metabolism of nutrients by organs and tissues (Verschuren et al., 2021). As the animal grows older, their nutrient digestibility improves as the digestive system develops and matures (Ouweltjes et al., 2018). Noblet and Shi, (1994) found energy and nutrient digestibility increased with BW however the rate of increase depends on feed characteristics like fibre-rich feeds having the most variation. In agreement,

Noblet et al. (2013) and Ouweltjes et al. (2018) also reported an increase in nutrient digestibility as BW or age increased.

2.5 Digestibility methodology

2.5.1 *In vivo* studies

The most common method to determine digestibility is *in vivo* digestibility (Zhang and Adeola, 2017). Basically, feed is provided to the animal, and the feces are collected. Depending on if a single or multiple feed ingredient is being tested, the procedure can be direct or indirect (Zhang and Adeola, 2017). With the direct procedure the feed ingredient of interest is formulated as the sole source of the whole diet to test a component of the ingredient (Zhang and Adeola, 2017). However, the direct procedure cannot be used on a diet with multiple feed ingredients that supply similar components (Zhang and Adeola, 2017). In these cases, indirect procedures will be used, like substitution and regression procedures (Zhang and Adeola, 2017).

There are two types of collection methods which are total collection method and index method (Zhang and Adeola, 2017). In any *in vivo* feed study, an adaptation period is first conducted, lasting about 3-5 days (Zhang and Adeola, 2017). For the total collection method, animals are kept in a collection pen or cage, and it requires quantitative feed and fecal collection (Zhang and Adeola, 2017). This method is a simple calculation of what goes in subtracted by what comes out will equal what is digested. Another collection method is the index method which requires a marker that is added to the feed and then the marker is analyzed in the feces (Zhang and Adeola, 2017). Less labour is required for the index method compared to the total collection method (Zhang and Adeola, 2017). Furthermore, quantitative collection of feed and feces is not required (Zhang and Adeola, 2017). An ideal marker should be 1) totally indigestible and

nonabsorbable, 2) nontoxic to the digestive tract, 3) pass through the digestive tract at a relatively uniform rate with digesta, and 4) easy to be analyzed (Moughan et al., 1991). The most common markers used are chromium oxide, titanium dioxide and acid-insoluble ash (Moughan et al., 1991). The total collection and index methods require wet chemical analysis to determine nutrient digestibility; however, the index method requires a more precise chemical analysis of the indigestible markers (Kong and Adeola, 2014). Both the feces and digesta can be analyzed for digestibility depending on the objective of the experiment. Total collection of feces will result in apparent total tract digestibility (ATTD). Even ATTD values provide valuable information, it does not correct for endogenous secretions which include digestive secretions, mucus, shedded epithelia cells and microbial matter (Danfaer and Fernández, 1999). Nutrient absorption mainly occurs in the small intestine (Vigors et al., 2016). Indeed, the apparent ileal digestibility is more accurate representation of the pig's nutrient digestibility (Albun et al., 2001). Sampling the digesta either requires the insertion of T-cannulas (Cunningham et al., 1963) or euthanizing the animal followed by intestinal dissection (Vigors et al., 2016) T-cannulas are implanted at the end of the ileum and allow researchers to perform repeated sampling of the digesta (Cunningham et al., 1963). However, apparent ileal digestibility also contains endogenous secretions (Danfaer and Fernández, 1999) including basal ileal amino acids (AA) (represent quantities of AA lost by the animal regardless of the diet) and specific ileal AA (represent AA losses from feed ingredient composition) (Zhang and Adeola, 2017). True ileal digestibility would be the most accurate representation of nutrient digestibility of pigs by correcting apparent ileal digestibility values for total (basal plus specific ileal AA) or just basal ileal AAs which will results in standardized ileal digestibility (Zhang and Adeola, 2017). The most common method to estimate basal ileal AA is feeding a nitrogen free diet (Adeola et al., 2016).

In vivo studies have many benefits and are very useful for predicting nutrient digestibility. However, living animals make it challenging to control the environment and manage other factors. There is also a high cost associated with *in vivo* measurements, especially with large-sized animals such as pigs (Bastianelli et al., 2015) and time-consuming (Boisen and Fernández, 1999).

2.5.2 *In vitro* studies

The goal of *in vitro* studies is to stimulate *in vivo* conditions. *In vitro* methods mimic an animal's gastrointestinal digestion (Chen et al., 2014). The complexity of the digestion process makes it near impossible to precisely repeat the same results with *in vitro* methods (Hur et al., 2011). *In vivo* methods are considered the "gold standard" for determining digestibility, but due to cost, time and resources, there is a need for *in vitro* methods (Lucas-González et al., 2018). *In vitro* involves 3 steps; 1) gastric digestion using pepsin, 2) small intestine digestion using pancreatin and 3) large intestine digestion using viscozyme (Boisen and Fernández, 1997). Depending on the objective of the experiment, the choice of enzymes and incubation conditions can change (Boisen and Eggum, 1991). Such methods like single-enzyme methods can predict digestion of single nutrients, or multi-enzyme methods can predict digestion of multiple nutrients (Boisen and Eggum, 1991). Digestion of one nutrient can be influenced by the digestion of other nutrients so even though multi-enzyme methods can be more difficult, they give more reliable values (Boisen and Eggum, 1991). For simulating large intestine fermentation, often *in vitro* incubations use live bacteria from intestinal fluids or feces extracts (Boisen and Eggum, 1991).

Recharla et al. (2019) evaluated the effect of multi-enzyme complex on various swine feed ingredients with *in vitro* digestibility methods and the *in vitro* total tract digestibility was increased with corn meal and Oriental herbal extract with the addition of enzymes. Tiwari et al. (2018) used *in vitro* methods to determine the fermentation characteristics of distillers dried grains with

solubles (DDGS) and the effect of enzymes (xylanase and mannanase) on the production of short chain fatty acids and branched chain fatty acids.

One benefit to *in vitro* digestibility is that protein and AA values are not influence by protein and AA endogenous secretions (Danfaer and Fernández, 1999). Because *in vitro* methods involve manual procedures, human errors can occur and the accuracy and repeatability of prediction might be unsatisfactory (Chen et al., 2014). Computer-controlled stimulated digestive system (CCSDS) has been developed that stimulates gastric pH change, peristaltic movements, gastric emptying rates, intestinal transit times, enzyme secretion, and small intestine absorption (Minekus et al., 1995; Święch, 2017). *In vitro* methods to study nutrient digestibility are, nevertheless, an useful alternative to using animal models (Lucas-González et al., 2018).

2.5.3 Near infrared spectroscopy (NIRS)

Because the nutritive value of feeds can vary substantially, *in vivo* evaluations take too much time and cost too much, thus NIRS is extensively used in agriculture. NIRS is an analytical technique that involves the absorption of light by the chemical bonds of samples and by this way determines the chemical composition of samples (Bastianelli, 2013; Bastianelli et al., 2015). Energy is absorbed by covalent bonds of a sample which cause a vibration specific to the covalent bond and is recorded in a spectrum (García-Sánchez et al., 2017; Noel et al., 2022). This gives structural information about the chemical compositions of the sample and NIRS can predict both the physical and chemical properties (Noel et al., 2022). Compared to chemical analysis, it is cheap and rapid, however, it requires many reference data from *in vivo* values to make strong calibrations (Wang and Zijlstra, 2018). It can take many years to build a database of samples that have been evaluated *in vivo* (Noel et al., 2022). It is also non-destructive and does not require a large sample quantity (Bastinelli, 2013). NIRS analyses the chemical composition of the sample with which the

nutritional value is estimated using prediction equations that are based on a calibration curve of reference data (Bastinelli, 2013).

Estimating energy and nutrient digestibility is important to optimize the nutrients supplied to the growing pig. Additional nutrients are extracted through the waste system of the body which is considered a production loss. Finding the optimal diet to meet the nutrient requirements of a pig can be complex, however, it is essential for precision feeding. However, food digestion can be a complex process in which many factors are involved.

2.6 Energy

2.6.1 Definition of dietary energy

Energy is a difficult concept as it is not a nutrient but rather a characteristic of a diet (Patience, 2012) but its accurate supply is essential for optimizing pig production (Kil et al., 2013). It is an important topic as energy represents 70 to 90% of dietary dry matter (DM) (Gutierrez and Patience, 2012). Energy can be supplied by either simple carbohydrates (starch), complex carbohydrates (fibre), fats and proteins, and their bioavailability is different from each source as well as each is utilized with a different metabolic efficiency (i.e. maintenance energy) (Patience et al., 2015) For example, the pig's efficiency for starch is much higher compared to fiber, and fiber digestibility can vary depending on levels of acid detergent fiber (ADF) (lower digestibility) and neutral detergent fiber (NDF) (higher digestibility) (Patience et al., 2015). Pigs consume feed until they meet their energy requirements is an important and well-known concept (Nyachoti et al., 2004). Thus, the level of energy in the feed influences feed intake and the quantity of other nutrients. In extreme cases when energy level of the feed is too high, feed intake would be reduced, and other essential nutrients would be limiting.

To measure energy, a calorie is defined as the quantity of heat required to raise the temperature of 1 gram of water from 25°C to 26 °C at one atmospheric air pressure (Patience et al., 2015; Russo and Silver, 2011). Since energy represents 50% or more of the total cost of feed, (Patience et al., 2015), it is critical to accurately match the energy requirements of the pig with energy values of the feed (Kil et al., 2013).

2.6.2 Energy systems

Energy is the costliest portion of the feed (Noblet et al., 2020) so accurate prediction is critical. Underestimating energy will impact the pig's growth whereas overestimated energy will increase feed costs with no added benefit (Noblet et al., 2020). Thus, it is necessary to accurately estimate the energy in the diet and with this, four energy systems have been defined to estimate the energy content of the feed (Kil et al., 2013).

Gross energy (GE) is the measure of the total energy content in the feed or ingredient (Patience, 2012) and depends on the concentration of carbohydrates, lipids, protein, and minerals (Gutierrez and Patience, 2012). Fat has a high GE content whereas carbohydrates have a low GE content (Noblet and van Milgen, 2013). GE can be measured using a bomb calorimeter (Noblet and van Milgen, 2013). Given that it does not truly represent usable energy by the pig, GE has little value in animal nutrition (Kil et al., 2013). As the feed is ingested, a portion of GE is not used by the animal and thus is wasted in the feces (Gutierrez and Patience, 2012). The measure of digestible energy (DE) corrects GE for energy lost in feces (Patience, 2012) and is calculated by subtracting energy lost in feces from the GE content of the feed (Gutierrez and Patience, 2012; Kil et al., 2013). The DE content can be measured using digestibility cages and fecal collection either total collection over a set number of days or using indigestible markers in feed (Noblet and van Milgen, 2013). However, energy is also lost in urine and gasses as the energy is metabolized and

this is metabolizable energy (ME) (Gutierrez and Patience, 2012). The level of energy lost in the urine depends on the pig's capacity to retain energy as protein thus both the pig's physiological state and diet characteristics determine energy lost in urine (Noblet and van Milgen, 2013). The ME content can be measured using metabolism crates (Noblet and van Milgen, 2013). As energy is metabolized some energy is lost in the form of heat. ME minus heat increment represents net energy (NE) (Kil et al., 2013; Gutierrez and Patience, 2012). Heat increment (HI) includes energy lost as a result of digestion, absorption, and metabolism (Gutierrez and Patience, 2012) and a "normal" level of physical activity (Noblet and van Milgen, 2013). The HI-to-ME ratio of the feed depends on the level of ME supplied and the final utilization of ME for either fat or protein deposition (Noblet and van Milgen, 2013). NE content can be measured by heat production through the use of direct or indirect calorimetry (Noblet and van Milgen, 2013). NE most closely represents the portion of the energy used by pig from the ingredients in the diet (Kil et al., 2013).

With the increasing energy costs, the NE system is the most popular method in measuring energy as to not overfeed pigs and waste feed (Gutierrez and Patience, 2012). However, variation can still exist with NE system, as there are different energy efficiencies with energy used for maintenance, protein accretion or lipid accretion (Patience, 2012). With pigs, both DE and ME systems are mostly used because these values are relatively easy to measure (de Lang and Birkett, 2005). The goal of energy systems is to estimate energy values in feed ingredients to accurately formulate diets that meets the requirements for optimal growth and to minimize feed costs (Kil et al., 2013).

2.6.3 Factors affecting energy utilization

Energy is released when carbon-containing compounds such as fat, carbohydrate and protein are oxidized (Patient et al., 2015). Efficiency of energy utilization is determined by the

animal's ability to extract energy from the diet and utilize the energy towards metabolic processes. Energy is naturally lost in the feces, urine, gasses and as heat produced when pigs consume feed (Kil et al., 2013) thus some energy is always expected to be lost. To maximize NE of the diet fed to the pigs it is important to reduce how much energy is lost.

Typically, DE can represent about 85% of GE (Patience, 2012) but can vary between 70 and 90% (Noblet and van Milgen, 2004). Most variation of DE utilization is related to the presence of dietary fibre (DF) as DF is less digestible compared to other nutrients such as starch, fat, and protein (Noblet, 2013; Noblet and van Milgen, 2004). A negative correlation exists between DE utilization and DF (Noblet, 2013). The level of fibre digestibility can vary with different sources of fibre (Noblet, 2013) or its botanical origin (Noblet and van Milgen, 2013). DF provides very little energy to the young growing pig, so adding DF will dilute the feed and decrease the energy density (Noblet & van Milgen, 2004). In other words, more energy will be lost in the feces. In contrast, another factor for DE utilization is the presence of fat (Noblet & van Milgen, 2004). Fat has a high gross energy content, and high digestibility, increasing energy density of the diet (Noblet & van Milgen, 2004). Digestibility of energy can also depend on feed processing treatments (Noblet & van Milgen, 2004). Pelleting combines all necessary nutrients into one bite and increases energy digestibility (Noblet, 2013) and pelleting treatments involves mechanical pressure and moderate temperatures which may disrupt cell walls and structures (Le Gall et al., 2009). In study involving four diets of varying fiber levels, pelleting improved overall digestibility of organic matter and energy however the positive effects of pelleting were not sufficient to compensate for negative effects of DF in the diets (Le Gall et al., 2009). BW is also a significant factor contributing to digestible energy utilization (Noblet, 2013). As pigs increase in age and BW, digestibility of energy increases (Noblet, 2013; Noblet & van Milgen, 2004) due to an improved

digestive capacity of DF, which is related to the source of the fibre (Noblet, 2013). The improved digestive capacity of DF with age is attributed to a maturation of the hindgut capability (Noblet, 2013) and a slower rate of digestive passage (Le Goff et al., 2002). Digestibility coefficient of energy for fibre rich feeds improved by 40 % with 150 kg pigs compared to 45 kg pigs. (Noblet and Shi, 1994). With diets high in starch, DE utilization is not improved with BW as starch is totally digested at all growth stages of the pig (Noblet and Shi, 1994).

ME represents about 82% if the GE and 96% of digestible energy since urine and gasses lost represent 3-4% (Patience, 2012). The energy lost in gasses can range from 0.4% in growing pigs (Noblet et al., 1994) to 1.5 % and may reach 3% in sows (Noblet and Shi, 1993). Variations in energy lost in gasses depend on BW and DF level in the diet (Noblet and Shi, 1993). From 45 kgs to 150 kgs of BW increased energy losses as methane and in urine by 50% (Noblet and Shi, 1994). Therefore, both contribute to the methane production, increasing energy lost by gasses (Noblet and van Milgen, 2004). As for urine loss, this depends on the diet's urinary nitrogen excretion and protein content (Noblet and van Milgen, 2004). As protein content is increased in the feed, more nitrogen is excreted in the urine (Noblet and van Milgen, 2004).

As for the metabolic utilization of metabolizable energy which is NE, energy is lost at the cost of ingestion, digestion, and physical activity (Noblet and van Milgen, 2004). These represent the metabolic cost of converting ME into usable energy for the pig (Patience, 2012). This metabolic cost is largely dependent on the chemical characteristics of the feed (Noblet and van Milgen, 2004). Some nutrients are more easily digested such as starch and dietary fat compared to more difficult ones such as fibre and protein (Noblet et al., 1994). The heat increment is higher for CP and DF as they are more difficult to digest (Noblet et al., 1994). Thus, the metabolic utilization of ME is dependent on the chemical characteristics of the feed and the nutrient being deposited.

The dietary energy that is actually absorbed by the pig is used towards maintenance or retention of body protein or lipids (van Milgen and Noblet, 2003; Kil et al., 2013) with about 34%, 19% and 47% of the total ME intake partitioned to each in a 70 kg pig, respectively (Patience, 2012). Thus, efficiency of metabolizable energy utilization is dependent on the pig's efficiency of energy utilized for maintenance, protein gain and fat gain (Gaillard et al., 2020). Energy utilization for maintenance is associated with the continuous maintenance of vital physiological functions of the body that are not associated with protein and lipid gain (Patience, 2012). Energy required for maintenance are used for functions like protein turnover, basal metabolism, thermoregulation, immune function and nutrient digestion and absorption (Knap, 2009). The quantity of energy allocated towards maintenance or retention is dependent on growth stage, genetics, thermal environment, and nutritional composition of the diet (Kil et al., 2013). Addition energy after maintenance requirements are met, are used towards growth or body tissues. The efficiency of using ME towards protein gain and lipid gain was estimated to be 60% and 80% respectively (Noblet et al., 1999).

2.6.4 Energy utilization efficiency as a measure of feed efficiency

FE can be expressed as energy consumed rather than feed consumed which is an intuitive concept as energy is the costliest component of the diet (Patience, 2012). Given that feed intake is influenced by the energy concentration of the feed (Li and Patience, 2017), selection for greater FE has consequently enhanced energy efficiency rather than nutritional efficiency (Kasper et al., 2020). The term "Mcal of energy per unit of gain' is used to express energy utilization efficiency (Patience, 2012). However, expressing FE as energy utilization efficiency poses some errors with how the energy content of the diet is determined (Patience et al., 2015). Firstly, quantifying dietary energy concentration is often a book value rather than determined biologically (Patience et al.,

2015). Due to variation among feed ingredients, the book value may not truly reflect the true energy content (Patience et al., 2015). The second error is the method of expression of dietary energy concentrations. Even though net energy is the true representation of useable energy, digestible and metabolizable energy systems are still continued to be used (Patience et al., 2015). Thus, inaccurate energy systems would cause variations in FE that are not related to the pig's ability to use the energy. Nonetheless, expressing FE as an energy utilization efficiency approach has potential and will force the estimation of the energy content of ingredients to improve (Patience, 2012).

2.7 Body weight gain

BW is measured as grams or kilograms per day, however the chemical composition of BW gain is important. BW gain can consist of lean tissue, fat tissue and visceral organs mass. As the pig grows, protein and lipid deposition simultaneously increases at a similar rate until PD_{max} (genetic potential for lean tissue gain) is achieved or other factors limit protein deposition (van Milgen and Noblet, 2003). Beyond PD_{max}., the lipid deposition rate would be much higher then the protein deposition rate (van Milgen and Noblet, 2003). Factors that determine energy partitioned to protein and lipid deposition are the genetic potential for lean tissue gain, dietary energy content and AA supply (van Milgen et al., 2008). PD_{max}. is determined by the genetics of the animal and is closely related to ADG (van Milgen et al., 2008). A linear relationship exists between the energy content of the feed and protein deposition (van Milgen and Noblet, 2003; Bikker et al., 1995) thus as energy content of the feed increases, so does protein deposition. Essential AA content of the feed also can determine protein deposition of the pig (van Milgen et al., 2008). Lysine-deficient diets of both 90 and 70% have shown to decrease protein deposition (Mŏhn et al., 2000). Deficiencies of lysine and energy intake have independent effects on protein

deposition such that when energy intake is limiting protein deposition, lysine intake does not affect protein deposition and conversely, when lysine intake is limiting protein deposition, energy intake will not affect protein deposition (Mŏhn et al., 2000).

The ME utilization efficiencies are 60% and 80% for protein and lipid deposition respectively (Noblet et al., 1999) however protein deposition costs 9.1 MJ of ME per kg whereas lipid depositions require 29.2 MF of ME per kg (Gaillard et al., 2020). In addition, of the daily metabolizable energy consumed, lipid accretion requires three times the energy content compared to protein accretion (Noblet et al., 1999). Thus, protein gain is much more efficient than lipid gain. The chemical composition of BW gain is dependent on the intake of nutrients and the digestive and metabolic utilization of the nutrients by the pig (Whittemore and Fawcett, 1976) which are both determined by genotype, sex, BW, factors (Noblet et al., 1999) and diseases (Schweer et al., 2017).

Composition of BW gain is associated with differences in voluntary feed intake and feed behaviours (Quiniou et al., 1999). Meishan is considered a fattier breed compared to the leaner breed Piétrain (Quiniou et al., 1999). Given their different body compositions they have similar voluntary feed intake however different feed strategies (Quiniou et al., 1999). Meishan pigs consumed half the amount of meals per day (7.3 vs 14.4 meals/day) but meal size was double the size (250 vs 125 g/meal) compared to Piétrain pigs. Protein deposition can be associated with high number of small meals per day.

Genetics can determine the composition of BW gain resulting in breeds that differ in carcass characteristics. Meishan is considered a fattier breed compared to the leaner breed Piétrain with Large white considered the intermediate, conventional breed (Noblet et al., 1999). Protein

deposition was higher in the synthetic line and Piétrain males compared to the Large white and Meishan males (Noblet et al., 1999) resulting in a different body composition weight gain.

Between genders, boars usually have higher protein deposition compared to females and castrated males. Within the large white breed, boars had the highest protein deposition (3.9 MJ/d) compared to the females (3.2 MJ/d) and castrated males (3.1 MJ/d) (Noblet et al., 1999). For lipid deposition, castrates had the highest (9.4 MJ/d) compared to females (7.6 MJ/d) and boars (7.7 MJ/d) (Noblet et al., 1999). This will result in leaner carcass with boars and fattier carcass with castrated males.

Diseases cause a reduced feed intake and in addition can change nutrient utilization and reduce protein and lipid deposition rates. The effect of Porcine Reproductive and Respiratory Syndrome virus (PPRS) over 80 days after inoculation was evaluated on lean tissue accretion. The challenged pigs had decreased whole body accretion of lean, protein (10% reduction) and fat (20 % reduction) compared to the controlled pigs (Schweer et al., 2017).

2.8 Research advances and gaps

FE is misunderstood by researchers due to the lack of knowledge of the biological basis as well as how to measure and express FE (Patience et al., 2015). Furthermore, due to the fact that financial returns are strongly influenced by FE, many attempts have been made in research to improve FE. Often attempts fail to acknowledge all the factors that have an effect and costs are increased rather than decreased (Patience et al., 2015). Nutritionists have tried to increase dietary energy in feed while geneticists have selected solely for improved FE (Patience et al., 2015). Both are single-minded attempts that only focus on one factor involved rather than the many factors involved. Nevertheless, the effects of pig genetics on FE should be studied when all the other

factors such has diet and rearing and management conditions are kept constant for the genotypes tested. Furthermore, diet and rearing conditions should be adjusted to the requirements as the animal growths as only in this situation the true growth potential can be achieved, and genotypes compared, and this was investigated in this thesis. Moreover, comparison between genotypes on FE should be comprehensive and include not only growth performance measures but also evaluate the nutrient digestibility and energy utilization efficiencies as this will vary as a function of the composition of the body growth, i.e., lean versus lipid body deposition.

CHAPTER 3: HYPOTHESES AND OBJECTIVES

3.1 Hypothesis

The following hypothesis were tested in this thesis:

1. Selecting pigs for high feed efficiency will produce pigs with unchanged or better growth performance and carcass characteristics
2. Feed intake differences can explain some of the differences observed between high and low efficiency pigs, with high efficiency pigs having a lower ADFI.
3. Improved nutrient utilization and digestibility in high feed efficiency pigs can explain some of the differences observed between high and low efficiency pigs

3.2 Objectives

1. To establish the effect of low or high feed efficiency animals within breed on nutrient digestibility, growth performance and carcass characteristics.

CHAPTER 4: MANUSCRIPT I

The effect of selecting for feed efficiency on digestibility, growth performance, and carcass characteristics of two Large White lines

4.1 Abstract

In pig breeding, one of the main goals is to improve the feed efficiency (FE) in pigs and estimated breeding values on feed conversion ratio (EBV_FCR) can be used to select animals within breed; however, the influence of EBV_FCR on growth performance, nutrient digestibility and carcass characteristics needs further investigation. Our objective was to determine the effect of selecting for high (HFE) or low (LFE) FE based on EBV_FCR within a Large White dam and sire line on growth performance, apparent total tract nutrient digestibility (ATTD) and carcass traits. From 11 to 23 weeks of age, boars were fed ad libitum and feed intake and body weight was recorded. At 23 weeks of age, pigs were sedated, and live carcass composition was measured using CT scans. As expected, sire line was superior compared to dam line in terms of FE, growth performance and carcass characteristics ($P < 0.05$); and the sire line had a tendency for a higher Ca ATTD ($P = 0.09$). HFE pigs consumed less feed ($P < 0.05$), had thinner fat depth ($P < 0.05$) and had greater loin depth ($P < 0.05$) then LFE pigs. In addition, HFE pigs had a significantly higher ATTD for Ca ($P = 0.05$) and a tendency for a higher ATTD for CP ($P = 0.06$), and phosphorous ($P = 0.10$) compared to LFE pigs. In conclusion, HFE pigs had a better growth performance, carcass characteristics, and nutrient digestibility compared to LFE pigs. Selection on EBV_FCR can improve FE via improvements in growth performance, carcass traits and nutrient digestibility.

Keywords: feed efficiency, growth performance, feed conversion ratio, carcass characteristics, apparent total tract digestibility

4.2 Introduction

Feed accounts for approximately two-thirds of the total cost of production; thus, it can significantly impact the profitability of any swine operation (Patience et al., 2015). Therefore, improving feed efficiency (FE) is a major goal in swine production in terms of production and environment costs. FE is described as the pig's ability to turn feed into the end product, such as pork. Thus, production costs can be reduced by increasing the pig's FE (Bergamaschi et al., 2020). FE can be expressed as feed conversion ratio (FCR), which is defined as feed intake (FI) over body weight gain (BW) (Houque et al., 2007). An animal with a low FCR consumes less feed per unit of BW and is desired compared to an animal with a higher FCR that consumes more feed (Bergamaschi et al., 2020) for the same BW gain. However, FE is a complex trait involving efficient utilization and body storage of energy and nutrients from feed. Body tissues such as muscle, adipose tissue, organs and bones, require different nutrients for their growth as well as different nutrient efficiencies. For example, muscle growth requires amino acids (AA) and energy while adipose tissue requires fatty acids and energy (Patience, 2012). The efficiencies of nutrient utilization for protein and lipid deposition are different (Patience, 2012) such that efficiency of ME utilization for protein deposition is 0.51 while for lipid deposition is 0.81 (van Milgen et al., 1999).

In pig breeding, purebred pigs are selected for FE at the nucleus level. Selection to improve feed utilization continues to be a challenge in livestock species, which is necessary for economic and environmental reasons. One method to genetically improve FE is by using estimated breeding

values (EBV) which is the genetic value of an animal and an estimation of the animal's potential for specific traits (Van der Peet-Schwering et al., 2021). The EBV for FCR could be an effective selection index that aims to maximize FE and in turn, improve growth performance and carcass composition (Patience et al., 2015). Other experiments that selected for FE over several generations, not only resulted in divergent lines of FE (high and low) but also differences in nutrient digestibility, growth performance and/or carcass characteristics in Yorkshire pigs (Cai et al., 2008) and Large White pigs (Gilbert et al., 2007). Because the main biological factors causing differences in FE are not well understood, and the results are inconsistent among experiments comparing high and low efficiency pigs, the various biological factors behind differences in FE need to be investigated. Key biological factors that cause variation in FE include heat production (Barea et al., 2010; Boddicker et al., 2011), maintenance energy utilization (Barea et al., 2010; Boddicker et al., 2011), feed intake and patterns (Young et al., 2011), nutrient digestibility (Harris et al., 2012; Vigors et al., 2016; Mauch et al., 2018), and body composition (Cai et al., 2008; Smith et al., 2011; Young et al., 2011; Hewitt et al., 2020; Lefaucheur et al., 2011; Hoque et al., 2007).

Selection responses for EBV-FE in pigs within Large White lines in relation to digestibility, growth performance, and leanness remain to be investigated. Thus, the objective of this study was to evaluate the apparent total tract digestibility (ATTD), growth performance and live carcass composition using CT-scan on pigs with diverse EBV-FE (low or high FE animals) within Large White breed lines.

4.3 Materials and Methods

The experimental procedures were approved by the University of Manitoba Animal Care Protocol Management and Review Committee (F20-026) for compliance with the guidelines of the Canadian Council on Animal Care (CCAC, 2009).

4.3.1 Management of pigs

Total of 2000 male pigs of Large White lines (dam-line vs sire line) were raised at the Topigs Norsvin Delta Nursery facility in consecutive baches, representing low, intermediate, and high efficiency, which was based on the EBV_FCR. At 11 weeks of age, piglets were transferred to Topigs Norsvin Delta Canada facility and housed in 8 pens of 12 pigs every week. Each pen was equipped with an automatic feed station where feed intake was monitored individually every visit. Individual bodyweight was recorded as the median of all weights registered at visits to the feeding station. All pigs were monitored for 80 days. Pigs were fed a corn-wheat-canola meal-based diet (Table 1.) and had ad libitum access to feed and water throughout the experiment.

Table 4.1 Ingredients and nutrient composition of diet

Ingredient Name	Amount*	Nutrient Name	Actual
Ground Barley	299.92	Crude Protein (%)	14.34
Corn Clean Ground	250.00	Crude Fat (%)	3.52
Ground Wheat	207.50	Crude Fiber (%)	4.56
Wheat Shorts	80.00	Non Fiber CHO[1] (%)	61.25
Soybean Meal 46%	50.00	NE[2] Swine (kcal/kg)	2350.01
Distillers Grain	34.50	Calcium (%)	0.721
Oat Hulls (Ground)	22.00	Phosphorous (%)	0.583
Monacol Phos >10KG bulk	10.00	Phosphorous available (%)	0.437
Vegoil	10.00	Chloride (%)	0.380
Coarse calcium (>5kg)	9.10	Magnesium (%)	0.166
Boilys (60%)(Lysine)	8.00	Potassium (%)	0.530
Potash salt bulk (>5 kg)	5.10	Sodium (%)	0.230
Threonine-L	2.25		
DL-Methionnie	1.43		
Tryptophan-L	0.540		

Lysine-L HCL 78%	0.450
FR Vit E 100000 IU/KG	0.250

*based on 1000 kg
[1]Carbohydrate; 2Net Energy

4.3.2 CT scanning

At 23 weeks, computed tomography (CT) scan was performed on each pig, according to Kongsro et al. (2017). Pigs had free access to water but no solid feed for a minimum of 8 h before weighing and scanning. On the day of CT scanning, boars were transferred to CT scan restroom (one animal/pen), mildly sedated, and then placed into a purpose-built cradle on the scanning unit. Pigs were sedated intramuscular. With a cocktail composed of ketamine, acepromazine, and xylazine to minimize disturbances in the CT images due to movement. Animals were fully scanned with a General Electric HiSpeed Zx/I tomograph, located in Topigs Norsvin Delta Canada Facility (Woodlands, Manitoba), and the instrumental settings were 140 kV, 145 mA, matrix 512 × 512, axial, 7 mm thick (30 kg TBW), and 10 mm thick (70, 100, and 120 kg TBW). A custom-built half-tube cradle (PVC, Ø 0.30 m, length: 1.2 m for 30 kg pigs; and Ø 0.46 m, length: 1.8 m for 70, 100, and 120 kg pigs) was used to hold the pigs in the prone position during scanning.

In the CT scanning machine, the animal passed through a circular gantry, and low dosage X-rays were beamed around it while detectors measured the absorption of the rays. A longitudinal scan of the whole body of the animal was initially taken, and landmarks lines were placed on the image at specific anatomical positions. The animal was scanned in a position that allowed for mapping the areas of interest for measuring commercial traits. The CT scanning process determines the weight of muscle and fat across the whole carcass. Fat, muscle, and bone appeared on the scans in different shades of grey. Both lean and fat depositions were measured.

4.3.3 Determination of FCR

The EBVs of individual pigs were estimated using the ssGBLUP method in MIXBLUP (Ten Napel et al., 2018). To create the genomic relationship matrix, a 25K single-nucleotide

polymorphism chip was used. The EBV_FCR was estimated by Topigs Norsvin Research Center (Beuningen, The Netherlands). Feed intake was measured individually using radio frequency identification devices (RFID) and bodyweight was recorded as the median of all weights registered at visits to the feeding station. FCR was calculated for each boar using the following equation: $\text{FCR} = \frac{\text{ADFI (kg)}}{\text{ADG (kg)}}$. The lower values represented high efficiency pigs and high values represented low efficient pigs.

4.3.4 Fecal sample collection for digestibility

Fecal samples were collected from pigs on the day of the CT scanning. Before CT scans, pigs were transferred to clean individual pens. Fresh fecal samples were collected from individual pigs by hand using sterile plastic bags. Samples were carried on ice and stored in a -20°C freezer.

4.3.5 Chemical analysis

Fecal samples and finisher diets were analysed at the University of Manitoba Animal Nutrition Laboratory. Before the proximate analysis, the feed sample was grinded down to 1 mm using a Wiley mill (Thomas Model 4 Wiley Mill) prior to further analyses. Dry matter was determined according to the AOAC 934.01. An empty aluminium tin with lid was weighed (W1), then the tin with 1-2 g of the sample was measured (W2). Measurements were repeated in duplicates and both samples were placed in a preheated oven set to 104°C. The lid of the tin was left ajar to allow the moisture out. Samples were dried overnight in the oven and were placed in a desiccator to cool afterwards. After cooling, the tins were weighted again (W3). To calculate the dry matter, the equation below was used:

$$\text{DM (\%)} = \frac{\text{W3 -W1}}{\text{W2}} \times 100$$

NDF and ADF were determined using an Ankom fiber analyzer (Ankom Technology, Macedon, NY) and according to the AOAC 973.18. The weight of the empty F57 filter bag was recorded and then the bag was filled with 0.5g of the sample. Bags were sealed closed within 0.5 cm from the open edge using a heat sealer. Samples were spread uniformly inside the filter bags and were loaded into trays. Trays were loaded into the digestion vessel and 2L of ADF or NDF solution was added. For ADF, the solution contained sulphuric acid, hexadecyltrimethylammoniumbromide, and tris hydroxymethyl aminomethane. For NDF, the solution contained EDTA, sodium borate, sodium lauryl sulfate, ethylene glycol and sodium phosphate. Since the sample contained starch, 4.0 ml of alpha amylase was used for the NDF analysis. The machine ran through its cycle for NDF, and the replicate of samples ran the cycle for ADF. After their cycles, samples were submerged in Acetone for 5 mins and then air dried for 20 mins. Samples were placed into a preheated 102°C oven overnight. The next day, samples were weighed again to calculate NDF and ADF using the following equation:

$$\text{NDF. ADF (\%)} = \frac{\text{Final weight} - (\text{Bag weight} \times \text{Bag correction})}{\text{Sample weight (DM basis)}} \times 100$$

Dietary gross energy was measured using an adiabatic bomb calorimeter (Model 6400, Parr Instruments, Moline, IL) calibrated using benzoic acid as a standard. Samples were formed into 1.0-1.5 g pellets into capsules and weights were recorded. Capsules were loaded onto a bomb head and a combustion string was tied from the heating wire and dangled down so it made contact with the pelleted sample. The bomb head was loaded into the calorimeter and the machine ran its course. After each sample, the acid waste was collected and acid correction was performed using titration with 0.0724 N Na_2CO_3. Methyl Orange was used as an indicator. The mL used was recorded and inputed into the machine to calculate the gross energy.

Calcium (Ca) and phosphorous (P) contents were determined using a Varian Inductive Coupled Plasma Mass Spectrometer, ash was determined according to the method AOAC 942.05. 1.0 g of sample was weighted into a 25 x 150 Kimax tube. Samples were ashed for 12 hours at 600 °C. 10 ml of 1% HNO_3 5N HCl was added, and the solution was digested for 1 hour in a sonication bath that was preheated to 70°C. Next, samples were mixed and diluted with deionized water. Samples were filtered through Q5 filters and analysed using the ICP Spectrophotometry. Samples were calculated using the following equation:

$$\text{Mineral (\%)} = \left(\frac{\text{ppm Mineral} \times \text{Dilution Factor}}{\text{Sample weight}}\right) \div 10{,}000$$

Ash was determined according to the method AOAC 942.05. The weight of a crucible was taken (W1) and then 1 to 2 g of the sample was weighed with the crucible (W2). The samples were dried in a muffle furnace for 2 hours at 600 °C. After 2 hours, samples were then cooled for 15-30 mins in the oven and were removed to a desiccator. Samples in the crucible was weighed (W3) and % of ash was calculated using the following equation:

$$\text{Ash (\%)} = \frac{\text{W3 -W1}}{\text{W2}} \times 100$$

Acid-insoluble ash (AIA) was determined using the method described by McCarthy et al. (1974). 10 g of the sample was weighted into a beaker, 100 mL of 4N HCl was added and boiled for 30 mins. The slurry was filtered through Whatman 541 filter paper and washed with 500 ml of boiling distilled water until free of acid. The residue was ashed at 600 °C for 12 hours and then the ash was weighed and recorded. Acid insoluble ash was calculated using the following formula:

$$\text{AIA}(\%) = \frac{\text{Ash wt.}}{\text{Sample wt.}} \times 100$$

Crude protein was analysed at Central Testing Laboratory Ltd. (Winnipeg, MB) according to AOAC 990.03 method.

4.3.6 Statistical analysis

Data were analyzed using the PROC MIXED model procedure of SAS (SAS Inst. Inc., Cary, NC) version 9.2 (SAS 2003). The model used for the data was a CRD with a factorial arrangement. Genetic lines (dam-line vs sire-line), EBV-FC (low- vs and high-efficient groups) and their interactions were fixed effects. CT-scanning day was considered a random effect. Least squares means for unequal subclass numbers were separated (F test, $P < 0.05$) using the least significant differences generated through the PDIFF option. The degrees of freedom in the denominator were adjusted using the Kenward-Roger procedure.

In the present study, the initial weight at the beginning of the experiment was significantly different among genetic lines. Therefore, in order to determine whether performance or carcass traits differences could be due to the weight difference rather than to any genetic line, the data were submitted to a simple regression test to determine if initial weight were correlated with growth performance and carcass traits; respectively. Thus, initial weight was included as a covariate in the model when a significant correlation with any individual dependent variables was detected.

4.4 Results

The results of growth performance and carcass traits for genetic lines (sire line and dam line) characterized by EBV-FCR (low and high) are described in Table 2. Analysis of covariance (adjusted for initial BW) did not detect a significant effect of the genetic line x EBV-FCR interaction on the different variable responses except for FCR ($P = 0.03$). The sire line was heavier

at the end of the experiment ($P < 0.01$; final weight > 9.69 kg), grew more rapidly ($P < 0.01$; ADG > 130.69 g/d), higher daily intake ($P > 0.01$; >149 g) and reached the market in lesser days ($P < 0.01$; < 11.5 d) compared to dam line. At the same time, sire line showed an increase in ADFI with respect to the dam line ($P > 0.01$); however, its growth performance in term of FCR was significantly lower ($P > 0.01$; less feed per BW) than dam line. On carcass traits, the sire line had a greater loin depth ($P < 0.01$; > 6.92 mm) and thinner fat depth ($P < 0.01$; < 2.6 mm) than the dam-line. In terms of nutrient digestibility, there was a tendency for higher Ca ATTD (P = 0.09) for the dam line than the sire line for both high and low efficiencies groups.

On the other hand, for pigs of varying efficiency, there was no significant difference for final weight, ADG, and days to market (Table 2). In terms of feed intake, HFE pigs consumed less feed compared to LFE group for both lines ($P > 0.01$, sire line < 252.43 g/d; dam line < 292.87 g/d), resulting in lower FCR values for HFE. Overall, HFE pigs consumed less feed per BW. For carcass traits, there was no significant difference for carcass weight between the efficiency groups ($P = 0.95$). HFE pigs had the thinnest fat depth for both lines ($P > 0.01$) and presented a greater loin depth then LFE pigs ($P < 0.01$). Overall, regardless of genetic line, HFE pigs had leaner carcass than LFE pigs ($P < 0.01$).

Table 4.2 The effect of feed efficiency between two swine lines on growth performance and carcass traits

Variable	Sire Line		Dam Line			P-Value		
	High (n=52)	Low (n=52)	High (n=53)	Low (n=50)	SEM	L	E	L x E
Growth performance								
Initial Weight, kg	43.89	43.40	39.56	41.59	1.23	< 0.01	0.38	0.15
Final Weight, kg*	121.57	123.12	113.58	112.51	1.40	< 0.01	0.80	0.18
Days to market*	153.41	152.33	161.68	161.06	1.23	< 0.01	0.33	0.79
ADFI, g/d*	2,317.57	2,570.00	2,147.82	2,440.69	54.60	< 0.01	< 0.01	0.60
ADG, g/d*	1,107.24	1,131.66	978.09	971.09	22.64	< 0.01	0.58	0.34
FCR, kg/kg*	2.10[a]	2.27[b]	2.20[b]	2.51[c]	0.45	< 0.01	< 0.01	0.03
Carcass traits								
Carcass weight, kg*	92.69	93.71	86.48	85.38	1.09	<0.01	0.95	0.17
Back fat, mm	5.88	8.19	7.75	9.70	0.47	< 0.01	< 0.01	0.58
Loin depth, mm*	67.83	65.95	61.90	59.64	0.90	< 0.01	< 0.01	0.76
Leaness, %*	72.31	68.30	71.88	67.22	0.56	0.07	< 0.01	0.41

*: Adjusted by co-variance analysis, using initial weight as co-variable
ADG: Average Daily gain (g/d)
ADFI: Daily Feed Intake (g/d)
FCR: Feed Conversion Ratio (ADFI/ADG)

The results for the effect of FE and breed on the digestibility of nutrients are shown in Table 3. The sire line had a tendency for a higher ATTD for Ca (P =0.09) compared to the dam line and no significant difference for dry matter, NDF, ADF, CP, energy, P and ash (P > 0.1). HFE pigs had a higher Ca digestibility than LFE for both lines (P = 0.05). Also, HFE pigs had a tendency for a higher CP (P = 0.06), P (P = 0.10) and ash (P = 0.09) digestibility compared to LFE pigs. There was no significant difference in dry matter, NDF, ADF, or energy between HFE and LFE pigs.

Table 4.3 The effect of feed efficiency and lines on digestibility of nutrients of finisher pigs

Variable, %	Sire Line		Dam Line		SEM	P-Value		
	High (n=52)	Low (n=52)	High (n=53)	Low (n=50)		L	E	L x E
Dry matter	80.83	80.53	81.13	80.21	0.62	0.98	0.17	0.48
NDF	37.81	38.80	40.12	37.53	1.68	0.99	0.28	0.28
ADF*	25.12	26.23	23.64	23.98	1.61	0.11	0.52	0.73
CP	81.35	80.32	81.44	80.18	0.85	0.96	0.06	0.86
Energy	81.37	81.24	81.66	80.71	0.60	0.78	0.21	0.34
P	43.11	40.60	44.24	41.69	2.18	0.47	0.10	0.99
Ca	38.96	36.02	42.21	38.57	2.36	0.09	0.05	0.83
Ash	48.87	46.36	48.63	47.36	1.60	0.73	0.09	0.58

NDF: Neutral Detergent Fibre
ADF: Acid Detergent Fibre
CP: Crude Protein
P: Phosphorous
Ca: Calcium
Adjusted by co-variance analysis, using initial weight as co-variable

Based on the estimated protein deposition and the average feed intake one week before sampling, calculated dietary digestible lysine content diet met the requirements for the average pig (Table 4). Table 4 is a rough estimate of the lysine shortage or surplus from the feed that the pigs may have experienced. With their feeding behavior, both LFE groups experienced a surplus of lysine (Sire line > 1.8; dam line > 3). As expected, with HFE groups reduced ADFI, they experienced a lysine shortage from the feed (Sire line > -3.9; Dam line > -0.6).

Table 4.4 Estimation of lysine shortage or surplus from the feed

		Sire line		Dam line	
Variables*	Average Pig	High	Low	High	Low
DFI (g/d)	2378	2333	2668	2088	2428
DFI_Last_Wk (kg/d)	3.031	2.94	3.57	2.7	3.01
ADG (g/d)	1038	1081	1150	954	976
PD_avg (g/d)	249	277	275	227	218
Required lys (g)	26.6	29.6	29.3	24.2	23.3
Actual lys (g)	26.5	25.7	31.2	23.6	26.3
Lysine Shortage (g)	-0.01	-3.9	1.8	-0.6	3.0

*Based on 200 animals
DFI: Daily Feed intake
DFI_Last_Wk: DFI of week before fecal samples were collected
ADG: Average daily gain
PD_avg: Average protein deposition calculated using formula described in Bergsma et al. (2013) with ADG

Required lys = $\frac{(\mathrm{PD_{avg}} \times \text{lysine (per g of protein)}}{\text{effeciency of lysine}}$

*SID Lysine/ g of protein = 0.07 g (according to NRC, 2012)
*Efficiency of lysine use from feed = 0.656 (according to NRC, 2012)
Actual lys = DFI last wk $\times$ lysine content in the feed
* lysine content in feed = 8.736 g SID lysine per kg (based on feed formula Table #)
Lys Shortage = Actual – required

4.5 Discussion

The boars from the sire line proved to be the more superior line compared to the boars from dam line in terms of FE, growth performance and carcass characteristics. This can be explained by the differences in genetic background. Sire lines are selected for traits that favor production goals like faster growth rates, leaner carcass, or uniformity (Whittemore, 2006). In contrast, dam lines are selected for traits that favor reproduction goals like large litter size, high piglet survival or mothering abilities (Whittemore, 2006). With different selection goals, it is not by surprise that in this study, there are differences in results between the two dam and sire lines. In contrast, Saintilan et al. (2013) compared castrated males of Large white dam line and sire line and found no significant difference between them for growth performance and carcass characteristics

Differences in growth performance and carcass composition can be observed among offspring sex classes within the same White Large breed genetic line. For example, Morales et al. (2011) compared immunocastrated males (IMC), surgically castrated males (CM), and intact females (IF) in two terminal Large White sire lines (Top York = TY and Tempo = TE) and observed no interactions between sex classes and sire lines for any growth performance and any carcass traits at the end of the experiment. Regardless of the genetic line, IMC and CM pigs grew at a faster rate had IF, and IMC were more efficient than the other sexes ($P < 0.001$), but IMC and IF pigs also had less ($P < 0.001$) backfat depth and more lean percentage than CM. At the same time, regardless of the sex class, crossbreds from TE sires grew at a faster rate ($P < 0.001$) than crossbreds from TY sires, but no differences were found for feed intake, efficiency, back fat thickness or carcass lean percentage (Morales et al., 2011). The pigs used in this experiment were entire intact male pigs which are known to have superior growth performances compared to other

sex classes due to present of testosterone (Needham et al., 2017) and to have higher rates of protein deposition (de Lange et al., 2012).

In the current study, EBV-FCR groups did affect the adjusted final weight, ADG and days to market; however, as expected, high efficiency pigs resulted with lower FCR values compared to low efficiency pigs and produced a leaner carcass with consuming less feed. In agreement, Barea et al. (2010) studied two lines of purebred French Large White castrated male pigs (high and low RFI lines) and observed a reduced ADFI and an improved FCR with no changes to ADG compared with the low RFI line. Also, Lefaucheur et al. (2011) observed in French Large White gilt lines, lower ADFI, FCR and unaffected ADG in low RFI pigs (more efficient). Similar results were seen with Yorkshire gilts with a lower ADFI, higher FE and unaffected ADG in the low RFI pigs (Harris et al, 2012). Using genetics to improve FE has repeatedly shown to have no effect on ADG in the current study and others. From an economic standpoint, higher efficiency pigs consumed less feed and showed lower FCR with no change to ADG or market weight so thus these pigs would cost less to produce to same product making them valuable commercially. In this current experiment, live carcass composition was measured using CT scans. We observed leaner carcasses from HFE pigs than LFE pigs, which is in agreement with other studies (Smith et al., 2011; Hewitt et al., 2020; Lefaucheur et al., 2011; Hoque et al., 2007; Cai et al., 2008).

Lean tissue accretion in skeletal muscle is to be associated with rates of lower protein turnover and higher protein deposition which are high energy demanding processes of the body (Hewitt et al., 2020). Animals with higher rates of lean tissue accretion would be associated with higher requirements of energy and protein; however, it does not imply that animals could have higher digestibility for those nutrients and others. Instead, high lean tissue accretion may suggest better utilization efficiency of dietary nutrients and energy (Riverra-Ferre et al., 2006). Rivera-

Ferre et al. (2006) reported differences with nitrogen digestibility and retention among Landrace and Iberian gilts and suggested that pigs with leaner faster growth traits, have a greater capacity for protein synthesis and deposition.

In our study, HFE pigs had a significantly higher Ca digestibility and a tendency for higher CP, P, and Ash digestibility, which would increase the nutrients available towards growth. Thus, we might consider the nutrients was used towards producing lean tissue and explain their leaner carcasses. Higher nutrient digestibility with HFE pigs has been reported in other studies (Harris et al., 2012; Montagne et al., 2014; Vigors et al., 2016; Mauch et al., 2018). In our study, rate of protein turnover was not measured, consequently, the rate for protein accretion could not be established. Hewitt et al., (2020) measured protein turnover and no detected difference between divergent genetic selections for FE was reported, although HFE pigs presented leaner carcasses. Interestingly, the authors suggested that the basis for the differences in leanness could be due to lower fat deposition instead (Hewitt et al., 2020).

Differences in digestion processes and metabolisms between pigs can vary (Barea et al., 2010). And individual pig genotypes play a role in determining ATTD of nutrients and energy due to the genetic merit or phenotypic potential (Harris et al., 2012). In the current study, pigs were fed ad libitum the same diet, thus nutrient digestibility is assumed to be determined by phenotypic potential for FE. Variations in selection for FCR responses could indicate HFE have an improved ability to digest nutrients and energy more efficiently. More efficient pigs have also shown an increase in expression in gene encoding for the enzymes involved in intestinal nutrient transport (Vigors et al., 2016); so, the genetic merit could improve digestibility process. However, results for nutrient digestibility among pigs of divergent FE have been inconsistent. For example, both Barea et al., (2010) and Montagne et al., (2014) reported no differences in nutrient digestibility

among pigs divergently selected for FE within Large White pigs; while Harris et al. (2012) saw greater digestibility values for dry matter, nitrogen and gross energy for higher efficiency Yorkshire gilts of two lines (high and low RFI).

Other factors such as body composition, maintenance requirements, physical activity, feed digestibility, energetic efficiency, and feed behaviours may possibly contribute to differences in FE (Young et al., 2011; Young and Dekkers, 2012). In this study, HFE pigs had a reduced ADFI which was also observed in Young and Dekkers (2011) who measured feeding behaviours and found HFE pigs ate faster, spent less time at the feeder and overall ate less compared to the control line. Table 4 estimates the results of a lower feed intake and possible lysine shortage pigs from the trial may have experienced. Based on feed intake of the previous week before sampling, high efficiency pigs of both sire and dam line may have experienced a lysine shortage (sire line = -3.9; dam line = -0.6). Thus, a lower feed intake in HFE pigs may have caused a shortage of lysine and other nutrients which could have improved nutrient digestibility. When nutrients are undersupplied, the marginal efficiency of retention is at its highest (Gaillard et al., 2020), so improved nutrient digestibility may be attributed to the lower feed intake.

4.6 Conclusion

High FE animals show advantageous growth performance and offer a favorable response in greater loin and leaner animals in the current study and others. HFE pigs also showed a greater nutrient digestibility which is beneficial in terms of body growth, environmental impacts, and feed costs. Nutrient digestibility may be a key biological mechanism that makes one pig more efficient than another and thus it can be used to predict FE. However, it is unclear if the extra nutrients were used towards lean tissue growth. It is also unclear whether the improved nutrient-digestibility is

caused by the lysine-shortage due to a reduced ADFI or the consequence of the differences in genetic merit for FE.

CHAPTER 5: GENERAL DISCUSSION

One of the primary goals for producers is to use the least number of resources to produce the best quality product while reducing feed costs and negative impacts on the environment. The pig industry has made efforts to improve FE which has been done through nutrition and breeding. Pig breeding has significantly improved FE by selecting traits like leanness and ADG (Knap and Wang, 2012). With nutrition, diets are formulated to match the nutrient requirements of pigs by using a balance of nutrient sources. However, nutrient requirements of individual pigs are often not used but rather the group requirements in grower-finisher pigs. Selection to improve FE in livestock has shown promising results however it remains a challenge to evaluate the outcome and the biological mechanisms involved. Even with the significant improvements in genetics and nutrition, feed costs still represent about two-thirds of production costs in pig production (Gilbert et al., 2017).

FE is generally expressed as kg feed per kg bodyweight gain however this statement ignores the biological processes of FE which is much more complicated. It involves digestion, absorption and metabolism processes to convert dietary nutrients into body tissues. The biological processes behind FE are exceedingly complex, and it's not certain that their heritability in the offspring (Cruzen et al., 2013). Key biological factors that cause variation in FE include heat production (Barea et al., 2010; Boddicker et al., 2011), maintenance energy utilization (Barea et al., 2010; Boddicker et al., 2011), feed intake and patterns (Young et al., 2011), nutrient digestibility (Harris et al., 2012; Vigors et al., 2016; Mauch et al., 2018), and body composition (Cai et al., 2008; Smith et al., 2011; Young et al., 2011; Hewitt et al., 2020; Lefaucheur et al., 2011; Hoque et al., 2007).

For many reasons, it is important to understand the biological determinants of animal-to-animal variation for FE. Reasons include 1) it could reveal the negative consequences of selection for FE; 2) it could help design balanced breeding programmes; 3) may provide insights for managements and diet strategies to maximize FE in commercial settings; and 4) it could lead to the development of low-cost, quick approaches (biomarkers) for ranking pigs for genetic purposes without requiring the feed intake measurement (Richardson et al., 2004; Cantalapiedra-Hijar et al., 2018). Chapter 4 evaluated fecal digestibility which could be used as a biomarking for ranking pigs.

The main objective of my thesis was to investigate the effect of selecting for FCR through genetics and identify plausible mechanisms that might be causing variation between pigs of diverse EBV-FCR.

5.1 Genetic potential

In the current study, the pigs were fed the same diet and were raised in similar conditions, and genetic selection for FE resulted in phenotypic variation between high and low efficiency pigs. Pigs selected for high FE, have consistently shown to eat less (Young et al., 2011; Vigors et al., 2016; Harris et al., 2012; Montagne et al., 2014; Cai et al., 2008), and tend to be leaner (Cai et al., 2008; Smith et al., 2011; Young et al., 2011; Hewitt et al., 2020; Lefaucheur et al., 2011; Hoque et al., 2007) with no change in ADG resulting in a lower FCR. These results are consist and concordant with findings from various experiments with different designs, diets, breeds and other factors, which support the importance of the genetic selection. These results are consist and concordant with findings from various experiments with different designs, diets, breeds and other factors, which support the importance of the genetic selection. However, the underlying biological mechanism of what makes one pig more feed efficient than another is still inconclusive. This is

important to understand because it could change how producers make breeding selections and improve selection accuracy.

5.2 Biological mechanisms causing improved FE

5.2.1 Nutrient digestibility

Studies have attempted to investigate the biological mechanisms involved in determining FE, one being the digestibility of nutrients. Nutrient digestibility is the result of the interaction between the feed and the animal. It is dependent on the bioavailability of the diet (determined by properties of the feed) and the animal's potential to digest (determined by species, age, sex, and physiological state) (Bastinelli, 2013). Thus, nutrient digestibility and FE are associated. In Chapter 4, fecal nutrient digestibility was measured; since the animal's ability to digest nutrients determines the quantity and quality of nutrients available for growth and body composition, genetics is more than likely controlling the processes involving digestion and absorption of nutrients. Pigs of different sires have shown to have different fecal digestibility of DM, organic matter (OM), CP, and energy which indicates genetics could cause animal digestibility variation (Noblet et al., 2013). Even of the same genetics, individual pig genotypes can play a role in determining digestive processes and metabolisms of nutrients and energy which cause variation between pigs of the same breed (Barea et al., 2010, Harris et al., 2012). Thus, it is assumed that the genetic selection for FE could influence nutrient digestibility and protein deposition. Chapter 4 showed higher nutrient digestibility in HFE pigs, which is in agreement with other studies (Harris et al., 2012; Vigors et al., 2016; Mauch et al., 2018). The genetic advantage potentially allows the pigs to efficiently utilize nutrients towards lean tissue growth. To support this, Vigors et al, (2016) revealed that more efficient pigs have an increased expression in gene encoding for enzymes

involved in intestinal nutrient transport. This suggests that these enzymes may be one of many key mechanisms important in improving FE (Vigors et al., 2016).

Improving nutrient digestibility is beneficial for many reasons such as reducing feed costs and environmental impacts. Feed costs represent approximately 60-70% of total cost of production (Patience et al., 2015) thus increasing nutrient digestibility has to potential to lower feed costs. Pig production also has significant environmental impact particularly with the excretion and emission of nitrogen (Déru et al., 2020). Nitrogen digestive efficiency can be improved to reduce the environmental footprint of pig production (Kasper et al., 2020). Thus, increasing FE and nutrient digestion in pigs could lower feed costs, lower resources used and reduce environmental impact.

Nonetheless, many discrepancy results exist on nutrient and energy digestibility among studies. For example, some studies reported no differences in nutrient digestibility between divergent FE lines and concluded that digestion is not an essential source of variation of RFI in growing pigs (Montagne et al., 2014; Barea et al., 2010). In addition, the results of chapter 4 were not significant but rather a tendency for higher nutrient digestion for HFE pigs. Other studies have reported differences in nutrient digestibility among FE groups (Harris et al., 2012; Vigors et al., 2016; Montagne et al., 2014)) and digestibility has shown to contribute significantly to RFI in beef cattle (Herd and Arthur, 2009). Inconsistent results may be due to differences in weight, age during the digestibility test, breeds, sex and diets during the selection process of pigs (Montagne et al., 2014), feed intake, gut microbiota composition (Déru et al., 2020) or the method of measuring nutrient digestibility.

Nutrient digestibility increases with age and BW (Ouweljes et al., 2018; Noblet, 2013; Noblet and van Milgen, 2004). With age, the hindgut capability matures (Noblet, 2013) and the rate of digestive passage slows (Le Goff et al., 2002) and as a result the digestive capacity of

nutrients improves especially of dietary fibre (DF). However, the digestibility rate increment differs among individual pigs (Verschuren et al., 2021). Thus, the time point of sampling within the growing periods will most likely cause variation in the digestibility results. In chapter 4, faeces were sampled at about 130 kg BW whereas Harris et al., (2012) sampled at about 62 kg BW, Vigors et al., (2016) sampled at about 85 kg, Montagne et al., (2014) sampled at about 28 kg BW, Barea et al., (2010) sampled at 25 -95 kg BW (sampled over three periods) and Mauch et al., (2018) sampled at about 40-60 kg BW. Thus, it is difficult to compare digestibility studies when pigs were sampled at different ages and BW. In addition, it would be beneficial to perform multiple-day sampling over the entire grower-finisher period rather than single-day sampling to accurately represent the animal's nutrient digestibility (Agudelo et al., 2010) and it its due to genetic selection by FE.

The digestibility results can vary depending on the guts portion where digesta (ileum, cecum and colon) or fecal materials were collected. Nutrient absorption mainly occurs in the small intestine (Vigors et al., 2016), while fecal samples are subjective to microbiome activity (McCormack et al., 2017) thus, digesta would be a more accurate representation of the pig's nutrient digestibility (Albun et al., 2001). But, sampling the digesta either requires the insertion of T-cannulas (Cunningham et al., 1963) or euthanizing the animal followed by intestinal dissection (Vigors et al., 2016). Both processes raise welfare concerns and large sample sizes are difficult. Vigors et al. (2016) measured coefficient of apparent ileal digestibility (CAID) and coefficient of apparent total tract digestibility (CATTD) and HFE pigs had increased CAID of GE and increased CATTD of GE, N and DM compared to LFE. In contrast, Montagne et al. (2014) measured digestibility of ileum, cecum, colon and feces and reported no differences in digestibility between

the different sampling areas. In the current study, apparent total tract digestibility (ATTD) was measured using feces and acid-insoluble ash as an indigestible marker from fecal samples.

The type of energy measured can also cause discrepancies in energy digestibility. Four types of energy systems exist (GE, DE, ME, and NE) with NE being the most accurate representation of energy used by the pig towards maintenance and growth (Kil et al., 2013). As stated above, lean tissue accretion is an energy demanding process however energy measured from the feces did not change with FE in chapter 4. This may be caused by the type of energy measured rather than the pig's inefficiency. In chapter 4, energy digested was measured in the feces representing DE and was compared to the GE present in the feed. DE does not accurately represent energy left over after digestion from the pig as it does not correct for energy lost in the urine, as heat production, and for endogenous contributions (Patience, 2012). In addition, GE of the diet overestimates the available energy for metabolisms and does not correct for losses through the feces, urine, heat production and gas production. A more accurate representation of energy utilization is the direct or indirect calorimetry methods which measures heat production (direct) or O_2 consumed, and CO_2 produced (indirect) (Li et al., 2018). DE and ME were greater in HFE pigs when energy was measured using metabolism crates after adjusting for ADFI (Harris et al., 2012). This potentially points to differences in digestion, absorption and utilization of energy for maintenance and growth. Interestingly, another study using respiration crates, after adjusting for feed intake, reported no significant differences in DE, ME or NE utilization between high and low RFI pigs (Barea et al., 2010). Thus, it is possible the inaccurate method of measuring energy rather than the genetic potential of the pig resulted in no difference between FE groups. However measuring NE can be time-consuming, expensive, complex and heavily depends on methodology

(Li et al., 2018) thus NE estimation is not a viable option to estimate energy utilization in swine for commercial farms.

5.2.2 Feed intake and lower energy requirements

Feed behaviors (Young et al., 2011) and energy requirements (Boddicker et al., 2011) (Barea et al., 2010) might contribute to differences in FE. Since pigs consume feed to meet their energy requirements (Nyachoti et al., 2004), lower energy requirements would decrease feed intake and ultimately FE. Furthermore, HFE pigs have also shown different feed behaviours compared to LFE pigs such that they spend less time eating but ate at a faster rate (Young et al., 2011) indicating that they are physically less active. In addition, the feed intake of a pig has a mechanical impact on digestibility (Déru et al., 2020). A lower feed intake slows the rate of passage of digesta, which will ultimately increase the time to digest nutrients and energy (Déru et al., 2020). In Chapter 4, results from the study indicated that HFE consumed less feed compared to the LFE pigs which is consistent with other studies (Young et al., 2011; Vigors et al., 2016; Harris et al., 2012; Montagne et al., 2014). Boddicker et al. (2011) placed pigs of divergent lines on either ad libitum or a weight statis feeding regime and LRFI (high FE pigs) consumed 9% and 20% less feed one each feeding regime; respectively. A lower ADFI suggests that the energy requirements were decreased, and the diet contained more nutrients than what was required by HFE pigs (Boddicker et al., 2011. This provides evidence that high FE pigs have lower maintenance requirements. This may be explained by the size of the visceral organs (Gilbert et al., 2017) and/or energy utilization efficiency. Visceral organs such as the gastro-intestinal tract and liver are associated with high metabolic cost thus the size of function may influence energy requirements (Cantalapiedra-Hijar et al., 2018; Boddicker et al., 2011). In addition, lower maintenance requirements can be explained by increase in energy utilization efficiency. Skeletal

muscle makes up about 50% of the body mass and accounts for 25% of the basal metabolic rate (Henriksson, 1990), indeed changes in metabolic properties of skeletal muscles could benefit the energy utilization efficiency and explain phenotypic differences with FE (Lefaucheur et al., 2011). In fact, HFE pigs showed hypertrophy of fast-twitch fibers and a greater glycogen content in glycolytic muscles (Lefaucheur et al., 2011). Thus, the differences in muscle properties could increase energy utilization efficiency for protein gain and may be another key biological mechanism.

CHAPTER 6: CONCLUSIONS AND FUTURE DIRECTIONS

6.1. Conclusions

Pigs selected for high FE, have consistently shown to eat less (Young et al., 2011; Vigors et al., 2016; Harris et al., 2012; Montagne et al., 2014; Cai et al., 2008), and tend to be leaner (Cai et al., 2008; Smith et al., 2011; Young et al., 2011; Hewitt et al., 2020; Lefaucheur et al., 2011; Hoque et al., 2007) with no change in ADG resulting in a lower FCR. Chapter 4 evaluated nutrient digestibility as a biological factor that may cause phenotypic variation between FE groups. The current study resulted in a tendency for higher CP, P, Ca and ash ATTD for HFE pigs compared to their counterparts.

Improved nutrient digestibility is beneficial for many reasons including: 1) increasing quantity of nutrients available towards body growth; 2) lowering feed costs; and 3) decreasing nutrient waste into the environment. Nutrient digestibility may be a major biological mechanism that makes one pig more efficient than another. Many studies have shown improved nutrient digestibility with HFE pigs (Harris et al., 2012; Vigors et al., 2016; Mauch et al., 2018) while others disagree (Montagne et al., 2014; Barea et al., 2010). In addition, many discrepancies exist among nutrient and energy digestibility studies which may be due to differences in weight, age, breed, sex and diets during the selection process of pigs (Montagne et al., 2014). In research, other possible major biological mechanisms that have been suggested are feed behaviours (Young et al., 2011), energy requirements (Boddicker et al., 2011; Barea et al., 2010), and energy utilization efficiency (Barea et al., 2010). It is important to note that no single biological mechanisms are responsible for determining animal FE (Herd et al., 2004). In fact, it is a myriad of all biological functions which each one having its own importance.

6.2 Prediction tools for FE

Using predication techniques to estimate phenotypic potential of pigs selected for FE can aid with breeding selection program accuracy. Measuring digestibility and CT scans can be used to predict efficiency of pig. Measuring digestibility coefficients can be done routinely on farm specifically in genetically selecting facilities to predict FE in pigs. It would be ideal to analyse on farm to eliminate storage and logistically issues (Déru et al., 2020). A valuable source of information comes from the feces since they contain the indigestible residue portion of the feed that was resistant to the digestion process (Schiborra et al., 2015). Fecal sampling is less invasive and less stressful to the pig compared to other methods like blood collection. Including digestibility in breeding schemes is advantageous as fibre content will increase in pig's diets as feed available and costs change in the future (Déru et al., 2020).

The nutrient digestibility can be analysed in laboratory settings using wet chemistry analysis. In Chapter 4, fecal nutrient digestibility was measured using standard wet chemistry analysis procedures however this is time consuming and expensive method. It is also labour intensive and can contain human errors. Therefore, research is needed to facilitate a rapid, low-cost method to evaluate digestibility coefficient that is effective for large numbers (Déru et al., 2020).

Using NIRS allows the analysis to be cheaper and results are acquired faster (Bastinelli, 2013). Measuring digestibility of individual pigs on a large scale using wet chemistry analysis is not feasible thus, NIRS analysis would allow large scale operations to measure digestibility more readily. However, it requires a large number of reference data (Bastinelli, 2013). But once the reference data is established, the results precision is similar to laboratory chemical analysis

(Bastinelli, 2013) and is a feasible option to predict chemical composition of faeces (Schiborra et al., 2015).

6.3 Optimizing efficiency with precision feeding

In chapter 4, estimation of lysine requirements of HFE pigs based on ADFI of the previous week before sampling revealed that HFE might have experienced a shortage of lysine. The diet fed to the pigs in the experiment were formulated to meet the needs of the "average" pig thus the diet fed to the HFE pigs was oversupplied in nutrients. The efforts of genetic selection can be impaired if diets fed during the selection process are not optimized for the individual pig. Diet can explain a significant part of the phenotypic variation (Ouweltjes et al., 2018), thus future research should focus on how we can utilize the full potential of FE with precise feed formulation and scientific feed techniques to accurately meet the nutrition requirements of HFE pigs (Wu et al., 2018). Precision feeding ensures that a ration with a quantity and composition adapted to the requirements of each individual animal is delivered at the right time (Gaillard et al., 2020). However, many challenges reside such as estimating individual requirements and distributing specific rations to individual pigs of the same group (Gaillard et al., 2020). Nonetheless, precision feeding would be beneficial to maximize FE in pigs.

CHAPTER 7: REFERENCES

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