Genetic analyses of feed efficiency traits in pigs

Genetiske analyser av fôreffektivitetsegenskaper hos svin

Philosophiae Doctor (PhD) Thesis

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Table of contents

Acknowledgement i

Summary 7

Sammendrag 9

List of abbreviations 11

List of papers 13

1. General introduction 15

  1.1 Background 15

  1.2 Pig breeding in Norway 16

    1.2.1 Norwegian Landrace 17

    1.2.2 Norwegian Duroc 17

  1.3 Phenotype recordings 18

  1.4 Breeding for improved feed efficiency 19

2. Aim and outline of the thesis 21

3. PAPER I:

4. PAPER II:

5. PAPER III:

6. General discussion 85

  6.1 Genetic improvement 85

  6.2 Statistical analysis of feed intake 88

  6.3 Maintenance requirement and body composition 89

  6.4 Data quality 90

    6.4.1 Boar records 90

    6.4.2 Sow records 91

  6.5 Recommendations 92

7. Conclusions 93

References 95

Papers I-III have individual page numbers

Summary

The main objective of this thesis was to establish more detailed measurements feed efficiency in Norwegian Landrace and Norwegian Duroc in order to genetically improve this trait without negative consequenses for other (mainly sow) traits. In addition, genetic analyses of the new efficiency measurements were developed. The data was provided by Topigs Norsvin, and consisted of records from the boar testing station and the Norwegian litter recording system. In total, data from 8,161 Norwegian Landrace boars and 7,202 Norwegian Duroc boars were used in the thesis, recorded from 2008 to 2014. Individual feed intake and weight were recorded daily and all boars were computed tomography-scanned to determine their deposition of lean meat and fat at the end of test. In addition, data from 90,945 purebred Norwegian Landrace and hybrid sows (50% Norwegian Landrace and 50% Yorkshire) was available from Norway and foreign countries, recorded between 2002 and 2014.

The aim of paper I was to investigate two new measures of feed efficiency, lean meat- and fat deposition efficiency. These measures are direct measures of feed efficiency rather than indirect traits that may change the body composition of the pig. Total feed intake in the test period was analyzed in a univariate animal model, where fat and lean meat deposition were included as random regression covariates. These covariates were considered as the new efficiency measurements expressing the amount of feed needed to produce an extra kg lean meat or fat, respectively. Significant genetic variation in these new efficiency measurements was detected. The fraction of total genetic variance due to lean meat deposition efficiency differed between breeds, where lean meat deposition efficiency explained a bigger part of the total genetic variation in feed intake in the test period in Norwegian Duroc than Norwegian Landrace (Norwegian Landrace = 12%, Norwegian Duroc = 15%). The opposite was observed for the fraction of genetic variation due to fat deposition efficiency (Norwegian Landrace= 20%, Norwegian Duroc= 10%). These two new efficiency traits might be used to select animals with a high genetic potential for lean meat and fat deposition efficiency rather than selecting for reduced feed conversion ratio and back fat.

Genetic correlations between lean meat deposition efficiency, fat deposition efficiency and economically important sow traits in Norwegian Landrace were estimated in paper II. The sow traits included in the analysis were stayability (stayability up to be inseminated for a second litter), body condition score at weaning, total number of piglets born and total litter weight at

three weeks of age. All traits were recorded on first parity sows and were analyzed using multivariate animal models. Only two significant genetic correlations were found, between fat deposition efficiency and stayability (0.21 ± 0.11) and between fat deposition efficiency and total litter weight at three weeks (0.21 ± 0.10). There were no significant genetic correlations between lean meat deposition efficiency and the sow traits. These results suggest that selection for fat deposition efficiency could give poorer stayability in sows and reduce the litter weights at three weeks. Selection for efficient lean meat deposition should not affect the sow traits and might be beneficial for genetic improvement of efficiency in pork production.

Paper III estimated the economic values for lean meat- and fat deposition efficiency in Norwegian Landrace. Economic values were calculated in a simple economic model including five traits; lean meat- and fat deposition efficiency, lean meat percentage, days from 40 to 100/120 kg and fat content on the carcass (kg). Input data was from the boar test station. The standardized economic values for lean meat- and fat deposition efficiency were high (8.9 EUR/σ_a and 2.9 EUR/ σ_a), suggesting the traits are of high economic importance. An index including lean meat- and fat deposition efficiency as feed consumption trait showed a bigger variance than an index with a traditional feed consumption trait, total feed intake in the test period. This suggested that there is a big potential for genetic gain in profit by using the breeding goal including the new efficiency traits, and that the new efficiency traits contained additional information to improve the genetic evaluation of boars.

Genetic variation existed in lean meat- and fat deposition efficiency and few unfavorable genetic correlations were found between the new efficiency traits and important sow traits. It might be possible to select for improved lean meat deposition efficiency without a negative effect on important sow traits. Both efficiency traits had a high economic importance in pork production. When selecting for the new efficiency traits, their genetic correlation to other production and quality traits should be accounted for.

Sammendrag

Hovedmålet med dette doktorgradsarbeidet var å studere nye og mer detaljerte egenskaper for å forbedre fôreffektivitet hos norsk landsvin og norsk duroc uten negative konsekvenser for viktige purkeegenskaper. I tillegg ble det utviklet en modell for å kjøre genetiske analyser av de nye egenskapene. Dataene kom fra Topigs Norsvin, og var registrert på råneteststasjonen, Norsvin Delta og fra Ingris, som er et registrerings- og styringsverktøy for alle svineprodusenter. Totalt ble data fra 8161 norske landsvinråner og 7202 durocråner brukt. Data var registrert fra 2008 til 2014. Individuelt fôropptak og vekt ble registrert daglig og alle råner ble datatomografi- skannet ved slutten av testen for å finne ut hvor mye kjøtt og fett som var avleiret ved slutten av testen. Data på purkene var fra 90,945 reinrasede norsk landsvinpurker og hybridpurker (50 % norsk landsvin og 50 % yorkshire) fra Norge og utlandet, registrert mellom 2002 og 2014.

I første artikkel ble det utviklet to nye fôreffektivitetsegenskaper; kjøtt- og fetteffektivitet. Egenskapene var et direkte mål på grisens utnyttelse av fôret i stedet for indirekte egenskaper som forbedrer effektivitet gjennom endringer i kroppssammensetning og redusert fôropptak per kg tilvekst. For å utvikle de nye egenskapene ble totalt fôropptak i testperioden analysert i en univariat dyremodell. I modellen ble mengdefett og kjøtt på slaktet inkludert som tilfeldige regresjonskovariater. Disse kovariatene representerte hvor mye fôr som trengtes for å produsere en ekstra kg kjøtt eller fett på slaktet, og var de nye fôreffektivitetsegenskapene. Signifikante genetiske varianskomponenter tydet på at genetisk variasjon eksisterte i de nye egenskapene. Andelen av total genetisk variasjon i fôropptak som skyldtes kjøtteffektivitet varierte mellom rasene. Kjøtteffektivitet forklarte en større del av den totale genetiske variasjonen i fôropptak i test perioden hos norsk duroc enn norsk landsvin (norsk landsvin = 12%, norsk duroc = 15%), mens det motsatte ble observert for fetteffektivitet (norsk landsvin = 20%, norsk duroc = 10%). De to nye effektivitetsegenskapene kan brukes for å selektere dyr med et høyt genetisk potensiale for å avleire kjøtt effektivt i stedet for dyr med lavt fôropptak per kg tilvekst og lite fett på slaktet.

Genetiske korrelasjoner mellom kjøtt- og fetteffektivitet og viktige purkeegenskaper hos norsk landsvin ble beregnet i artikkel II. Purkeegenskapene som ble inkludert i analysen var holdbarhet (evne til å bli inseminert med andre kull), purkas hold ved avvenning, totalfødte grisunger og kullvekt ved treukers alder. Alle egenskapene var registrert på førstekullspurker,

og egenskapene ble analysert i multivariate dyremodeller. To signifikante genetiske korrelasjoner ble funnet; en mellom fetteffektivitet og holdbarhet (0.21 ± 0.11) og en mellom fetteffektivitet og kullvekt ved treukers alder (0.21 ± 0.10). Ingen signifikante genetiske korrelasjoner ble funnet mellom kjøtteffektivitet og purkeegenskapene. Resultatene tydet på at seleksjon for fetteffektivitet kan gi dårligere holdbarhet ved avvenning hos purker og lavere kullvekter ved treukers alder. Seleksjon for økt kjøtteffektivitet skal, basert på disse resultatene, ikke ha noen effekt på purkeegenskapene og kan være gunstig for avlsarbeidet for forbedret fôreffektivitet.

I Paper III ble økonomiske verdier for kjøtt- og fetteffektivitet i norsk landsvin beregnet. De økonomiske verdiene ble beregnet i en enkel bio-økonomisk modell som inkluderte fem egenskaper: Kjøtteffektivitet, fetteffektivitet, kjøttprosent, dager fra 40 til 100/120 kg levendevekt og fettmengde på slaktet (kg). Gjennomsnittsdata som ble brukt i den økonomiske modellen var fra råneteststasjonen til Norsvin. De standardiserte økonomiske verdiene for kjøtt- og fetteffektivitet var høye (8.9 EUR/σ_a and 2.9 EUR/σ_a), noe som tyder på at egenskapene er av økonomisk betydning for svineproduksjon. En indeks som inkluderte kjøtt- og fetteffektivitet som fôropptaksegenskap i avlsmålet viste en større variasjon enn en indeks med en tradisjonell fôropptaksegenskap; totalt fôropptak i test perioden. Resultatene tydet på at avlsmålet som inkluderte de nye effektivitets egenskapene gir mulighet for større genetisk framgang enn avlsmålet som hadde totalt fôropptak i test perioden som fôropptaksegenskap og at de nye egenskapene bidrar med ny informasjon som kan bedre de rutinemessige avlsverdiberegningene.

Genetisk variasjon eksisterte i både kjøtt- og fetteffektivitet og studiet fant få ugunstige korrelasjoner til viktige purkeegenskaper i norsk landsvin. Det kan være mulig å selektere for økt kjøtteffektivitet uten at dette har en negativ effekt på viktige purkeegenskaper. Begge egenskapene hadde en klar økonomisk betydning i norsk svine produksjon. Ved seleksjon for de nye fôreffektivitetsegenskapene er det viktig å ta hensyn til genetiske korrelasjoner til andre produksjonsegenskaper i avlsmålet.

List of abbreviations

BCSw– Body condition score at weaning

FCR – Feed conversion ratio

FE – Fat efficiency

FI – Total feed intake in the test period

LME – Lean meat efficiency

LMP– Lean meat percentage

ND – Norwegian Duroc

NL – Norwegian Landrace

RFI – Residual feed intake (intercept)

STAY – Stayability up to insemination for a second litter

TLW – Total litter weight at three weeks

TN – Topigs Norsvin

TNB – Total number of born piglets

List of papers

I. **Martinsen, K. H., J. Ødegård, D. Olsen and T. H. E. Meuwissen.** 2015. Genetic variation in efficiency to deposit fat and lean meat in Norwegian Landrace and Duroc pigs. *Journal of Animal Science 93:3794-3800.*

II. **Martinsen, K. H., J. Ødegård, T. Aasmundstad, D. Olsen and T. H. E. Meuwissen.** 2016. Genetic relationships between the boar feed efficiency and the sow piglet production, body condition score and stayability in Norwegian Landrace pigs. *Accepted in Journal of Animal Science.*

III. **Martinsen, K. H., J. Ødegård, D. Olsen and T. H. E. Meuwissen.** 2016. Economic values for lean meat- and fat efficiency in Norwegian Landrace nucleus pig population. *Submitted to Journal of Animal Science.*

1. General introduction

1.1 Background

Feed efficiency is an important trait in pig breeding due to global issues such as human population growth, climate changes and economics in pork production. FAO (2009) stated that the global human population is expected to exceed 9 billion people by 2050 and that food production needs to increase by 60%. On the other hand, decreased availability of feeds is expected as climate changes may have a negative effect on crop yields in the world (Nelson et al., 2009; Åby et al., 2014). Therefore, an efficient pig is important in order to defend the use of resources such as cereals, which could be human food, for pork production. Smith and Gregory (2013) concluded that "measures that improves the efficiency of agriculture will be beneficial for both food security and greenhouse gas emission- reduction". Studies have shown that selection for different feed efficiency traits have led to reduced greenhouse gas emissions from ruminants (Hegarty et al., 2007) and nitrogen excretion in pigs and poultry (Nahm, 2002; Shirali et al., 2012). As climate changes and increased human population leads to an increased scarcity of resources, the prices of agricultural commodities will increase. Feed is the major cost in pork production and therefore, feed efficiency is important for the profit of the farmer (Niemi et al., 2010). The Norwegian Landrace (**NL**) is highly feed efficient and has a high ability to mobilize energy from body reserves (Kolstad and Vangen, 1996; Kolstad et al., 1996). This is a result of systematic selection for reduced feed intake per kg growth (**FCR**), increased lean meat growth and reduced back fat. This selection strategy has been widely used by breeding companies. However, studies have shown that such selection may result in reduced appetite in lactating sows (Kerr and Cameron, 1996). This may have unfortunate consequences on profitable traits in piglet production in maternal lines (Prunier et al., 2010). A reduced appetite among high-producing lactating sows might lead to severe body condition losses during lactation (Rydhmer, 2000), which again increases the risk of premature culling (Thaker and Bilkei, 2005; de Jong et al., 2014).

To meet future challenges and thus, ensure a sustainable pork production, genetic improvement of feed efficiency is necessary. The aim of this thesis was, therefore, to investigate new measures of feed efficiency in pigs that could be beneficial to meet the addressed challenges and contribute to further improvement of feed efficiency in pig breeding.

1.2 Pig breeding in Norway

Pig breeding in Norway is organized by the farmer-owned cooperative, Norsvin SA. In 2014, Norsvin merged their international part of the company with the Dutch pig breeding company Topigs. This company is named Topigs Norsvin (**TN**) and is now the second largest provider of pig genetics in the world. Today, national breeding programs exists for two breeds in Norway, Norwegian Duroc (**ND**) (paternal line) and NL (maternal line).

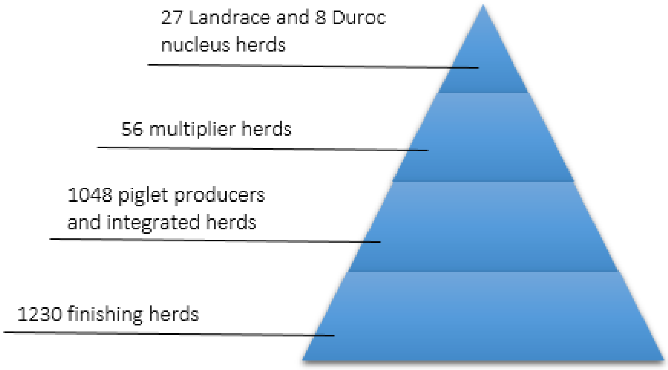

Figure 1 The Norwegian pig-breeding pyramid (Norsvin, 2016)

The Norwegian pig breeding is organized in a pyramid structure (Figure 1). The nucleus herds produce purebred NL- and ND-boars for the test station, Norsvin Delta. The sows are used for self-recruitment or sold to multiplier herds as dams for the hybrid sow. In the multiplier herds, NL-sows are inseminated with Yorkshire semen (produced in Norway) to produce the hybrid sow used as a dam for the commercial fattening pig. The sire of the commercial fattening pig is normally purebred ND. The multiplier herds transfer the genetic gain from the nucleus herds on to the production herds, which are the main producer of pork in Norway. Therefore, the production herds are the main target group for the breeding program. The production herds are divided in three groups: piglet producer, finisher herds or combined herds. The combined herds produce piglets and keep them as grower-finisher pigs (Norsvin, 2011).

1.2.1 Norwegian Landrace

Today, there are 27 NL nucleus herds in Norway and Figure 2 shows the historical changes in the breeding goal for NL. Organized breeding for NL started in the late 1950s, and today NL is a maternal breed in the TN system. Originally, the breed was selected as a "multi-purpose"-breed, and this is why emphasis was put on typical fattening pig traits such as feed efficiency, growth and slaughter quality traits. Later, the breeding goal included more traits like maternal productivity, health and robustness. The three maternal trait groups included in NL's breeding goal today are litter size, maternal ability and reproduction. In 2014, the average age of the sows at first farrowing in NL nucleus herds was 326 days, and average number of live born piglets per litter was 12.5 (Ingris, 2014).

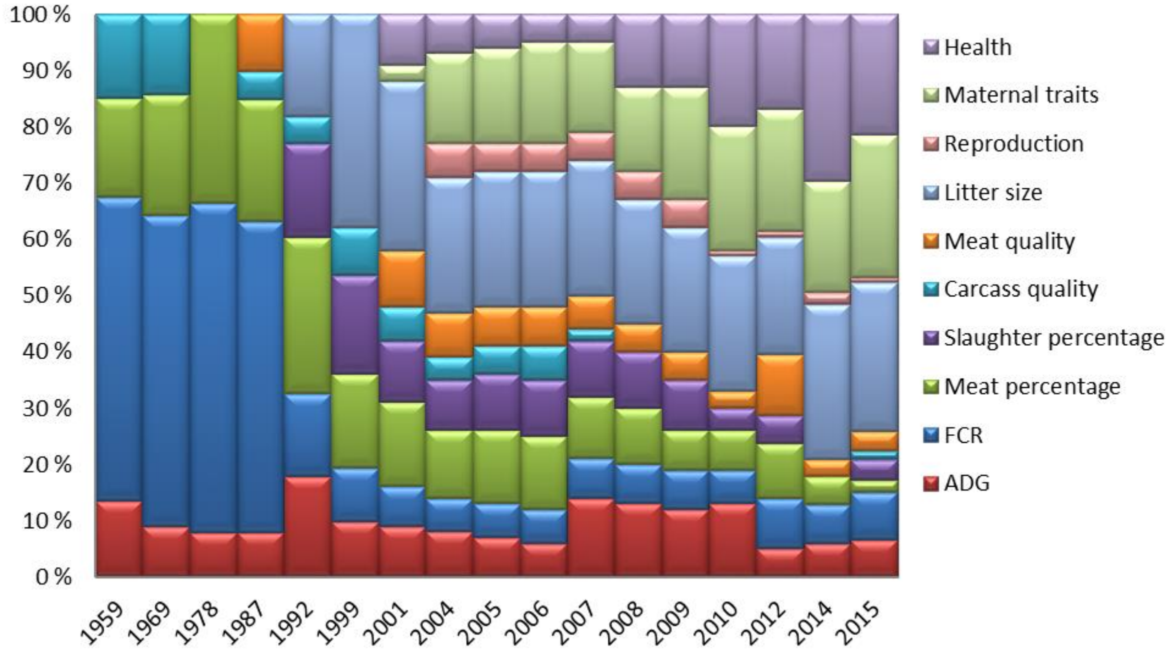

Figure 2. The historical changes in the breeding goal for Norwegian Landrace from 1959 to 2015. Note that the timeline interval (x-axis) is not constant throughout the period.

1.2.2 Norwegian Duroc

The organized breeding for ND has a significantly shorter history of selection than NL, as systematic breeding started in the 1990s. Back then, the breeding goal included feed efficiency and growth along with carcass and meat quality traits. Later, health traits such as conformation, osteochondrosis and hernia were included in the breeding goal (Norsvin, 2015). Figure 3 shows the historical changes in the breeding goal of ND. Systematic breeding for improved meat quality, such as increased portion of intramuscular fat, has made the ND superior in meat quality compared to NL (Gjerlaug-Enger et al., 2010). Today, eight nucleus herds deliver boars to the test station, and average number of litters born in each herd was 188 in 2014 (Norsvin, 2015).

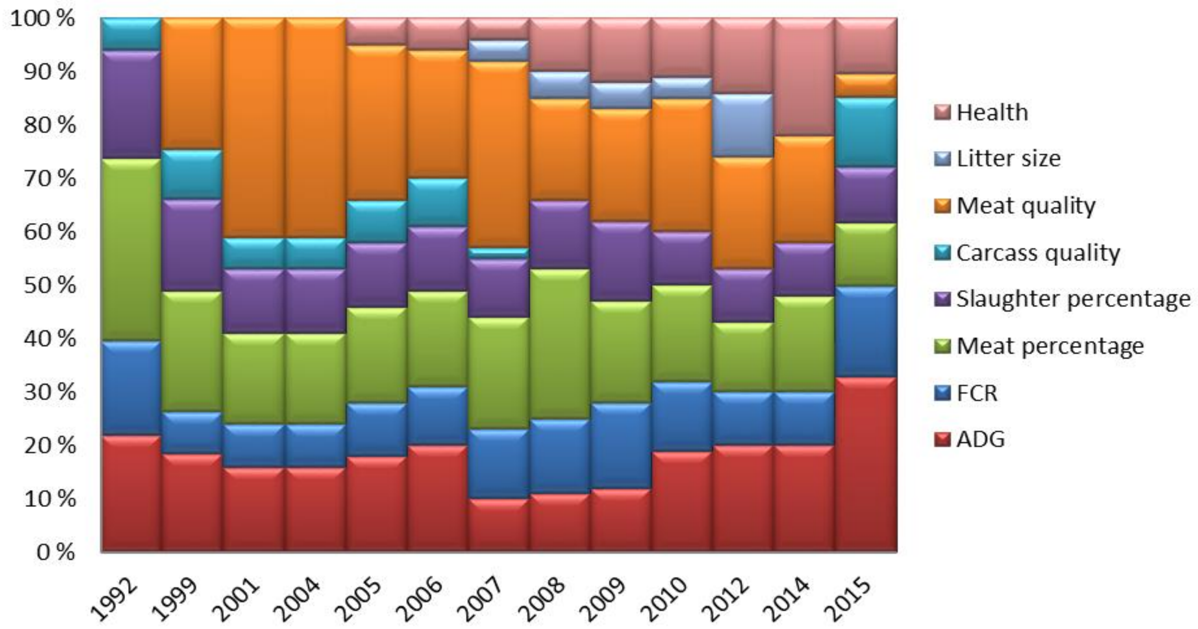

Figure 3. The historical changes in the breeding goal for Norwegian Duroc from 1992 to 2015. Note that the timeline interval (x-axis) is not constant throughout the period.

1.3 Phenotype recordings

In TN, breeding for improved feed efficiency in NL and ND is done through selection for improved FCR and reduced number of days between 40 and 120 kg live weight. In addition, lean meat percentage (**LMP**) is included in the breeding goal to ensure lean growth. In 2008, a new boar test station was built in Norway. The station has a test capacity of 3,500 boars per year. The station is divided into 16 sections, where each section includes 6 pens with 12 boars per pen. For all boars entering the test station, detailed phenotype recordings are carried out. In each pen one FIRE- station (FIRE; Osborne Industries Inc., Osborne, KS, USA) is available. The FIRE-station records individual weight and feed consumption each time the boar enters the FIRE-station. When the boars end the test, they undergo a detailed exterior scoring and are scanned in a computed tomography (**CT**). High quality phenotypes for carcass composition on live selection candidates are obtained from image analyses of the CT-scans. For each boar, 1,100 pictures are taken, one picture per 1.2 millimeter of the boar. Based on different densities of different tissues, an image analysis is carried out and the amount of bone, lean meat and fat are calculated (Gjerlaug-Enger et al., 2012). Figure 4 shows a sedated pig in the CT-scanner and typical images from a CT-scan.

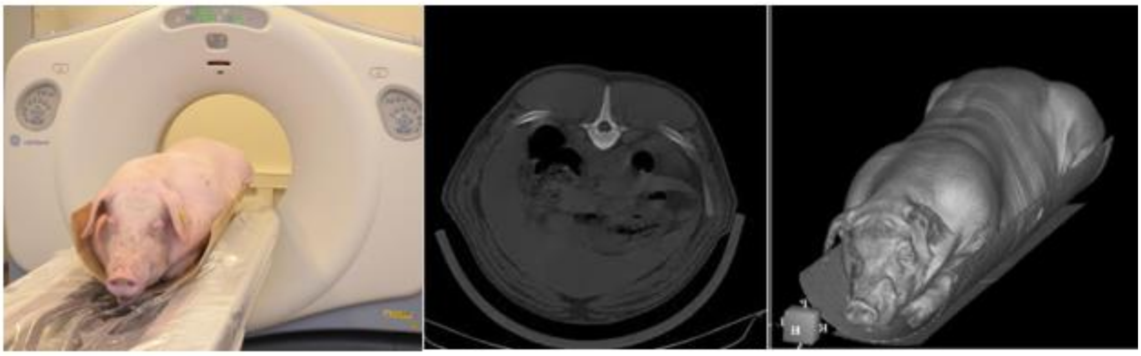

Figure 4. (1) Boar sedated for scanning in the computed tomography (CT) (Norsvin, 2016). (2) Cut image from CT. (3) Spiral scan from CT (Kongsro, 2009).

Internationally, TN is the only commercial breeding company who has included CT-scanning as a part of the routine phenotype collection (Norsvin, 2016). This implementation has led to genetic improvement of economically important traits such as LMP (Kongsro, 2014).

In addition to information from the test station, the farmer records production results in the Norwegian litter recording system (Ingris; Norwegian Meat and Poultry Research Centre, 2016). For the nucleus and multiplier herds, the recordings are at animal level and important traits regarding the production cycle of the sow are registered. These are traits related to insemination, farrowing, weaning and culling of the sow. These data are the basis for TN's breeding program for maternal productivity in NL. In addition, all potential boar dams are tested on-farm by a trained breeding consultant. The consultant registers the weight of the animal at approximately 150 days, measures back fat and loin depth with ultrasound and carries out a detailed exterior scoring of the pig.

1.4 Breeding for improved feed efficiency

Feed efficiency in fattening pigs is a complex trait, and we do not have a direct measurable phenotype. An efficient fattening pig has a low input (feed) and a high output (lean meat percentage and growth), and several approaches to obtain such a result have been proposed. Bernard and Fahmy (1970) showed that indirect selection for feed efficiency through selection for lean growth was a success. The study was important for future selection strategies for feed efficiency, and the traditional way of improving feed efficiency has been through selection for increased lean growth, reduced back fat and reduced FCR. This selection has led to huge genetic improvement of production efficiency in fattening pigs (Sather and Fredeen, 1978; Rauw et al., 1998; Nguyen and McPhee, 2005). This selection has focused on the part of feed intake that is explained by production. Koch et al. (1963) introduced a new measure for feed efficiency, which focused on the part of the variation in feed intake that was not explained by the production, later named residual feed intake. Residual feed intake is defined as the difference between observed feed intake and the expected feed intake which is calculated based on standardized requirements for production and maintenance (Kennedy et al., 1993). Variation in residual feed intake is caused by differences in body composition, maintenance, physical activity, digestibility, immune response, thermoregulation and energy efficiency (Young and Dekkers, 2012). Residual feed intake is moderately heritable, ranging from 0.1 to 0.4 depending on breed and calculation method of residual feed intake (Johnson et al., 1999; Do et al., 2013; Saintilan et al., 2013). Lines selected for low residual feed intake have shown reduced physical activity, lower maintenance requirement and leaner carcasses (Barea et al., 2010; Boddicker et al., 2011).

Compared to the approach of Koch et al. (1963), this thesis used an extended residual feed intake model, where production (lean meat – and fat content) were included as random regression covariates. This splits the traditional genetic component for residual feed intake into three components: one for the animal intercept (**RFI**), one for lean meat efficiency (**LME**) and one for fat efficiency (**FE**). These traits describe the genetic potential of the animal to deposit lean meat and fat efficiently, and includes individual differences in efficiency to deposit lean meat and fat. These new traits are more specific than the traditional residual feed intake described in Kennedy et al. (1993).

2. Aim and outline of the thesis

The main aim of this thesis was to find new measures for feed efficiency that described how well the pig utilized the feed and perform the first genetic analyses of these new efficiency traits in Norwegian Landrace and Duroc. The study also aimed to investigate if selection for these new feed efficiency traits would have a negative impact on other economical traits in the breeding goal of Norwegian Landrace and if they had any economic value in pork production.

The thesis had three sub goals:

1. Develop new feed efficiency measures and investigate if genetic variation in these traits exists.
2. Investigate genetic relationships between the new efficiency traits and economical important sow traits.
3. Evaluate the economic importance of the new efficiency traits in pork production.

This aims were investigated through three studies. First, an extended residual feed intake model was developed to establish new efficiency measurements and used to estimate genetic variation in the new traits. Secondly, heritabilities were estimated and the genetic correlations between the new feed efficiency traits and economically important sow traits were calculated. Last, a bio-economic model describing pork production in Norway was developed to calculate the economic importance of the new feed efficiency traits in pork production.

3. PAPER I:

Genetic variation in efficiency to deposit fat and lean meat in Norwegian Landrace and Duroc pigs

K. H. Martinsen, J. Ødegård, D. Olsen and T. H. E. Meuwissen

Journal of Animal Science 93:3794-3800

Photo: Topigs Norsvin

Genetic variation in efficiency to deposit fat and lean meat in Norwegian Landrace and Duroc pigs[1]

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ABSTRACT: Feed costs amount to approximately 70% of the total costs in pork production, and feed efficiency is, therefore, an important trait for improving pork production efficiency. Production efficiency is generally improved by selection for high lean growth rate, reduced backfat, and low feed intake. These traits have given an effective slaughter pig but may cause problems in piglet production due to sows with limited body reserves. The aim of the present study was to develop a measure for feed efficiency that expressed the feed requirements per 1 kg deposited lean meat and fat, which is not improved by depositing less fat. Norwegian Landrace (*n* = 8,161) and Duroc (*n* = 7,202) boars from Topigs Norsvin's testing station were computed tomography scanned to determine their deposition of lean meat and fat. The trait was analyzed in a univariate animal model, where total feed intake in the test period was the dependent variable and fat and lean meat were included as random regression cofactors. These cofactors were measures for fat and lean meat efficiencies of individual boars. Estimation of fraction of total genetic variance due to lean meat or fat efficiency was calculated by the ratio between the genetic variance of the random regression cofactor and the total genetic variance in total feed intake during the test period. Genetic variance components suggested there was significant genetic variance among Norwegian Landrace and Duroc boars in efficiency for deposition of lean meat (0.23 ± 0.04 and 0.38 ± 0.06) and fat (0.26 ± 0.03 and 0.17 ± 0.03) during the test period. The fraction of the total genetic variance in feed intake explained by lean meat deposition was 12% for Norwegian Landrace and 15% for Duroc. Genetic fractions explained by fat deposition were 20% for Norwegian Landrace and 10% for Duroc. The results suggested a significant part of the total genetic variance in feed intake in the test period was explained by fat and lean meat efficiency. These new efficiency measures may give the breeders opportunities to select for animals with a genetic potential to deposit lean meat efficiently and at low feed costs in slaughter pigs rather than selecting for reduced the feed intake and backfat.

Key words: computer tomography, feed efficiency,
genetic variation, landrace, residual feed intake, random regression

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INTRODUCTION

Production efficiency is of importance in livestock production because of greater competition for feed resources due to growth in human food consumption and an increasing scarcity of feeds due to climate change (Åby et al., 2014). In addition, Shirali et al. (2012) showed that selection for feed efficiency could reduce total protein excretion, which is the greatest pollution factor in pig production. These factors make improvement of total pork production efficiency an important goal for future pig breeding to meet the likely prospective challenges. The profitability of pork production is dependent on feed requirements, as feed costs are the greatest costs in pork production (Niemi et al., 2010). Based on current market economy, feed efficiency is a trait of importance for genetic improvement of production efficiency (Kanis et al.,

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Table 1. Number of boars, average, SD, minimum, and maximum values for total feed intake during the test period (FI), lean meat, fat, live weight (LW) and slaughter percentage (SP) for Norwegian Landrace (NL) and Duroc (D)

	No. of boars		Average		SD		Minimum		Maximum	
	Breed									
Parameter	NL	D	NL	D	NL	D	NL	D	NL	D
FI, kg	8,161	7,202	152.0	157.0	29.4	29.9	97.2	80.1	270.6	258.2
Lean meat, kg	8,161	7,202	52.3	48.6	3.6	3.7	40.5	35.8	68.2	64.8
Fat, kg	8,161	7,202	15.9	19.4	4.3	4.5	7.2	8.0	33.0	35.6
LW, kg	8,161	7,202	111.8	111.5	11.8	11.8	93.9	93.4	140.7	149.2
SP, %	8,161	7,202	69.2	69.9	2.1	1.7	56.3	48.0	82.9	86.7

2005). Bernard and Fahmy (1970) proved that selection for changed body composition, such as carcass leanness and reduced backfat, lead to indirect selection for feed-efficient animals. Since then, this has been a common way to select for improved feed efficiency in commercial breeding companies (Patience, 2012). Other approaches as gross feed intake, residual feed intake, feed conversion ratio, and feed intake relative to growth rate in the breeding goal are also used (Korver, 1988; Gilbert et al., 2007; Do et al., 2013). These traits have moderate heritabilities, and selection for these traits has resulted in more cost-effective production (Suzuki et al., 2005; Chen et al., 2010; Saintilan et al., 2013). However, based on selection responses for these traits, a hypothesis might be that the traditional traits are related to allocation of nutritional resources to lean meat and fat growth rather than how efficient the animal converts feed into product (Rauw et al., 1998; Cai et al., 2008). Moreover, selection for reduced feed intake and reduced body reserves may cause problems for lactating sows that raise large litters (Eissen et al., 2000). The objective was, therefore, to develop a novel measure of feed efficiency expressed as feed consumed (kg) per 1 kg lean meat or fat deposited and to test whether genetic variation in efficiency to deposit fat and lean meat existed within Norwegian Landrace and Duroc pig populations.

MATERIALS AND METHODS

Data and Trait Recording

Data were provided by the Topigs Norsvin company in Norway and recorded on Norwegian Landrace and Duroc boars born from 2008 to 2014 at their boar testing station (“Delta”). Annually, about 3,500 boars from the Topigs Norsvin’s nucleus herds in Norway are tested, equally divided between the 2 breeds. Boars are housed in pens of 12. In each pen, there is 1 feed station (FIRE; Osborne Industries Inc., Osborne, KS), where individual amount of feed consumed at each visit, number of visits, and time spent per visit in the feed station is recorded. In addition, individual BW is recorded as the median of all weights registered at visits to the feeding station that day. Boars are fed ad libitum on conventional concentrate containing 194 and 164 g digestible protein and 9.79 and 9.61 MJ NE/kg before and after 65 kg live weight. Boars enter the test at approximately 40 kg live weight, with an average age of 90 d for Duroc and 85 d for Landrace, respectively. As a standard, the test is terminated and computed tomography (**CT**) scans performed when boars reach approximately 120 kg (approximately 100 kg before March 2012) live weight. Boars are sedated during CT scanning and do not eat on the scanning day; that is, feed intake recording is terminated the day before scanning. Through image analysis of the scans, CT provides information directly on the selection candidate boars for the traits lean meat (kg) and fat (kg) on the carcass. In total, 8,161 Norwegian Landrace and 7,202 Duroc boars had information on total feed intake (over the test period), lean meat (kg), and fat (kg) in the data set. Pedigree information for the boars was traced back 11 generations and included 18,843 and 13,901 animals for Norwegian Landrace and Duroc, respectively.

Estimation of Total Feed Intake in Test Period

The trait analyzed was total feed intake during the test period (**FI**). For both breeds, the trait was a summation of the feed intake from different stages of the growth curve. These stages were 40 to 60, 60 to 80, and 80 to 100 kg live weight. In addition, for boars that entered the test after March 1, 2012, the feed intake from 100 to 120 kg live weight was also included in the summation. Descriptive statistics for the data sets are shown in Table 1, and each boar had 1 record for FI, 1 for lean meat content, and 1 for fat content. Slaughter percentage was similar for the 2 breeds, but the Duroc had a generally greater average and variation in feed intake during the test period compared with the Norwegian Landrace. In addition, the Duroc had a lower average amount of lean meat and a higher fat content in the carcass compared with Norwegian Landrace.

Statistical Analysis

Records more than 4 SD from the mean within breed were discarded as outliers. Boars with missing values for at least 1 of the subtraits (i.e., FI from 40 to 60 or from 80 to 100 kg) were deleted from the data sets and all records were standardized as a deviation from the mean within breed.

The data were analyzed in a univariate animal model, and estimation of variance and covariance components was performed using the DMU software package (Madsen and Jensen, 2013). Lean meat and fat in carcass were included as both fixed and random regression cofactors in the model. In addition, the analysis included each boars' maintenance requirement in the model as a fixed regression cofactor. The maintenance requirement was estimated as the integrated metabolic growth curve for each boar, with the assumption that the metabolic BW (**MBW**) was proportional to the BW raised to 0.75. The function integrated was MBW = $(\mu + bx)^{0.75}$, in which *b* was the linear regression coefficient of MBW, *x* was the age of the boar, and μ was the overall mean. The linear regression was used to estimate accumulated metabolic BW (**AMW**) for each boar. The lower limit (*z*) was age at 40 kg and upper limit (*w*) was age at 100 or120 kg:

$$\mathrm{AMW} = \int_z^w (\mu + bx)^{0.75}dx = \left[(bx+\mu)^{1.75} / b(1.75)\right]_z^w .$$

The efficiency traits were expressed as the genetic regression coefficients that represented the extra feed needed to increase lean meat and fat deposition with 1 kg. This method was based on nutritional models with fixed regression earlier addressed by, for example, van Milgen and Noblet (1999) and also by Aggrey and Rekaya (2013), which used a random regression model for calculating residual feed intake (**RFI**) for maintenance and RFI for growth in broiler chicken.

The following model [1] was fitted separately for both breeds:

$$\begin{aligned} Y_{ijknoq} &= \mathrm{HY}_i + \mathrm{BM}_j + \mathrm{ST}_k + \mathrm{SEC}_n + \beta_{\mathrm{lm}} \times \mathrm{LMEAT}_o \\ &+\beta_{\mathrm{fat}} \times \mathrm{FAT}_o + \beta_{\mathrm{amw}} \times \mathrm{AMW}_o + a_o + \mathrm{pen}_q + a_{p_o} \\ &\times \mathrm{lmeat}_o + a_{f_o} \times \mathrm{fat}_o + e_{ijknoq} \end{aligned} \qquad [1].$$

In the model, Y_{ijknoq} was total feed intake from 40 to 100 or 120 kg of live weight (kg), depending on when CT scanning occurred. Fixed effects included were herd–year (**HY**), birth month (**BM**), scanning time (**ST**), and section (**SEC**). In the model, a_o and pen_q were the random effects of the breeding value of the boar and the pen they were housed in. Pen was included as a random effect because of small numbers of animals in each pen.

The regressions $\beta_{\mathrm{lm}} \times \mathrm{LMEAT}_o$ and $\beta_{\mathrm{fat}} \times \mathrm{FAT}_o$ were the fixed regression on lean meat (kg) and fat (kg), respectively. Lean meat and fat was estimated by the CT. The regression $\beta_{\mathrm{amw}} \times \mathrm{AMW}_o$ was the fixed regression on AMW. Random regressions were also included and $a_{p_o} \times \mathrm{lmeat}_o$ was the random regression on lean meat (kg), in which a_{p_o} was the measure for the feed efficiency to deposit lean meat and represented the amount of feed used to produce 1 kg lean meat (lean meat efficiency of boar *o*).

The regression $a_{f_o} \times \mathrm{fat}_o$ expressed as was the random regression of fat (kg) for boar *o*, in which a_{f_o} was a measure for the feed efficiency to deposit fat and represented the amount of feed used to produce 1 kg fat (fat efficiency of boar *o*). The residual variance in the model was e_{ijknoq} for boar *o*.

In the model, the animal intercept (a_o) explained the variation in FI caused by other factors, such as the part of activity not related to the animals' size (AMW). These factors could be the maintenance requirement part that is not explained by the MBW (e.g., the animal's activity, heat production, disease status). In general, the effect includes all genetic variation in feed intake caused by the animal that is not explained by the animals' MBW, deposition of lean meat and fat, or other effects included in the model.

After variance component estimation, the fraction of total genetic variance in FI due to lean meat and fat efficiency was defined as $\sigma^2_{\mathrm{efficiency}_{(k)}} / \sigma^2_g$, in which $\sigma^2_{\mathrm{efficiency}_{(k)}} = E_{X_k}\left[X_k^2 \times \sigma^2_{a_k}\right]$ was the average over all boars' squared amounts of lean meat (kg), denoted by X_p^2, ($k = p$) or fat (kg), X_f^2, ($k = f$), with the corresponding variance, $\sigma^2_{a_k}$, estimated by model [1]. The variance ($\sigma^2_{a_k}$) represented the variation in the regression coefficient for lean meat or fat. Estimation of total genetic variance in FI (σ^2_g) was an average over all boars' amounts of fat (X_f) and lean meat (X_p) and was estimated using the following formula:

$$\sigma^2_g = E_{X_p,X_f}\begin{bmatrix} \sigma^2_a + X_p^2 \times \sigma^2_{a_p} + X_f^2 \times \sigma^2_{a_f} + 2X_p \times \\ \sigma_{a_p,a} + 2X_f \times \sigma_{a_f,a} + 2X_pX_f \times \sigma_{a_p,a_f} \end{bmatrix},$$

in which $E_{X_p,X_f}[]$ denotes average over all X_p and X_f. In the formula, σ^2_a was the genetic variation in FI that could not be explained by the other factors included in the model. To investigate the importance of lean meat and fat efficiency, variance components were also estimated with a simpler animal model [2], analyzing residual feed intake:

$$\begin{aligned} Y_{ijklmn} &= \mathrm{HY}_i + \mathrm{BM}_j + \mathrm{ST}_k + \mathrm{SEC}_l + \beta_{\mathrm{lm}} \times \mathrm{LMEAT}_m + \beta_{\mathrm{fat}} \times \\ &\mathrm{FAT}_m + \beta_{\mathrm{amw}} \times \mathrm{AMW}_m + a_m + \mathrm{pen}_n + e_{ijklmn} \end{aligned} \qquad [2].$$

Model [2] included the same effects as model [1] but excluded the random effects of lean meat and fat deposition.

Table 2. Fixed regression coefficients (SE) for lean meat (β_{lm}), fat (β_{fat}), and accumulated metabolic BW (β_{amw}) for Norwegian Landrace and Duroc

Regression coefficient	Norwegian Landrace	Duroc
β_{lm}	–0.027 (0.06)	0.073 (0.10)
β_{fat}	2.241 (0.06)	2.495 (0.07)
β_{amw}	0.050 (0.00)	0.046 (0.00)

RESULTS

Fixed Effects

Table 2 includes the fixed regression coefficients for lean meat efficiency, fat efficiency, and AMW. There was no effect of lean meat deposition on total feed intake for any of the breeds, whereas fixed regression coefficients for fat efficiency and AMW were different from zero (Table 2). For Norwegian Landrace, the fixed regression coefficient for fat efficiency indicated that a boar, on average, used 2.24 ± 0.06 kg extra feed/kg fat growth. Duroc, on the other hand, needed slightly more additional feed (2.49 ± 0.07 kg feed/kg fat growth). The regression coefficient for AMW reflected the average amount of feed needed for maintenance per kilogram MBW; the estimates were both different from zero but lower for Duroc than Norwegian Landrace. This suggests that the Norwegian Landrace had a greater average maintenance requirement than Duroc per kilogram MBW (Table 2).

Genetic Variance Components and Genetic Correlations

Genetic variance and covariance components (SE) estimated with model [1] for the effect of animal, lean meat efficiency, and fat efficiency are shown in Tables 3 and 4 for Norwegian Landrace and Duroc, respectively. All variance components for both breeds were greater than zero (Tables 3 and 4). For Norwegian Landrace, the genetic variation in fat efficiency was greater than for lean meat efficiency, whereas the opposite was true for the Duroc. Genetic variance components calculated with models [1] and [2] are shown in Table 5. Genetic variation was greater for both breeds when model [1] was used, whereas residual variation was lower.

The correlation between the random regression coefficients for fat and lean meat was close to zero and nonsignificant for both breeds. The genetic correlation between animal intercept for FI and fat and lean meat efficiencies were, respectively, 0.72 and 0.24 for the Norwegian Landrace and 0.58 and 0.44 for the Duroc. This indicates that those animals with a low feed intake are also likely to have lower feed requirements per unit fat deposited and are thus more fat/lean meat efficient.

Table 3. Variance components (SE) for the intercept of total feed intake during the test period (a), regression coefficients for lean meat in kilograms (a_p) and fat in kilograms (a_f) for Norwegian Landrace on the diagonal and genetic correlations (SE) among a, a_p, and a_f for Norwegian Landrace on the off-diagonal

	a	a_p	a_f
a	17.38 (1.42)	0.24 (0.06)	0.72 (0.05)
a_p	–	0.23 (0.04)	–0.17 (0.11)
a_f	–	–	0.26 (0.03)

Fraction of Total Genetic Variance

Table 6 summarizes that genetic variation in the lean meat and fat efficiencies contribute substantially to the total genetic variance in FI. In Norwegian Landrace, fat efficiency was more important than lean meat efficiency with respect to genetic variation in FI (20 and 12%, respectively), whereas the opposite was the case for Duroc (10% for fat efficiency and 15% for lean meat efficiency).

DISCUSSION

Although approaches to improve feed efficiency through recording of feed intake, reduced backfat, increased carcass leanness, and daily gain exists, it is not obvious that these selection efforts result in pigs with more efficient fat and lean meat deposition. The increased feed efficiency may be due to nutrient resources increasingly being allocated to fat and lean meat growth and less to other processes (e.g., disease resistance). At some point, this reallocation reaches a biological limit and it would be necessary to breed for actual efficiency of fat and lean meat deposition instead of reallocation of resources. The current research investigated whether this was possible and 1) developed statistical methodology to perform the breeding value estimation and 2) found that there were genetic differences between pigs in efficiency of fat and lean meat deposition. Selection for growth rate remains important, next to a selection for lean meat efficiency, because it reduces the costs of housing of the animals and the maintenance requirements. If further reduction in backfat is not desired, as Norwegian Landrace are very lean (Gjerlaug-Enger et al., 2012), selection for fat efficiency may replace the current selection against backfat.

In practice, selection against feed intake is accompanied by selection for (lean meat) growth and is closely related to residual feed intake (Kennedy et al., 1993). In terms of the present study, Kennedy's residual feed intake is similar to the residual feed intake modeled by model [2]. Model [1] in the current study ex-

Table 4. Variance components (SE) for the intercept of total feed intake during the test period (a), regression coefficients for lean meat in kilograms (a_p) and fat in kilograms (a_f) for Duroc on the diagonal and genetic correlations (SE) among a, a_p, and a_f for Duroc on the off-diagonal

	a	a_p	a_f
a	26.04 (2.15)	0.44 (0.05)	0.58 (0.07)
a_p	–	0.38 (0.06)	–0.24 (0.14)
a_f	–	–	0.17 (0.03)

Table 5. Variance components (SE) for the animal, pen, and residual for Norwegian Landrace and Duroc based on models [1] and [2]

	Model [1]		Model [2]	
Breed	Norwegian Landrace	Duroc	Norwegian Landrace	Duroc
Animal	24.93	34.19	13.69 (1.49)	21.83 (2.14)
Pen	5.66 (0.52)	5.41 (0.61)	6.49 (0.58)	5.74 (0.64)
Residual	17.83 (0.93)	23.69 (1.36)	26.18 (1.14)	33.12 (1.56)

tends model [2] residual feed intake model by splitting a_m into components that are due to the actual efficiency of deposition of fat and lean meat (a_f and a_p). With model [1], it is thus possible to select for actual fat and lean meat efficiency without affecting the reallocation of feed resources. Therefore, the model for analyzing FI in the routine genetic evaluation for boars would be superior if fat and lean meat efficiency were included and it would be useful to get a better understanding of the components underlying overall feed efficiency.

Fixed Regression Coefficients

The fixed regression coefficients of lean meat deposition were not different from zero for Landrace and Duroc (Table 2). This could partly be due to the negative correlation between backfat and lean meat content on the carcass, which makes the lean meat regression coefficient difficult to estimate (Lo et al., 1992). Furthermore, the pigs were CT scanned at approximately the same live weight, which means that a pig with a high lean meat content typically has reduced noncarcass body mass (differences in fat deposition are corrected for in the model). Hence, these pigs may have reduced feed intake due to the lower costs of depositing noncarcass body mass. This suggests that the lean meat regression coefficient reflected the costs of depositing lean meat subtracted from the costs of depositing noncarcass body parts. The results in Table 2 implied that this difference was not different from zero. The same argument also holds for the regression on fat deposition, but the difference was positive due to the great costs of depositing fat compared with lean meat and noncarcass body parts.

Genetic Variance Components and Genetic Correlations

The fractions of total genetic variance due to fat and lean meat efficiency and fixed regression coefficients differed between breeds. Based on the present study, individual differences between the boar's efficiency to deposit lean meat and fat and differences between breeds existed. A high regression coefficient for lean meat (a_p) implies that a boar is expected to consume a large amount of feed to produce 1 kg lean meat and is inefficient. In Norwegian Landrace, a smaller fraction of the total genetic variance in FI was explained by lean meat than fat efficiency, but the opposite was true for Duroc. These breed differences may be caused by different breeding goals and different selection strategies in the past. The Norwegian Landrace has been selected for lower feed intake, increased lean meat percentage, and lower backfat thickness for many years (Kolstad, 2000). In Duroc, the selection has been more focused toward carcass and meat quality traits such as intramuscular fat. The fraction of genetic variance due to lean meat and fat efficiency were small, suggesting that the genetic variation in total feed intake at the test station was also due to other genetic factors.

Aggrey and Rekaya (2013) reported variance components for maintenance efficiency and growth efficiency in chickens estimated with the same method as this study. Our results could not be directly compared to these due to different efficiency measures, but their study proves that genetic variation in efficiency for growth exists between animals and is supporting our results. Sizeable estimates of genetic variation have been reported for lean meat and fat on the carcass and FI and in maintenance requirements (Cameron, 1990; Hermesch et al., 2000; Gjerlaug-Enger et al., 2012). The abovementioned components affect the new efficiency traits, fat and lean meat efficiency, and therefore, genetic variation was expected to exist in these new traits.

Genetic correlations between the animal intercept and the random regression coefficients were significantly different from zero. The results indicated that animals with low feed intake (intercept) were more efficient in deposition of fat compared with animals with a high feed intake (Tables 3 and 4). In agreement with this, Barea et al. (2010) found that a pig line selected for high RFI was energetically less efficient due to greater basal metabolism and higher physical activity, whereas there was no significant line effect on N retention (i.e., lean meat growth).

Table 6. Fraction of total genetic variation due to lean meat and fat efficiency in Norwegian Landrace and Duroc

Parameter	Norwegian Landrace	Duroc
Fraction of total genetic variance due to lean meat efficiency	0.12	0.15
Fraction of total genetic variance due to fat efficiency	0.20	0.10

Statistical Analysis

When comparing model [1] with model [2] in Table 5, the variance components for residual and pen were greater with model [2], suggesting that the model [1] explained more of the heritable variation in FI, that is, due to the explicit modeling of fat and lean meat efficiency (Tables 3, 4, and 5). It also attempted to fit the individual boar's maintenance requirement as a random regression coefficient in the model. However, these analyses did not converge (in DMU [Madsen and Jensen, 2013] or ASReml [Gilmour et al., 2009]). According to Kolstad and Vangen (1996), there are breed differences in maintenance requirements due to body composition, heat production, temperature, and activity, suggesting there could be individual variation in maintenance requirements. Individual differences in maintenance requirements can be partly due to differences in the same factors as mentioned above and could affect the regression coefficients for fat and lean meat depositions. Hence, the fat and lean meat deposition itself may also influence maintenance requirements, making these effects hard to disentangle. The latter could explain the convergence difficulties of a model with individual regression coefficients on fat deposition, lean meat deposition, and AMW, that is, maintenance requirement.

In general, variation in lean meat and fat efficiency may be caused by 1) actual differences in fat and lean meat efficiency; 2) differences in body composition, which may affect heat production and general activity of the animal; and 3) individual differences in which fraction of the fat is deposited around intestines or on the carcass. By including CT scans of the whole pig (and not just the carcass part), differences due to individual differences in which fraction of the fat is deposited around intestines or on the carcass could be eliminated by correcting for total fat and lean meat deposition.

Implications

The results indicated that significant genetic variation existed in Norwegian Landrace and Duroc in efficiency for deposition of lean meat and fat during the test period and that a significant part of the total genetic variance in feed intake was explained by efficiency in fat and lean meat deposition. A challenge in swine genetics is to make the slaughter pigs more feed effective and be lean but have fatty (juicy) meat and at the same time maintain sufficient feed intake and body condition on the sows. Lean meat and fat efficiency, as defined in model [1], gives the breeders opportunities to select animals that have genetic potential to efficiently deposit lean meat at low feed costs, rather than animals that eat less (due to reallocation of feed resources) or produce less fat. Our novel model enables selection for a feed-efficient pig, with a high fat and lean meat efficiency, without the aforementioned problems.

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4. PAPER II:

Genetic relationships between boar feed efficiency and sow piglet production, body condition score and stayability in Norwegian Landrace pigs.

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Paper II

Running head: Boar feed efficiency and sow performance

Genetic relationships between boar feed efficiency and sow piglet production, body condition score and stayability in Norwegian Landrace Pigs[1].

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ABSTRACT

Both feed efficiency and sow production are economically important traits in pig breeding. One challenge in a maternal line such as Norwegian Landrace is to breed for highly feed efficient fattening pigs and at the same time, produce sows with high daily feed intake to maintain their body condition score in multiple parities. The aim of this study was to estimate genetic correlations among novel feed efficiency measurements on Norwegian Landrace boars and piglet production, stayability and body condition in Norwegian Landrace sows. The feed efficiency measurements were lean meat- and fat efficiency. These measurements were calculated using an extended residual feed intake model where total feed intake in the test period was the response variable and fat (kg) and lean meat (kg) on the carcass were included as both fixed and random regressions. The random regression coefficients that resulted from this model were breeding values, which represented amount of feed used to produce an extra kg lean meat and fat. The sow traits were stayability of the sow from first to second parity, body condition score at weaning, litter weight at three weeks and total number of piglets born. All traits were recorded on first parity purebred Norwegian Landrace and analyzed using multivariate animal models. All genetic correlations were low between fat efficiency and sow traits. Significant genetic correlations were found only between fat efficiency and stayability (0.21 ± 0.11) and between fat efficiency and total litter weight at three weeks (0.21 ± 0.10). The results indicate that selection for efficient deposition of fat could give poor stayability and lower litter weight at three weeks in first parity sows. The genetic correlations between lean meat efficiency and sow traits were not significantly different from zero and signified no genetic relationships between these traits. Selection for efficient deposition of lean meat should not affect the sow traits and is thus beneficial.

Keywords: body condition score, feed efficiency, genetic parameter, maternal line, stayability

INTRODUCTION

In the late 1950s, systematic breeding of Norwegian Landrace pigs began and the breeding goal consisted mainly of growth and feed intake within a certain weight interval. Growth and feed intake are still economically important traits in pork production (Kanis et al., 2005): A feed efficient pig with high growth rate is desired. Traditionally, selection for lean meat growth is accomplished by including growth rate, reduced back fat and feed intake per kg growth (**FCR**) in the breeding goal (Hermesch, 2004). Cameron and Curran (1994) showed that intense selection for lean food conversion or lean growth rate may have resulted in reduced feed intake in *ad libitum* feeding systems. Additionally, Kerr and Cameron (1996) showed that animals selected for low daily feed intake over seven generations ate significantly less during lactation and had a poorer litter growth than animals selected for high daily feed intake. This suggested that such selection strategies might give an undesired reduction in voluntary feed intake in the sow during the lactation period. Litter size is an economically important production trait for maternal lines; as the number of piglets increase, the energy requirement for milk production increases (Rothschild, 1996; Rydhmer, 2000). Kolstad et al. (1996) showed that Norwegian Landrace had a high ability to mobilize energy from body reserves. Hence, increased litter size and reduced appetite increases the risk of a negative energy balance of the sows. High mobilization of body reserves during lactation could lead to a poor body condition at weaning. Poor body condition and increased weight loss in sows are associated with lower reproductive performance (Yang et al., 1989; Thaker and Bilkei, 2005), and low reproductive success is a major reason for culling of sows (Dagorn and Aumaitre, 1979; Stein et al., 1990; Lucia et al., 2000; de Jong et al., 2014). Stalder et al. (2003) found that sows needed at least three parities to become profitable. Therefore, one of the major challenges of pig breeding is to produce a highly feed efficient fattening pig with a low FCR and a high production level, and at the same time maintain the sow's body condition score to be able to produce multiple litters. Martinsen et al. (2015) found genetic variation in new feed efficiency measurements for Norwegian Landrace and Duroc, which gave the possibility to select for animals that utilized their feed efficiently. The aim of this current study was therefore to estimate genetic relationships between the new feed efficiency traits of Norwegian Landrace boars and body condition score, stayability and piglet production of Norwegian Landrace sows.

MATERIAL AND METHODS

This study was based on phenotypic records that existed in the databases of Topigs Norsvin (**TN;** Vught, The Netherlands) and hence, the Animal Care and Use Committee approval was not needed for this specific study. Data material was provided by TN and included purebred boars from TN's boar testing station and purebred Norwegian Landrace sows from TN's breeding nucleus and multiplier herds. Data on piglet production, body condition and stayability was extracted from the Norwegian litter recording system (Ingris; Norwegian Meat and Poultry Research Centre, 2016), while feed intake data on the boars was extracted from TN's database from the test station. The traits analyzed were total feed intake in the test period (**FI**) measured on boars on the test station and body condition score after weaning of first litter (**BCSw**), stayability up to insemination for a second litter (**STAY**), total number of piglets born in first litter (**TNB**) and total litter weight of first litter at three weeks (**TLW)** measured on purebred Landrace sows and their litters in nucleus and multiplier herds. The feed efficiency measures were predicted by a random regression of total feed intake (in the test period) on lean meat and fat production (Martinsen et al., 2015). In total, data on all traits was extracted from 197 herds within TN's breeding nuclei in Norway and other countries.

Boar Test Recordings

Total feed intake in the test period measured on boars originated from 40 nucleus herds in Norway and was recorded at TN's boar station test. The boars selected for the test are from the best third of all litters born in the active breeding population. At the station test, individual feed intake and weight were measured daily on all boars by a Feed Intake Recording Equipment (FIRE) station (Osborne Industries Inc., Osborne, KS, USA) in each pen of 12 pigs. The average live weight of the boars at the start of the test was approximately 40 kg, and approximately 100 or 120 kg at the end of the test. If the boar finished the test before March, 1, 2012, they ended the test at 100 kg live weight, all boars finishing after this ended the test at 120 kg live weight. In this data set, FI was recorded on boars born from 2008 to 2014. In total, 8,161 Norwegian Landrace boars had information on FI. At the end of the test, all boars were scanned by computed tomography (**CT**). As part of this procedure, lean meat and fat content on the carcass of each boar were calculated by a TN developed MATLAB (The MathWorks Inv., 3 Apple Hill Drive, Natick, MA, USA) program for image analysis of CT- data (Gjerlaug-Enger et al., 2012). Martinsen et al. (2015) provided a more detailed description of the data.

Stayability, Body Condition Score and Piglet Production

Information on the sow traits came from 194 nucleus and multiplier herds in the TN system, from Norway and other countries. Due to strict animal welfare regulations, Norwegian pig production has some distinct characteristics. It is enforced by law that the minimum length of lactation shall be 28 days and sows are loose housed through all stages of production (Thingnes, 2013). Hence, the data are collected in herds that does not have identical management, as weaning takes place earlier and the sows are crated during lactation in some foreign countries. In Norway, farmers routinely record BCSw, TLW and TNB in nucleus and most multiplier herds. In this data set, TLW was defined as the sum of adjusted individual weights of all piglets at three weeks of age in the first litter. The piglets are weighed between 17 and 25 days of age, and their weight is adjusted to 3 weeks of age (21 days). Total number of piglets born in first litter included both live-born and stillborn piglets. Body condition score after weaning of first litter was a categorical trait where sows were scored from 1 to 9, where 1 was thin and 9 was obese. The farmer follows national guidelines for body condition scoring of sows provided by TN and Norwegian Meat and Poyltry Research Centre (Oslo, Hamar) to make the scoring as objective as possible (Norwegian Meat and Poultry Research Centre and Topigs Norsvin, 2015). In this data, STAY was defined as a binary trait and stated whether a sow was culled after first litter (STAY = 0) or if she was inseminated for a second litter (STAY = 1). Animals with an unsuccessful second insemination were not captured in this trait, as these were also registered as 1. Only information from first to second parity was used, but stayability from first to second parity is found to be highly correlated with stayability from second to third parity and later parities (Tholen et al., 1996; Engblom et al., 2009; Aasmundstad et al., 2014). Sows younger than 250 days or older than 730 days at farrowing and sows weaning piglets older than 70 days were discarded. Only sows with at least two piglets in the litter were included in the analysis. The traits were recorded on first parity sows born from 2002 to 2014. Table 1 shows descriptive statistics for the traits. Pedigree was traced ten generations back, and included 117,638 animals.

Statistical Analyses

The traits were analyzed using multivariate animal models, and estimation of variance components and genetic correlations were performed using the DMU software package (Madsen and Jensen, 2013). The fixed effects used in the models were determined based on a GLM analysis of the traits in SAS (SAS Inst. Inc., Cary, NC). For all traits, heritability was defined as: $h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2}$, where σ_a^2 is the genetic variance and σ_e^2 is the residual variance of the trait.

Total feed intake in the test period. The trait and model are defined according to Martinsen et al. (2015). For the trait FI in boars at the test station, the following model was used for analysis:

$$\mathbf{FI}_{\mathbf{ijknoqrs}} = \mathbf{HY}_{\mathbf{i}} + \mathbf{BM}_{\mathbf{j}} + \mathbf{ST}_{\mathbf{k}} + \mathbf{SEC}_{\mathbf{n}} + \boldsymbol{\beta}_{\mathbf{lm}} \times \mathbf{LMEAT}_{\mathbf{o}} + \boldsymbol{\beta}_{\mathbf{fat}} \times \mathbf{FAT}_{\mathbf{q}} + \boldsymbol{\beta}_{\mathbf{amw}} \times \mathbf{AMW}_{\mathbf{r}} + \mathbf{a}_{\mathbf{s}} + \mathbf{pen}_{\mathbf{t}} + \mathbf{a}_{\mathbf{p}_{\mathbf{s}}} \times \mathbf{lmeat}_{\mathbf{o}} + \mathbf{a}_{\mathbf{f}_{\mathbf{s}}} \times \mathbf{fat}_{\mathbf{q}} + \mathbf{e}_{\mathbf{ijknoqrst}} \qquad [1]$$

The fixed effects included in the model were birth herd-year (**HY**), birth month (**BM**), scanning time (**ST**) and section in the test station (**SEC**). Number of levels in HY (*i*) was 207 and for BM (*j*) it was 12. For ST (*k*) number of levels was 2 (finishing before or after March 1, 2012) and SEC (*n*) had 132 levels. The boars' phenotypes for carcass lean meat (**LMEAT**), carcass fat (**FAT**) and accumulated metabolic body weight (**AMW**) were included as fixed regression covariates. As a measure of feed efficiency, random regressions on amount of lean meat (**lmeat**) and fat (**fat**) ($\mathbf{a}_{\mathrm{p}_{\mathrm{s}}}$ and $\mathbf{a}_{\mathrm{f}_{\mathrm{s}}}$, respectively) were included in the model as in Martinsen et al. (2015). As each boar only has one measure each for lean meat and fat content (kg), respectively, the random regression model is fitted through the genetic relationships between boars with records of lean meat and fat. Thus, the model can utilize a situation with only one record per animal. The animals' additive genetic effect ($\mathbf{a}_{\mathrm{s}}$) and pen (**pen**) were included as random effects. In this model, a_{s} represents the genetic effect of the animal on FI that cannot be explained by the differences in deposition of fat and lean meat, and is from now on referred to as the (genetic effect on) residual feed intake of the animal (**RFI**). In the results, $\mathrm{a}_{\mathrm{p}_{\mathrm{s}}}$ is referred to as lean meat efficiency (**LME**) and $\mathrm{a}_{\mathrm{f}_{\mathrm{s}}}$ is referred to as fat efficiency (**FE**) of animals. Both LME and FE are random regression coefficients, which indicate the individual deviation (from the population mean) with respect to amount of feed needed to produce one kg of lean meat or fat. It should be noted that increased levels are unfavorable as this indicates a greater demand for feed per kg fat or lean meat deposited. Hence, low LME and FE are desirable.

Total feed intake in the test period was also analyzed in a second model [2], which was identical to model [1], but excluded the effect of accumulated metabolic body weight and the fixed and random regressions on carcass lean meat and fat.

$$\mathbf{FI_{ijklmn} = HY_i + BM_j + ST_k + SEC_l + a_m + pen_n + e_{ijklmn}} \qquad [2]$$

The fixed effect are the same as in model [1], while the random effect ($\mathbf{a_m}$) is the genetic effect of the animal on total feed intake in the test period. Model [2] was therefore a traditional linear animal model used to analyze FI, which did not correct for production. Model [2] was used to compare the results from the new model developed in Martinsen et al. (2015) with results from a traditional linear animal model for FI.

Body condition score. Body condition score after weaning of first litter was analyzed in the following model, which is used by TN for their routinely genetic evaluation of the trait:

$$\begin{aligned}&\mathbf{BCSw_{ijklmnopq} = M\_LNO_i + HY_j + SEA_k + BRYEAR_l + WEAN_m + \beta \times AGEM_n +}\\&\mathbf{\beta \times AGEW_o + animal_p + litter_q + e_{ijklmnopq}}\end{aligned} \qquad [3]$$

The fixed effects in the model was dam’s litter number (**M_LNO**, i= 1 to 3, where all M_LNO > 3 was assigned as 3), birth herd-year (**HY**, j= 1 to 593), season (**SEA**, k=1 to 4), breed of the litter-year of the record (**BRYEAR**, l= 1 to 65) and number of weaned piglets (**WEAN**, k=1 to 19). Sow’s age at farrowing (**AGEM**) and litter’s age at weaning (**AGEW**) were both included as fixed regression covariates in the model. The animal’s breeding value (**animal**), litter’s identity (**litter**) and the residual (**e**) were included as random effects.

Stayability. Based on previous work by Aasmundstad et al. (2014) STAY was analyzed as:

$$\mathbf{STAY_{ijklmno} = M\_LNO_i + BY_j + HYS_k + BR_l + \beta \times AGEM_m + animal_n + litter_o + e_{ijklmno}} \qquad [4]$$

In the model, M_LNO, birth year (**BY**), herd-year-season of the record (**HYS**) and breed of the litter (**BR**) were treated as fixed effects. Dam's litter number had 3 levels (M_LNO> 3 was assigned 3), BY had 13, HYS had 4936 levels and BR had 11 levels. The AGEM was included as a fixed covariate. The animal's breeding value (animal) and their litter (litter) were included as random effects, and **e** was the random residual effect.

Total number of piglets born and litter weight at three weeks. Total number of piglets born in first litter was analyzed by the model below, which is identical to TN's model in the routine genetic evaluation of this trait:

$$\mathbf{TNB_{ijklmno} = M\_LNO_i + HY_j + SEA_k + BRYEAR_l + \beta \times AGEM_m + litter_n + animal_o + e_{ijklmno}} \qquad [5]$$

The effects in model [5] were the same as for BCSw (model [3]), without the fixed regression covariate of age at weaning. The M_LNO (i= 1 to 3, where $i > 3 = 3$), the HY (j=1 to 1406), the SEA (k =1 to 4) and BRYEAR (l= 1 to 93) were included as fixed effects. For TLW, the model was the same as model [5] but also included the fixed effect of number of piglets weighed in the litter (weighed piglets= 1 to 27). This model was referred to as model [6].

RESULTS

Descriptive Statistics

Table 1 shows descriptive statistics of the data. The average FI was 152.1 kg with a high variation (97.2 to 270.6 kg). Boars had on average 52.3 ± 3.6 kg LMEAT and 15.9 ± 4.3 kg FAT. For BCSw measured on sows at weaning, the average was 4.2 ± 0.9 points (scale from 1 to 9). Few sows with BCSw = 1 were present, which indicated that some sows were very thin at weaning. The maximum BCSw was 8 which indicated that no obese sows were included in the data. For STAY, approximately 70% of the sows were inseminated for a second parity, whereas the rest were culled after weaning their first litter. For piglet production, TLW was 66.8 ± 19.7 kg on average, but with a high variation from 1.5 to 193.2 kg. This is mainly due to the substantial variation in number of piglets in the litters. Average TNB was 13 piglets, ranging from 2 to 29. The TNB included both live born and stillborn piglets. Table 2 contains number of animals with phenotypes for each trait combination. Registration of BCSw did not start until 2007, and therefore the number of observations was significantly lower than the other traits.

Variance Components and Heritabilities

Estimates of variance components and heritabilities for all traits are presented in Table 3. All (genetic) variances were significantly larger than zero. Significance was tested based on the estimate ± 1.96 x SE, which signifies a 95% confidence interval for the estimate ($P < 0.05$). Low to moderate heritabilities were found for TNB, STAY, BCSw, and TLW (0.07, 0.10, 0.13 and 0.16). The heritability for FI estimated with model [1] was remarkably high (0.59), whereas model [2] gave a moderate heritability for FI (0.22). The additive genetic variance was approximately the same in both models, but the residual variance was considerably lower with model [1].

Genetic Correlations

The estimated genetic correlations from the multivariate analysis are presented in Table 4. Genetic correlations were estimated among RFI, LME and FE measured on boars and BCSw, STAY, TLW and TNB were measured on sows. Overall, the genetic correlations were relatively low and mostly non-significant. Significant correlations were found between RFI and both efficiency measures (LME and FE), suggesting that animals with a high overall feed intake in the test period had a lower efficiency (higher feed intake per kg deposited lean meat and fat). The estimated genetic correlation between FE and LME was slightly negative, albeit not significant. The genetic correlation between FI estimated with model [2] and the sow traits where close to zero and non-significant between all traits.

The sow traits and Residual Feed Intake. The correlations between RFI and the sow traits were positive, but low and mostly not significantly different from zero. Still, a positive and significant correlation was found between RFI and BCSw, which implies that animals with an overall high feed intake (used for other purposes than fat and lean meat deposition) in the growth period would be expected to have a greater BCSw as first parity sows.

The sow traits and Fat Efficiency. The genetic correlations between FE and sow traits were positive (i.e., unfavorable), but low. Significant positive correlations were found between FE and STAY (0.21 ± 0.11) and between FE and TLW (0.21 ± 0.10). These results suggested that selection for fat efficient pigs might result in animals with poorer STAY and reduce TLW. Overall, the correlations between FE and sow traits were non-significant, except for the correlations between FE, TLW and STAY in first parity sows.

The sow traits and Lean Meat Efficiency. The genetic correlations found between LME and the sow traits were nonsignificant. All the correlations were negative, except the one between LME and TNB, which was positive but also nonsignificant.

DISCUSSION

This genetic analysis showed no genetic correlations between LME and the sow traits, whereas FE had a low and unfavorable genetic correlation to both TLW and STAY. Selection for LME is therefore not expected to deteriorate the sow traits BCSw and STAY and piglet production in first parity sows. Selection for FE is a possibility, but may cause some deterioration of TLW and STAY, unless the traits are actively selected for.

Variance Components and Heritabilities

For the piglet production traits (TNB and TLW), the heritabilities were in agreement with TN's genetic parameters and slightly lower than those found by Aasmundstad et al. (2014). Sevón-Aimonen and Uimari (2013) estimated a heritability of 0.08 for TNB in Finnish Landrace, which corresponds to this study and studies of other breeds (Hanenberg et al., 2001; Rydhmer et al., 2008). Bergsma et al. (2008) estimated a higher heritability, but included more than first litter in their analysis as well as data from crossbred sows. A review article by Bidanel (2011) showed that average heritability for TNB was 0.11. Hanenberg et al. (2001) found an increase in heritability as parity increased for TNB. This study only included first parity sows; therefore, a lower heritability might be expected. Total number of piglets born in first litter is influenced by embryo survival, uterus capacity and ovulation rate. Primiparious sows have a lower uterus capacity than multiparious sows, and Hermesch et al. (2000) suggested that this might cause a restriction on the genetic variation. This means that the genetic potential for the trait might not be fully expressed.

Bidanel (2011) also found an average heritability of 0.17 for TLW, in accordance with this study. A corresponding heritability was found in Norwegian Landrace for mean body weight at three weeks (Canario et al., 2010). Lundgren et al. (2014) estimated a greater heritability for TLW in Norwegian Landrace, in accordance with Aasmundstad et al. (2014). The data set in this study consist of data from Norway and foreign countries, thus may include more noise and underestimate the heritabilities. Heritability for BCSw was in accordance with earlier results found in Norwegian Landrace, analyzed as linear traits in multitrait animal models (Lundgren et al., 2012; Lundgren et al., 2014). Studies have also investigated the sow's body condition through other continuous traits, such as loss of live weight and loss of back fat from farrowing to weaning (Grandison et al., 2005; Bergsma et al., 2008). Heritabilities in these studies were slightly greater for weight loss and lower for back fat loss.

In the current study, STAY was defined as a binary trait with success (1) if the sow was inseminated again after first litter and a failure (0) if she was culled after first litter. The estimated heritability of the current study was 0.10, which was slightly lower than estimates obtained by Aasmundstad et al. (2014) for the same breed (0.13). The traits were not identically defined, as Aasmundstad et al. (2014) defined STAY as ability to give birth to a second litter, rather than insemination for a new litter. Knauer et al. (2011) defined stayability in the same way as Aasmundstad et al. (2014), included only first litter sows and analyzed the trait in a threshold model (0.14). The heritability of a threshold model is not directly comparable to that of a linear model. An ordinal threshold model may be beneficial for analysis of both BCSw and STAY, as simulation studies have shown that threshold models are beneficial to use for categorical traits and are expected to give better estimates of the underlying heritability and increased genetic gain if higher accuracy is achieved (Meuwissen et al., 1995; Abdel-Azim and Berger, 1999). Still, in real data studies, the use of threshold models is challenging because of an increased computational burden when working with large data sets, and extra gains have been limited (Varona et al., 1999; Ødegård et al., 2006). Ødegård et al. (2006) concluded that a longitudinal linear test day model for survival in Atlantic salmon gave the highest predictive ability, when compared to a threshold model and various other models. However, these methods are rarely implemented in organized breeding programs, as they are computationally challenging.

Stayability up to insemination for a second litter is a complex trait, influenced by several traits such as reproduction and lameness and also environmental factors such as herd management and temperature. A low heritability might be expected, as the genetic component of STAY may be difficult to depict. This might be because the binary outcome of the trait not only is a result of sows' biological capacity of coming into heat or producing a litter, but also because an insemination is an active decision made by the farmer. This decision is partly based on sows' biological capacity and partly a subjective judgement from the farmer. The herds in this dataset were selected to be inseminated for a second litter or not based on their total merit index and phenotypical functionality. Hence, the observed stayability is not only a result of the sows biological capacity for a second litter, but also an active decision made by the farmer partly influenced by the assumed EBVs at the time of insemination or culling. This means that sows with poor EBVs are not necessarily inseminated with a second litter, even though they are capable. Aasmundstad et al. (2014) performed a genetic analysis of stayability, comparing models with and without the fixed covariate of the animals' total merit index at time of culling. Inclusion of the total merit index as a covariate actually increased the estimated heritability for the stayability trait. This may be explained by several major changes in the breeding goal of Norwegian Landrace in the past (and, therefore, in the composition of the total merit index), and correcting for this may have removed some of the noise in the recorded phenotype (Aasmundstad et al., 2014). Furthermore, Aasmundstad et al. (2014) might have improved the model by comparing the EBV of the culled animals with the within herd level at time of culling, instead of population average.

The genetic variation in LME and FE was rather low for both traits, and Martinsen et al. (2015) found that LME and FE explained 12% and 20%, respectively, of the total genetic variation in FI. This suggested that a rather small part of FI was explained by LME and FE. The trait FE rather than LME explained a bigger part of the genetic variation in FI, and the study proposed that this might be caused by the selection strategy for Norwegian Landrace. The estimated heritability for FI was 0.59 and was calculated with the same formula as the sow traits, but the calculation of σ_a^2 was based on the variance components for RFI, LME and FE (Martinsen et al., 2015). Lower heritability estimates have been found for total feed consumption in performance test by earlier studies (Kerr and Cameron, 1996; Holm et al., 2004). The model used for analysis of total feed intake in the test period in this study was very complex. The residual variance decreased substantially as lean meat and fat were included in the model, and may be the reason for the increased heritability when model [1] was used in contrast to model [2] (Table 3). Model [1] has a heterogeneous genetic variance (due to differences in lean meat and fatness) and a constant error variance, which implies that the genetic variance is modelled with more flexibility than the error variance. This may have resulted in the genetic factor capturing some of the residual heterogeneity. Thus, an extension of model [1] would be to introduce also heterogeneous error variance, which would be a function of the lean meat and fat content (kg). No significant changes were observed in the heritabilities for the sow traits when model [2] was used for FI, as expected.

Genetic Correlations

In pork production, daily feed intake is a conflict of interest between the market hog producers and the piglet producers (Holm et al., 2004). For a market hog producer, low feed intake and high growth is important to maintain a good profit. For the piglet producer, a large appetite and high daily feed intake in the sow is crucial to produce large and heavy litters and to avoid high weight loss (Eissen et al., 2003). No information was available on the sows' feed intake in this study, but the sows' production (TLW) and BCSw could give an indication whether their feed intake was sufficient during lactation. To look at the genetic relationships between the new feed efficiency traits and these sow traits would be beneficial to see if potential selection for these new traits would have a deleterious effect on these important sow traits.

No significant correlations were estimated between any of the feed efficiency measures and TNB. Other studies have also found low or non-significant correlations between reproductive performance in sows and production traits in boars (Hermesch et al., 2000; Holm et al., 2004; Imboonta et al., 2007). Kaufmann et al. (2000) stated that the maternal genetic effect of the sow was a more important part of piglet weight at birth and weaning than the animal's own direct genetic effect, and Grandison et al. (2002) supported this conclusion. An inclusion of the maternal genetic effect in the model for analyzing piglet production might have been useful to depict a genetic correlation between efficiency traits and piglet production traits.

The carcass of a pig consists of lean meat, fat and bones. In Norwegian Landrace, there is minimal variation in the size of bone compared to lean meat and fat (Norwegian Meat and Poultry Research Centre, 2012). Therefore, more fat at a given body weight usually implies less lean meat and vice versa. This relationship may explain the overall opposite signs for the correlations between the sow traits and FE and between the sow traits and LME. If an animal consumes a given amount of feed, it is distributed to muscle or fat deposition. If the animal has a high muscle growth, it most likely deposits less fat tissue. This does not necessarily make the animal fat inefficient, as the energy cost of depositing one kg fat may be similar.

The Sow Traits and Residual Feed Intake. The sow data material in this study consisted of records on first parity sows. First parity sows have a greater risk of loss of body reserve during lactation compared to multiparous sows. This is due to not only their extra nutritional requirement for growth in addition to milk production and maintenance, but also their general lower feed intake capacity (Whittemore, 1996; Thingnes et al., 2012). Boddicker et al. (2011) found that animals selected for low residual feed intake ate less than a randomly selected group, and especially in the second half of the growth period (after 50 kg). These biological restrictions in first parity sows might influence the genetic relationship between RFI and BCSw.

In a review article, Veerkamp (1998) showed studies where positive correlations were found between live weight and dry matter intake in cows. Dunnington and Siegel (1996) showed that chicken lines selected for high body weight had a significantly greater feed intake than the line selected for low body weight. In addition, animals selected for low residual feed intake tended to have a higher body weight loss from farrowing to weaning than animals selected for high residual feed intake (Gilbert et al., 2012). These findings may support the current study's positive genetic correlation between RFI and BCSw in sows, suggesting that animals with a high overall feed intake in the growth period had an increased BCSw.

The genetic relationship between residual feed intake and sow performance is not clearly established in the literature. This study found no significant genetic correlations between RFI and piglet production (TNB and TLW), in accordance with Gilbert et al. (2012) who estimated weak and non-significant correlations between residual feed intake and total number of piglets born and litter weight at three weeks. In contrast, Young et al. (2010) investigated animals selected for reduced residual feed intake over six generations, and found that the line selected for low residual feed intake had a greater number of piglets in the litter and the piglets were heavier at birth. However, the study concluded that the sows had a greater body reserve loss than the control line. Based on the present and earlier studies, it might seem like the genetic relationship between the residual feed intake in the growth period and sow performance is rather weak. However, selection for reduced residual feed intake in the growth period might improve sows' ability to mobilize body reserves for piglet production.

The Sow Traits and Fat Efficiency. The significant unfavorable genetic correlation between FE and STAY suggested that animals that used a high amount of feed to produce one kg of fat had a better chance of staying in the herd. We found a positive correlation between fat content on the carcass (kg) and FE (unpublished results), implying that the animals with high fat content on the carcass being less fat efficient. Possibly, animals that overeat would produce more fat and appear less fat efficient. In the end, this overeating would result in the conversion of protein from feed to fat on the carcass, which is a highly inefficient use of feed. However, this may be beneficial for the sow as an energy resource for piglet production, which affects STAY. This explanation is supported by the significant positive correlation between FE and TLW (0.21), which signifies that animals that are less fat efficient produce heavier litters.

Kolstad (2001) investigated the fat deposition in Norwegian Landrace and Duroc. They argued that, due to the selection criteria, a relatively high proportion of total fat in Norwegian Landrace was deposited as visceral fat. The study also mentioned the importance of including deposition of visceral fat for the efficiency in pig production. When modeling FE in this study, the amount of visceral fat was not included in the analysis, only carcass fat (FAT) estimated from the CT images. Visceral fat deposition was, therefore, not directly corrected for in the model, although a positive genetic correlation between visceral and carcass fat (FAT) exists (D. Olsen, Topigs Norsvin, Hamar, Norway, personal communication). It is thus possible that animals that seemed inefficient in fat deposition had deposited a high amount of visceral fat in their body, which is not included in the CT image analyses. A correction for the slaughter percentage (i.e., amount of visceral fat) in model [1] was performed to investigate whether FE was dependent of where the fat was deposited. The results indicated that slaughter percentage did not have an effect on FE. No changes were observed in the results when slaughter percentage was included in the model. This suggested that the findings of the current study are robust, even though visceral fat is not included in the analysis of FE.

The Sow Traits and Lean Meat Efficiency. The amount of feed used to produce one kg lean meat did not have any significant genetic relationship with any of the sow traits. Hermesch et al. (2000) estimated genetic correlations between FCR and reproduction traits in sows. They found a negative, but low and favorable correlation between FCR and litter weight at birth. Lean meat efficiency in the current study describes the feed needed for lean meat deposition and is a more specific measure of feed efficiency. The genetic correlations between LME and litter weight showed the same relationship as Hermesch et al. (2000), but were not significant. Our results suggested that overall LME hardly affected the sow traits. This study found a significant correlation between RFI and BCSw, which suggests that selection for RFI could result in sows with poor BCSw. Because no genetic relationships between LME and the sow traits were found, this new trait could be less related to sow traits than traditional residual feed intake.

IMPLICATIONS

The results indicated that the genetic relationships between the new feed efficiency measurements and the sow traits in general were small and not significantly different from zero for Norwegian Landrace. Significant genetic correlations were found between FE and STAY and between FE and TLW (0.21, 0.21), suggesting that selection for better FE in boars may reduce TLW in first parity sows and result in poorer STAY. Lean meat efficiency had no significant genetic relationships with the sow traits. To meet future challenges with the maternal line, LME makes it possible to select animals that have genetic potential to deposit lean meat efficiently at low feed costs, without affecting economically important sow traits such as STAY, BCSw, TLW and TNB.

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Table 1. Average (mean), standard deviation (SD), minimum (min) and maximum (max) values for total feed intake in the test period (FI), lean meat and fat registered on boars in the test station and for body conditions score after weaning of first litter (BCSw), stayability up to insemination for a second litter (STAY), total litter weight of first litter at three weeks (TLW) and total number of piglets born in first litter (TNB) registered on sows off test.

Parameters	Mean	S.D.	Min	Max
FI (kg)	152.1	29.4	97.2	270.6
Lean meat (kg)	52.3	3.6	40.5	68.2
Fat (kg)	15.9	4.3	7.2	33.0
BCSw (point)	4.2	0.9	1	8
STAY(point)	0.7	0.5	0	1
TLW (kg)	66.8	19.7	1.5	193.1
TNB (number)	12.9	3.6	2	29

Table 2. Distribution of observations between total feed intake in the test period (FI), body condition score after weaning of first litter (BCSw), stayability up to insemination for a second littter (STAY), total litter weight of first litter at three weeks (TLW) and total number of piglets born in first litter (TNB)

	FI	BCSw	STAY	TLW	TNB
FI	8,161				
BCSw	-	38,251			
STAY	-	36,257	88,453		
TLW	-	34,128	68,319	70,321	
TNB	-	38,251	88,453	70,321	90,945

Table 3. Genetic variance components (σ_a^2), residual variance components (σ_e^2) and heritability (h^2) for total feed intake in the test period for boars (FI), body condition score after weaning of first litter (BCSw), stayability up to insemination for a second litter (STAY), total litter weight of first litter at three weeks (TLW) and total number of piglets born in first litter (TNB) for model [1] and [2]. The variance components for FI were based on genetic variance components for the animal (RFI), lean meat efficiency (LME) and fat efficiency (FE).

	Model [1]			Model [2]		
Trait	σ_a^2	σ_e^2	h^2	σ_a^2	σ_e^2	h^2
FI	25.58	17.50 (0.95)	0.59	23.34(3.26)	83.22(2.79)	0.22
RFI (a_s)	18.16 (1.47)	-	-	-	-	-
LME (a_{p_s})	0.22 (0.04)	-	-	-	-	-
FE (a_{f_s})	0.27 (0.04)	-	-	-	-	-
BCSw	0.07 (0.00)	0.46(0.00)	0.14	0.07 (0.00)	0.46(0.00)	0.13
STAY	0.02 (0.00)	0.14 (0.00)	0.10	0.02 (0.00)	0.13(0.00)	0.10
TLW	12.10 (0.66)	63.37 (0.59)	0.16	11.91 (0.63)	63.28(0.59)	0.16
TNB	0.80 (0.06)	11.08 (0.07)	0.07	0.81 (0.06)	11.07(0.07)	0.07

Table 4. Genetic correlations (standard error) between feed intake in the test period not explained by genetics of lean meat and fat efficiency, named residual feed intake (RFI), lean meat efficiency (LME), fat efficiency (FE), body condition score after weaning of first litter (BCSw), stayability up to insemination for a second litter (STAY), total litter weight of first litter at three weeks (TLW) and total number of piglets born in first litter (TNB) (Model[1]). Genetic correlations between total feed intake in the test period (FI) and BCSw, STAY, TLW and TNB (Model [2]).

	Model [1]			Model [2]
Trait	RFI	LME	FE	FI
LME	0.25 (0.07)	-	-	-
FE	0.71 (0.05)	-0.19 (0.12)	-	-
BCSw	0.16 (0.07)	-0.03(0.13)	0.13 (0.11)	0.13 (0.08)
STAY	0.12 (0.07)	-0.14 (0.12)	0.21 (0.11)	0.02 (0.08)
TLW	0.09 (0.06)	-0.16 (0.11)	0.21 (0.10)	-0.04 (0.07)
TNB	0.03 (0.08)	0.14 (0.14)	-0.05 (0.12)	0.06 (0.09)

5. PAPER III:

Economic values for lean meat- and fat efficiency in Norwegian Landrace nucleus pig population

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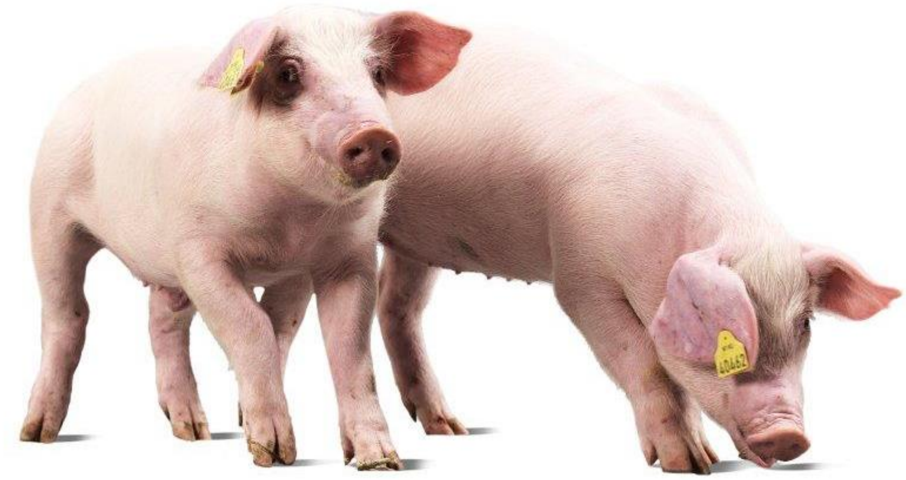

Photo: Topigs Norsvin

Paper III

Running head: Economic values for feed efficiency

Economic values for lean meat- and fat efficiency in Norwegian Landrace nucleus pig population[1].

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ABSTRACT

A simple bio-economic model was developed to estimate economic values for five traits for fattening pigs in Norwegian Landrace. The traits included in the model were lean meat efficiency (**LME**), fat efficiency (**FE**), days from 40 to 100/120 kg live weight (**DAYS**), lean meat percentage (**LMP**) and fat content on the carcass (**FC**). This model was referred to as breeding goal A. The model simulated the economic result on a per fattening pig-basis. The performance level was set to the average production results from Topigs Norsvin's boar test station in Norway. To compare the two efficiency traits with feed intake in the test period (**FI**), an economic model including FI, LMP and DAYS was developed. This was referred to as breeding goal B. Indexes for the two different breeding goals were made for comparison. The standardized economic values (SEV) for LME and FE were 8.9 and 2.9 EUR/σ_a, respectively, while for LMP and FC they were estimated to 4.5 and 1.1 EUR/σ_a. For DAYS, the SEV was 2.6 EUR/σ_a, while for FI it was 1.6 EUR/σ_a. There was a larger variation in the index for breeding goal A than breeding goal B, and the rank correlation between the two indexes was 0.77. The results suggested that the two new efficiency traits had a high economic importance in pork production, and that there was a big potential for increased genetic gain in profit by using breeding goal A. Breeding goal A included additional information and might improve the genetic evaluation of boars.

Keywords: economic model, economic value, lean meat efficiency, Norwegian Landrace

INTRODUCTION

The purpose of breeding programs is to improve the profitability of livestock production. Profitability is approximated by the breeding goal for the population. A breeding goal states which traits that are important to improve and could be of both economical and societal interest (Olesen et al., 2000; Kanis et al., 2005). The purpose of pig breeding is to meet the demands for high quality meat production in a sustainable way. The breeding goal should therefore include traits that increase the commercial producer's income and reduce their costs in pork production. This includes traits such as growth and feed efficiency, but also demands from the society, with traits such as meat quality, animal welfare and health (Kanis et al., 2005; Flint and Woolliams, 2008). The traits are often of different importance, and to weigh the traits in the breeding goal, their economic value needs to be estimated (De Vries, 1989). The Norwegian Landrace (**NL**) is a maternal breed and the breeding goal consists of seven trait groups with a number of traits within each group. These groups are production, carcass quality, meat quality, litter size, reproduction, maternal ability and robustness, and all have different weights in the total merit index (Norsvin, 2016). The NL is a feed efficient and lean breed with a low amount of back fat (Gjerlaug-Enger et al., 2012). This is due to extensive selection for reduced back fat, increased lean growth and reduced feed intake per kg growth (**FCR**) over 50 years. Martinsen et al. (2015) suggested that this selection was more related to resource allocation rather than selection for efficiency to utilize nutrients. The same study therefore established two new efficiency traits, indicating how well the animal utilizes the feed for lean meat and fat production. The traits were named lean meat efficiency (**LME**) and fat efficiency (**FE**) and describes how much feed needed for production of one extra kg lean meat and fat (as a deviation from the mean). The aim of this paper was to assess the economic importance of the new efficiency traits in pork production compared to a traditional feed consumption trait and estimate the economic values for the two new efficiency traits, lean meat- and fat efficiency.

MATERIAL AND METHODS

Model Description

The breeding company Topigs Norsvin (TN; Vught, the Netherlands) provided data from their boar test station in Norway, and this was used as input for the economic model. The model describes the income and costs in the purebred NL fattening pigs, from they are bought, as feeder pigs (40 kg) to they are slaughtered (100/120 kg).

Traits Evaluated

All traits were recorded on purebred NL boars from 40 nucleus herds in Norway at the boar test station. The boars are housed in pens with a Feed Intake Recording Equipment (FIRE) station (Osborne Industries Inc., Osborne, KS, USA), with 12 pigs in each pen. Here, individual feed intake and weight are recorded. The boars weight ~40 kg live weight when they enter the test, and about 100/120 kg when they end the test and their body composition is scanned by computed tomography (**CT**). Boars finishing the test before March 1, 2012 were CT-scanned at 100 kg live weight, while boars finishing after this date were scanned at 120 kg. Through image analysis from the CT-scans, lean meat- and fat content are registered. In total, 8,161 NL boars had information on the traits included in the bio-economic model. These traits were lean meat efficiency (**LME**) and fat efficiency (**FE**) (described in Martinsen et al. (2015)), number of days from 40 to 100/120 kg (**DAYS**), lean meat percentage (**LMP**) and fat content on the carcass (**FC**). To compare the new efficiency traits with total feed intake in the test period (**FI**), an economic model including FI, DAYS and LMP was developed. This was referred to as breeding goal B. The economic model including LME, FE, DAYS, LMP and FC was referred to as breeding goal A.

Days from 40 to 100/120 kg live weight (DAYS). Days from 40 to 100/120 kg live weight is a measure for the individual growth. The trait is number of days between the animal is bought as a feeder pig (40 kg) and slaughtered at 100/120 kg. A reduction in this trait is preferable, as a faster growing pig would use less days to reach the end weight, and thus less feed. In addition, the farmer save costs in housing and labor per unit produced when the animals are slaughtered earlier.

Lean Meat Percentage (LMP). Lean meat percentage is a measure for carcass quality in the pig, and influences the income of the farmer. The price per kg for the carcass is influenced by LMP, as the market prefers a lean carcass (high LMP). By improving this trait, the income of the farmer will thus increase.

Fat Content on the Carcass (FC). Fat content on the carcass represents the amount of fat on the carcass, which represents a cost for the farmer. By reducing FC on the fattening pigs, feed costs for fat deposition is reduced, and the farmers total cost decreases. This trait is included in the calculation of feed intake costs together with FE.

Total Feed Intake in the Test Period (FI). Total feed intake in the test period is a measure of individual total feed intake during the test period. A reduction in this trait is preferable, as animals with low feed intake saves feed costs in the production.

Estimation of Lean Meat and Fat Efficiency. Both efficiency measurements were analyzed in an random regression animal model, and prediction of breeding values was performed in a univariate analysis using DMU (Madsen and Jensen, 2013).The fixed effects used in the model were determined based on an analysis of the traits in SAS.

To estimate LME and FE, FI was analyzed as the trait with amount of lean meat and fat included through random regressions in the model. For analyzing FI the following model was used:

$$\begin{aligned}\mathbf{FI_{ijknoqrst}} &= \mathbf{HY_i} + \mathbf{BM_j} + \mathbf{ST_k} + \mathbf{SEC_n} + \boldsymbol{\beta}_{\mathbf{lm}} \times \mathbf{LMEAT_o} + \boldsymbol{\beta}_{\mathbf{fat}} \times \mathbf{FAT_q} + \boldsymbol{\beta}_{\mathbf{amw}} \times \mathbf{AMW_r} + \\ &\mathbf{a_s} + \mathbf{pen_t} + \mathbf{a_{p_s}} \times \mathbf{lmeat_o} + \mathbf{a_{f_s}} \times \mathbf{fat_q} + \mathbf{e_{ijknoqrst}}\end{aligned} \quad [1]$$

The fixed effects included in the model were herd-year (**HY**), birth month (**BM**), scanning time (**ST**) and section (**SEC**). Number of levels in *i* were 207 and for *j* it were 12. For *k* number of levels were two (finishing before or after March 1, 2012) and *n* had 132 levels. The boars' amount of lean meat (**LMEAT**) and fat (**FAT**) on the carcass and accumulated metabolic body weight (**AMW**) were included as fixed regression covariates. As a measure of the individual genetic potential for LME and FE, amount of lean meat (**lmeat**) and fat (**fat**) were also included as random regression covariates ($\mathbf{a}_{\mathrm{p_s}}$ and $\mathbf{a}_{\mathrm{f_s}}$, in the model) (Martinsen et al., 2015). Lean meat efficiency and FE represents the amount of feed needed to produce one extra kg of lean meat or fat, respectively, and are regression coefficients. The animals' breeding value ($\mathbf{a}_{\mathrm{s}}$) and pen (**pen**) were included as random effects. In this model, a_{s} represent the genetic effect of the animal on FI that is not explained by the genetic effect of fat and lean meat efficiency and is referred to as the residual feed intake of the animal (Martinsen et al., 2015).

Since LME and FE are derived from estimates of model [1], direct phenotypic recordings are not available for these traits. The fixed regression coefficients estimated by model [1] were set as the mean for LME and FE, and are used in the profit equation to estimate the economic value of these traits. The prediction of breeding values for FI, FC, LMP and DAYS was performed in univariate models using the DMU (Madsen and Jensen, 2013). The following model was used:

$$\mathbf{Y_{ijklmn} = HY_i + BM_j + ST_k + SEC_l + a_m + pen_n + e_{ijklmn}} \qquad [2]$$

Model [2] was identical to model [1], but did not include the fixed and random effect of lean meat and fat content nor the fixed effect of accumulated metabolic body weight.

Profit Function

The profit function is a function consisting of the input and output per unit, to describe the profitability of the unit. In this study, the profit was calculated per fattening pig. The input data and means are presented in Table 1.

Income. In fattening pig production in Norway, the revenue comes from the value of the fattening pig and subsidies. The value of the fattening pig is dependent on the settling price, which is associated with the SEUROP carcass grading system for pigs. The system organizes the carcasses into categories (S to R), depending on their LMP (Norwegian Meat and Poultry Research Center, 2012). During recent years, the average LMP has been above 60%, and in category S. The farmer is paid a bonus if LMP in the carcass is above 60% or given a reduced price if LMP is lower. This bonus was set to +/-0.03 EUR per LMP above/below 60% (Table 2). The settling price depends on the carcass weight. The settling price for the carcass weight was collected from Norsvin SA's economic analysis of pork production in 2014 (M. Narum, Topigs Norsvin, Hamar, Norway, personal communication). The subsidies for this given situation were set to 1.8 EUR/fattening pig (Table 2) and treated as a fixed income. The income (**I**) of a fattening pig (**fp**) was calculated with the following model:

$$\mathbf{I_{fp} = CW \times (Pr_{kg} + (LMP_{fp} - 60) \times AdPr) + S_{fp}} \quad [3]$$

where CW represents the carcass weight, Pr_{kg} is the settling price per kg. AdPr is the additional bonus per LMP above or below 60 % and S_{fp} is the fixed subsidies.

Costs. The costs included in the fattening pig production were the costs for feed for production and maintenance, costs to labor, machines and housing and fixed non-feed costs. The following model was used to calculate the costs (**C_{fp}**) of a fattening pig:

$$\begin{aligned}\mathbf{C_{fp}} &= \mathbf{P_{feed} \times (\beta_{lm} \times \mu_{lmc}) + P_{feed} \times (\beta_{fat} \times \mu_{fc}) + P_{feed} \times (MAIN_{day} \times DAYS_{fp})} \\ &\mathbf{+ (LAB_{day} \times DAYS_{fp}) + (HOU_{day} \times DAYS_{fp}) + FNF_{fp}}\end{aligned} \quad [4]$$

The feed costs for maintenance per day (MAIN) were calculated based on the equation for standard maintenance requirement given in NRC (2012), and multiplied by the number of feed days (DAYS). To calculate feed used for production of lean meat and fat, the fixed regression coefficients derived from model [1] ($\beta_{lm} = \mathrm{LME}$ and $\beta_{fat} = \mathrm{FE}$) were used with the amount of lean meat (μ_{lmc}) and fat (μ_{fc}) (Table 1). All feed requirements were multiplied by the cost per kg feed (P_{feed}) (Table 2). In addition, a fixed non-feed cost (FNF_{fp}) per fattening pig was included. This cost includes piglet price, veterinary, insurance, mortality and interests per fattening pig for all traits (Table 3). Since machines/buildings (HOU) and labor (LAB) were dependent on DAYS, these costs are not included in FNF. The cost function described in model [4] was related to breeding goal A. The estimated cost for breeding goal B (FI is analyzed instead of LME and FE) is identical to model [4], but parameters associated with feed intake estimation ($\beta_{lm}, \beta_{fat}, \mu_{lmc}, \mu_{fc}$ and MAIN) were replaced by FI multiplied with the feed price (P_{feed}). The profit per fattening pig was the difference between total income per fattening pig (I_{fp}) and total costs per fattening pig (C_{fp}) in both breeding goal A and B.

Economic Values

Economic values for the traits were estimated by improving the mean of the trait by 1%, while the other traits remained constant. The following formula was used to estimate the marginal economic value of the traits.

$$\textbf{Marginal economic value}_{\mathbf{n}}\,\mathbf{(MEV)} = \frac{\mathbf{P(\mu_n + \Delta n) - P(\mu_n)}}{\mathbf{\Delta n}} \qquad [5]$$

The difference in profit (P) between the original (μ_n) and the improved ($\mu_n + \Delta n$) mean was divided by the change in the trait (Δn) and represented the marginal economic value of the trait per trait unit. The marginal economic value was standardized by multiplying with the additive genetic standard deviation (σ_a) for each trait.

Indexes and Profit

To compare the two breeding goals for production an index was calculated for both breeding goals described below:

$$\mathbf{Index_i = \sum MEV_i \times EBV_{ij}} \qquad [6]$$

The index was calculated as the summation of the product of the marginal economic value for each trait (*i*) (MEV_i) and the estimated breeding value for the trait (EBV_{ij}) for each animal (*j*). An economically weighted phenotype including the traits in breeding goal B was estimated for each animal as showed in model [7].

$$\mathbf{PROFIT_j = \sum MEV_i \times phenotype_{ij}} \qquad [7]$$

Individual profit for animal (j) was calculated based on their phenotype for trait (*i*) included in breeding goal B and the economic value of the trait (j). This trait was named PROFIT and breeding values were calculated with model [2].

RESULTS

Economic Values

Table 1 gives the production means for NL pigs on the test station. The average carcass weight of a purebred NL boar was 79.1 kg and LMP of 67.9%. The average fat content on carcass was 16 kg, and the boars used on average 66 days from 40 to 100/120 kg live weight at the test. The marginal economic values (EUR per trait unit) are presented in Table 3. The marginal economic value of FI was estimated to 0.3 EUR/kg feed. A 1% improvement of LME increased the profit by 0.005 EUR, and feed used for lean meat production was reduced by 0.0015 kg. This gave LME the highest marginal economic value of 18.3 EUR/kg feed/kg lean meat deposited (unit regression coefficient). For FE, the 1% improvement gave a reduced use of feed for fat production of 0.3 kg, which increased the profit by 0.12 EUR. The marginal economic value for FE was 5.6 EUR/kg feed/kg fat deposited. In terms of carcass payment, LMP was an important trait (Table 2). By improving LMP by 1%, to 68.5%, the profit increased by 1.7 EUR. The marginal economic value for LMP was 2.5 EUR/percentage. Fat content on the carcass affected feed intake in this economic analysis of breeding goal A. A 1% improvement in the trait was assumed (from 15.99 kg to 15.83 kg), and resulted in increasing the profit by 0.12 EUR. The marginal economic value for FC was 0.8 EUR/kg fat. For growth in the fattening period, DAYS was included in the analysis. By reducing DAYS by 1% (0.7 days), profit increased by 0.6 EUR per fattening pig and the marginal economic value was 0.9 EUR/day.

Table 3 also include standardized economic values (SEV), which makes it possible to compare the economic values on the same scale i.e. change in profit from one genetic standard deviation increase in each included trait (EUR/$\sigma_{a)}$. Among the traits, LME was the trait that had the highest economic importance (8.9 EUR/σ_a), whereas FE (2.9 EUR/σ_a) was the third most important trait after LMP (4.5 EUR/σ_a). For DAYS, the standardized economic value was 2.6 EUR/$\sigma_{a.}$ The trait FC was least important (1.1 EUR/σ_a). The trait FI had the second lowest economic importance out of all six trait in the analyses (1.6 EUR/σ_a).

Breeding Goals

Table 4 shows the descriptive statistics for the EBV's for PROFIT and the indexes for breeding goal A and B. The standard deviation of the EBV's for PROFIT was 23.3, while for the index for breeding goal B the standard deviation was 36.3. For the index for breeding goal A, the standard deviation was estimated to 52.2. The standard deviation suggested that the index for breeding goal A had two times as high variation as the index for breeding goal B. The high variance indicates that there is a bigger variation in the genetic potential for profit using breeding goal A. Breeding goal A included LME and FE as feed efficiency measures, while breeding goal B included FI. The rank correlation between the two indexes was 0.77. There was a complete re-ranking of the ten best sires when breeding goal B was used instead of breeding goal A, with no overlap among the ten best boars for the two breeding goals. The best animals in breeding goal A had overall lower phenotypic FI than the best animals for breeding goal B. However, the animals had poorer growth (higher DAYS).

DISCUSSION

The study found economic values for LME and FE, together with directly observed traits DAYS, LMP, FC and FI. Higher variance was observed in the index containing LME and FE as feed consumption traits (breeding goal A) compared to the index for breeding goal B, containing FI as the feed consumption trait. The results suggested that both efficiency traits are important for profit and an inclusion of the traits in the breeding goal improves genetic gain, since the index of breeding goal A shows a substantially higher variance.

The model constructed for breeding goal A in this study was only dependent on five boar traits, as the aim was to estimate the economic value of LME and FE and not to describe the overall complexity of the pork production in Norway. Therefore, the model constructed was simple, but included the traits that are important regarding feed consumption and growth in pork production.

The quality of the input data used for the base situation are important when calculating economic values for traits. This study used input data from the boar test station, on purebred NL. These data are used for the genetic evaluation of the boars and are a part of the higher genetic level of the NL population as they are selected for the test station. This may influence the input data through high LMP and short growth period, but should not influence the economic value of the traits. The feed price and carcass price were market averages from 2014.

Economic Values

The marginal economic values in this study were presented per trait unit per fattening pig. Other studies have estimated economic values for production traits in different breeds, countries and with a different definition of production efficiency in the economic model (Hermesch et al. 2003; Houska et al. 2004; Serenius et al. 2007; Houska et al. 2010). Economic values across countries, breeding companies and breeds are difficult to compare due to different definitions of production efficiency, different market and management conditions across countries and different economic models (Houska et al., 2004). The standardized economic values estimated for DAYS and LMP in this study were higher than the economic values TN use. For FI, the economic value was slightly lower than what TN use. Still, the trait definitions are not exactly the same, and our economic model is not very complex.

Serenius et al., (2007) mentioned the importance of what a realistic change in the trait is, when marginal economic values are investigated. This study found a marginal economic value for LME of 18.3 EUR/kg feed/ kg lean meat, which is high. However, it may not be realistic to reduce the amount of feed used for one kg lean meat deposition by one kg. In 2014, the feed used for one kg growth in Norwegian commercial fattening pigs was 2.74 kg (Ingris, 2014). Feed for growth includes feed for deposition of fat, lean meat and other tissues as well as feed for maintenance (Schinckel and de Lange, 1996). To reduce the amount of feed for production of a kg lean meat by one kg might be unlikely, as there obviously is a biological limit for how efficient a pig could be.

The genetic standard deviation of LME was low (0.5), and the standardized economic value of the trait was 8.9 EUR/σ_a. Lean meat efficiency is not a phenotype that is observed, but a regression coefficient estimating the estimated cost for production of one additional kg lean meat (as a deviation from the mean). Lean meat efficient animals use less feed per kg lean meat deposited, i.e., the breeding value is negative and low. Even though the marginal economic value of LME was high per kg feed/kg lean meat, a small change in the trait was observed when improved by 1%. This small change reduced the feed cost and made a change in profit. This change in profit was big compared to the change in the trait and thus a high economic value per trait was calculated. The high economic value for LME is also dependent on the amount of lean meat on the fattening pig. As the trait is a result of FI as a function of amount of lean meat on the fattening pig, the trait is expressed as kg feed/kg lean meat. The same situation occurs for FE. The lower economic value is related to the lower amount FC on the carcass compared to lean meat. For both FE and LME, the economic value is dependent on the production level (amount of lean meat and fat), which makes it even more difficult to compare to other studies (Hermesch et al. 2003).

All feed related traits had high economic values, and a significant influence on the pork production profit. These economic values are highly dependent on the feed price, and a market change in the feed price would influence the economic importance of feed consumption traits in the breeding goal. The current situation in Norway is low feed prices and the importance of feed efficiency traits is expected to increase as feed prices rise.

Breeding Goals

The two breeding goals defined in this study contained few, but important, production traits in pig breeding. Breeding goal A represented the new traits LME and FE, established in Martinsen et al. (2015), while breeding goal B represented a more traditional breeding goal with FI, DAYS and LMP included. Profit as a trait (PROFIT) was the summation of the phenotypes of the traits included in breeding goal B multiplied with the economic value of each trait. This was a simple way of modelling profit (by phenotypes), but Meuwissen and Goddard (1997) concluded that profit was a quite robust trait for selection and Pérez-Cabal and Alenda (2003) suggested that profit as a trait should be implemented in the genetic evaluation of Spanish Holstein. As the standard deviation of the EBVs for PROFIT was lower than the standard deviation for the indexes for both breeding goal A and B, it seemed like more complex modelling of feed consumption increased the standard deviation. The index resulting from breeding goal A had the highest variance, which suggested that inclusion of LME and FE in the breeding goal would result in bigger genetic gain for profit. Still, it is important to take into consideration the use of univariate analyses of the traits. No genetic correlations among the traits are accounted for in the prediction of breeding values, and hence some breeding values might be over- or underestimated which might affect the index (Smith, 1983). The reason for not performing multitrait analyses was problems with convergence. Breeding goal A also included more traits in the index, which might influence the variation in the index. In addition, the traits included in breeding goal A have a considerably higher economic value than FI in breeding goal B.

The rank correlation between the indexes for the breeding goal was low (0.77), and suggested that the two breeding goals are not the same. The re-ranking of the sires suggested that the new efficiency traits contribute new information, not described in breeding goal B with FI as feed consumption trait. No sires were selected in common for the two breeding goals. The efficiency traits does not necessarily say which animals that have lowest feed intake or highest growth, but who deposit lean meat and fat most efficient. The animals with highest feed intake does not necessarily have to be less efficient. However, when comparing the best boars for the two breeding goals, the boar selected with breeding goal A had lower FI and poorer growth than the animals selected with breeding goal B. This highlights the importance of including genetic relationships between the traits in the breeding value estimation.

CONCLUSIONS

Both of the new efficiency measures had an economic importance in pork production. Lean meat efficiency had a high economic value compared to other production traits in NL. When comparing the breeding goals, including LME and FE in the breeding goal could potentially give a bigger genetic gain for profit than the breeding goal including FI. The rank correlation between the breeding goals proved that the new efficiency traits does not describe the same as FI, and includes additional information to improve the genetic evaluation of boars.

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Table 1. Input data, mean performance from pure bred Norwegian Landrace boars at test station.

Variable	Performance mean
Carcass weight (kg)	79.1
Days in test (days)	66.3
Total feed intake in the test period (kg)	152.1
Maintenance requirement/day (kg)	1.2
Lean meat percentage (%)	67.9
Average fat percentage (%)	20.4
Lean meat content (kg)	52.3
Fat content on the carcass (kg)	15.9
Average lean meat efficiency (kg feed/kg lean meat)	-0.03
Average fat efficiency (kg feed/kg fat)	2.24

Table 2. Market prices related to costs and income in fattening pig production (M. Narum, Topigs Norsvin, Hamar, Norway, personal communication). The currency was set at April 13, where 1 EUR = NOK 9.3.

Variable	EUR(€)
Price/kg carcass weight	2.75
Additional price per kg if lean meat percentage above or below 60 %	0.03
Subsidies per fattening pig	1.83
Cost /kg feed	0.34

Table 3. Marginal economic values (MEV) expressed in EUR (€), genetic standard deviation (σ_a) and standardized economic values (SEV) for the five traits; Total feed intake in the test period (FI) Lean meat efficiency (LME), fay efficiency (FE), days from 40 to 100/120 kg live weight (DAYS), lean meat percentage (LMP) and fat content on the carcass (FC). All traits are expressed on a fattening pig-basis. The currency was set at April 13, where 1 NOK = 9.3 EUR

Trait	MEV (€)	σ_a	SEV (€/σ_a)
FI (kg)	0.3	4.7	1.6
LME (kg feed)	18.3	0.5	8.9
FE (kg feed)	5.6	0.5	2.9
DAYS (days)	0.9	2.8	2.6
LMP (%)	2.5	1.8	4.5
FC (kg)	0.8	1.4	1.1

Table 4. Number of observations (n), standard deviation (SD), minimum value (Min) and maximum value (Max) for index calculated for breeding goal A, breeding goal B and breeding values for profit as a trait (EBVprofit). Breeding goal A contain lean meat efficiency (LME), fat efficiency (FE), fat content on the carcass (FC), lean meat percentage (LMP) and days between 40 to 100/120 kg live weight (DAYS). Breeding goal B contains total feed consumption in the test period (FI), lean meat percentage (LMP) and days from 40 to 100/120 kg live weight (DAYS). Profit as a trait was the summation of the product of the phenotypes for the traits included in breeding goal B and the economic value of each trait.

	Breeding goal A	Breeding goal B	EBVprofit
n	8161	8161	8161
Mean	41.9	21.1	9.6
SD	52.2	36.3	23.2
Min	-137.9	-135.8	-89.7
Max	311.3	160.4	135

6. General discussion

The overall aim of this thesis was to model new feed efficiency measurements that could be used for further genetic improvement of feed efficiency in pig breeding. New ways of modelling feed efficiency in pigs are desired due to concerns regarding a biological limit for improving feed efficiency through changes in body composition (increased lean growth and reduced back fat) and lower feed conversion ration (FCR). This thesis modelled total feed intake in the test period (FI) in a random regression model, where lean meat (kg) and fat (kg) were included as covariates in a random regression model. The model provided two new efficiency measurements, named lean meat efficiency (LME) and fat efficiency (FE). Genetic variation was found in both traits, and the economic value of each trait was calculated. Few unfavorable genetic correlations to important sow productivity traits were found. Both traits appeared to have an economic importance in the breeding goal, and contributed with new information to the genetic evaluation of potential elite boars.

6.1 Genetic improvement

The thesis found significant genetic variation in two novel measurements for both ND and NL and genetic improvement of both traits is possible through selection. Based on the variance components estimated in paper I, a heritability of 0.59 was calculated for FI (paper II). This estimate was high compared to earlier studies (Kerr and Cameron, 1996; Holm et al., 2004; Cai et al., 2008), and previous estimates of FI in TN. The heritability might be overestimated, as the model only allowed heterogeneity of genetic variance, while residual variance was homogenous. Some increased flexibility of the genetic effects in model [1] may be used to model potential heterogeneity of environmental variance. Hence, by including heterogeneous residual variance, the estimated genetic variance may be reduced. In NL, genetic variation due to LME described a smaller part of total genetic variation in FI than FE, while the opposite was observed in ND. The different selection history of the two breeds and the length of systematic breeding program for the two breeds might explain this (Gjerlaug-Enger et al., 2012).

Aggrey and Rekaya (2013) modelled feed intake in broilers with maintenance and growth as random covariates, and estimated significant genetic variation in these efficiency traits. Sánchez et al. (2015) had a similar way of modelling feed intake in a commercial Duroc line, but only found genetic variation for feed used for maintenance, not growth. These traits are not directly comparable to LME and FE, but indicates that this way of modelling FI is possible. Both traits explained a relatively small part of total genetic variation in FI for both breeds (paper I), suggesting that genetic variation in FI also is influenced by other genetic factors not discovered in this thesis. Cai et al. (2008) found that residual feed intake explained 34% of the phenotypic variation in average daily feed intake. Both LME and FE are smaller fractions of residual feed intake and the genetic variation is a fraction of the phenotypic variation. Hence, it may be expected that the fraction of total genetic variation in FI due to lean meat and fat efficiency was lower than this.

Daily feed intake is a conflict of interest trait between the fattening pig producers and the piglet producers (Holm et al., 2004). Low feed intake and high growth are important for fattening pig producers to maintain good profit, while higher appetite and daily feed intake in sows are crucial to produce large and heavy litters and to avoid substantial weight loss (Eissen et al., 2003). To investigate potentially unfavorable genetic relationships between LME, FE and other economically important traits in the breeding goal, genetic correlations between LME and FE and important sow traits in NL were estimated (paper II). The sow traits included in the analyses were stayability up to insemination for a second litter (**STAY**), body condition score after weaning of first litter (**BCSw**), total number of piglets born in first litter (**TNB**) and total litter weight at three weeks of first litter (**TLW**). The genetic correlations between FE and STAY (0.21) and FE and TLW (0.21) were significant, but low and unfavorable. These correlations suggested that selection for reduced FE could result in poorer STAY and lower TLW, while selection for LME had no genetic influence on the sow traits.

There are different biological explanations for the genetic relationships between FE and the sow traits. An animal that are fat efficient might have a low feed intake but deposited some fat, but not enough to maintain a sow in production (low STAY). On the other hand, the animal may have had a high feed consumption and deposited a high amount of fat (inefficient fat deposition), which might be beneficial for STAY in sows. The same arguments might hold for the genetic correlation between FE and TLW also. The exact biological explanation of the genetic correlations is uncovered by this thesis. The genetic relationship between feed efficiency in the growth period and important sow traits is not clearly established in the literature, although several studies have expressed their concern regarding the side effects of selection for feed efficiency during growth (Kerr and Cameron, 1995; Rauw et al., 1998; Eissen et al., 2003). Gilbert et al. (2012) estimated weak and non-significant correlations between residual feed intake and litter weight at three weeks and total born piglets. These correlations indicate the same relationship between feed efficiency and sow traits as found in this thesis (paper II). Still, studies have shown that lines selected for low residual feed intake had a higher number of piglets born and heavier litters than lines not selected for residual feed intake (Young et al., 2010; Renaudeau et al., 2014). This was explained by a higher mobilization of body reserves during lactation in animals selected for reduced residual feed intake to compensate for reduced feed intake and support the increased piglet production.

By showing low or no genetic relationship to important sow traits in NL, inclusion of LME and FE in the breeding goal seems of current interest. To define the traits in a breeding goal, the economic value of the new traits was estimated for NL (paper III). Both traits had high economic values (LME=8.9 EUR/σ_a and FE=2.9 EUR/σ_a). This result suggested there was an economic importance of the traits LME and FE in pork production. Even though the economic value per unit was high for both traits, the change in each trait was small. Since the economic value is the marginal change in the profit per unit change in the trait, the economic values became high. Serenius et al. (2007) pointed out the importance of considering whether the change in the trait is realistic or not. To reduce LME by 1 kg is might not be possible, as a certain amount of feed is needed to produce a kg of lean meat. When comparing the new traits with the traditional feed consumption trait FI in an index, it seems like the new efficiency measures includes additional information to improve the genetic evaluation of boars. The index including the efficiency traits had a significantly higher variance than the index including FI as feed consumption trait in the breeding goal measured in EUR. The index is describing the genetic variation in the breeding goals, and a higher variance in the index including the efficiency traits suggests that this breeding goal would provide an increased genetic gain in profit. As the rank correlation between the animals was 0.7, it is obvious that the two indexes do not include the same information on the selection candidates. The best boars selected for the index including the efficiency traits had lower FI and growth compared to the best boars selected for an index including FI. This highlights the importance of including information of genetic relationships between the traits included in the breeding goal (Smith, 1983). This information is valuable to see if the new traits provide any new information in the genetic evaluation, but also to see if selection would have a negative effect on existing important traits.

Genetic improvement of feed efficiency in NL and ND could be done through these new traits, as genetic variation exists. The new traits describe how efficient the animal utilizes feed for lean meat and fat deposition, and the genetic variances of these traits contribute to the genetic variance in FI. The consequences of selection for FE and LME with respect to other traits was not investigated here. As paper III showed, both LME and FE include additional information to the breeding goal including FI, and could be beneficial for further genetic improvement of feed efficiency in pork production.

6.2 Statistical analysis of feed intake

Analyzing feed intake in a random regression model has been done in several studies, for cattle, poultry and pigs (Wetten et al., 2012; Aggrey and Rekaya, 2013; Manzanilla Pech et al., 2014). These models included continuous covariates that extend over a certain period. This could be stage of lactation or growth period. This thesis included amount of lean meat and fat as covariates, measured once, at the end of the test. The model was therefore fitted through the genetic relationship between the test boars, e.g. especially through their sires, as each sire will have several offspring with records for amount of lean meat and fat. Thus, as the random regression model utilizes the relationship between the animals, it can be fitted in a situation where only one record per animal is available (paper I), which is an untraditional way of utilizing the properties of a random regression model. In January 2014, TN included genomic information in their breeding value estimation. This thesis included only pedigree information in the variance component estimation and prediction of breeding values. By including genomic information, the estimates for both LME and FE and their variance components could become more accurate.

In the extended residual feed intake model (paper I, II, III), fixed effects of amount of lean meat and fat are included, together with a fixed effect for maintenance requirement. Both lean meat and fat were also included as covariates through random regression. The random regression coefficients expressed how much extra feed (as a deviation from the mean) needed to produce one kg extra lean meat (LME) or fat (FE) and represents individual differences between animals. The intercept represents the genetic part of the animal not related to LME or FE, such as genetic components affecting e.g. physical activity, heat production and immune response not related to the animal’s size (metabolic body weight). Paper I pointed out that the difference in actual efficiency, body composition and where tissue was deposited may affect LME and FE. In addition, individual differences in maintenance might influence the efficiency traits. The efficiency traits are dependent on individual differences in carcass lean meat and fat, which influence the maintenance requirement, as lean meat is more expensive to maintain than fat (Kolstad and Vangen, 1996).

6.3 Maintenance requirement and body composition

Accumulated metabolic body weight was included as a fixed regression in the model for FI to correct for maintenance requirements. This was calculated as the integral of a linear function of metabolic body weight at the beginning and the end of the test. It was assumed that the maintenance requirement was proportional to the metabolic body weight ($W^{0.75}$ = body weight raised to the power of 0.75 (Kleiber, 1965)). However, studies have suggested that a systematic underestimation of maintenance requirement was performed when metabolic body weight was estimated by $W^{0.75}$ (van Milgen et al., 1998; Noblet et al., 1999). Tess et al. (1984) implied that this was due to that maintenance requirement was more related to lean tissue weight rather than whole body weight. NRC (2012) suggested that the maintenance requirement for fattening pigs should be proportional to $W^{0.6}$, based on more recent studies. Kolstad and Vangen (1996) showed that the highly lean breed NL had a significantly higher maintenance requirement than ND when including mobilized energy from body reserves and concluded that there are breed differences in maintenance requirement. It is expected that this component may vary between breeds, as some breeds have a higher fraction of lean meat, which is more energy costly to maintain than fat (Rivera-Ferre et al., 2006). Therefore, relationships between body weight and metabolic body weight may actually deviate to some extent between NL and ND.

The model in this thesis corrected for maintenance requirement related to a combination of body size and shape through the accumulated metabolic body weight. Maintenance requirement is a very complex trait influenced by several factors in the animal. These factors are age, growth stage, production level, external environment, weight of the animal, health status, body composition, visceral organs, heat production and activity (Kolstad and Vangen, 1996; van Milgen et al., 1998; Noblet et al., 1999). All these factors affect each other and to distinguish which effects are present in RFI (intercept) might be difficult. In addition, the data set included boars growing from either 35 to 100 kg or from 40 to 120 kg. To assume one linear fixed effect of accumulated metabolic body weight for both groups may not be entirely correct. Fat deposition increases later in the growth period, as the animal reaches maturity. In this thesis, animals with growth periods up to 120 kg live weight might have systematically deposited more fat than the animals with a recording period ending at 100 kg. Fat has an insulating effect and may actually reduce the maintenance requirement of animal due to reduced heat loss.

In this thesis, amount of fat and lean meat on the carcass was included in the data material based on CT-images. What was not accounted for was deposition of visceral fat. Kolstad (2001) proved that NL had a rather high portion of visceral fat compared to ND, which might be due to selection for both reduced back fat thickness and increased inter/intramuscular fat. The same study concluded that information on visceral fat depots should be used for further progress in efficiency in lean breeds, such as NL. This thesis corrected for slaughter percentage in the model to investigate whether the FE was dependent on where the fat was deposited (paper II), but no changes were observed. This suggested that the model was not dependent on where fat was deposited.

6.4 Data quality

6.4.1 Boar records

Records of FI were collected from the boar test station on purebred NL and D in Norway (paper I, II, III). In TN, all records on individual feed intake and weight are quality controlled and stored in a local data base. Originally, their test interval was from 25 to 100 kg live weight, but this was changed from March 1, 2012, so the boars finishing after this date were tested from 40 to 120 kg live weight. This change was done to adjust to the market demands, where actual slaughter weights are closer to 120 kg than 100 kg. The data contained approximately 60% boars who ended the test at 100 kg live weight and 40% at 120 kg live weight. Both mean and variance would differ, depending on when the boar ended the test. To address this problem a fixed effect with two levels was included in the model to correct for which period the boar finished the test. An alternative would be to treat these as two different traits, as estimated genetic correlations between daily feed intake in later periods in life vary between 0.29 to 0.77 (Von Felde et al., 1996; Schulze et al., 2002; Huisman and van Arendonk, 2004). A bivariate analysis was performed, but did not converge. This might be due to fewer observations (less information) per trait or possibly because of a high genetic correlation between the traits.

The data included in this thesis were of high quality. Still, it would have been preferable to have CT images also from the beginning of test. Then the model would include the amount of tissue deposited in the growth period, and not the amount deposited since the animal was born. Ideally, the boar should be scanned each time it entered the feeder system, so that a view of what the boar eats and deposits every day was available. This would provide an ultimate measure of how much fat and lean meat are deposited in the same period as feed intake is recorded.

Today, the boars are housed individually the day they are CT-scanned. This routine is highly suitable for sampling of feces and urine. This sampling could provide important information on individual digestibility and nitrogen excretion in the pig, which could be useful data for future research on feed efficiency. This has been studied earlier, but with rather few observations (Bastianelli et al., 2015; De la Roza-Delgado et al., 2015). Due to the already existing logistics for CT scanning of the boars, TN has the opportunity to do this recording in large scale, without a high additional cost.

6.4.2 Sow records

Records on the sow traits were from Ingris and included only information from first parity sows. Genetic relationships between sow reproduction traits in different parities are moderate to high ranging from 0.62 to 1, depending on trait and parity (Roehe and Kennedy, 1995; Tholen et al., 1996; Hanenberg et al., 2001). This implies that they should not be treated as repeated measures, but rather as different traits and analyzed in a multitrait model (Roehe and Kennedy, 1995). For this thesis, the multivariate analysis with RFI, LME, FE and the sow traits was restricted to first parity only. Genetic correlations to, e.g., BCSw or TLW in later parities might be different from estimates in this thesis (paper II).

The sow traits presented in paper II included records from several different countries. These countries differ in animal welfare regulations and management systems, which may influence the estimation of genetic variance for the sow traits. As an example, Norway is one of few countries where crating sows is prohibited at all stages of production. The models used for analyzing sow traits included herd effect, which corrected for a part of these differences (paper II).

In the genetic evaluation, TN discovered that STAY recorded in Norway had a high correlation to the total merit index of the animal (D. Olsen, Topigs Norsvin, Hamar, Norway, personal communication). The trait STAY measured in nucleus and multiplier herds is dependent on the active and subjective decision made by the farmer. These decisions are based on the animals breeding value (EBV) and its biological capacity to have a second litter. This relationship was lower in foreign herds, and to include only data from foreign countries is a good alternative for genetic evaluation of STAY.

6.5 Recommendations

In theory, selection for these new traits should not affect the resource allocation for different processes in the pig, but rather identify pigs that use the feed more efficient than others do. Hence, the new traits would be beneficial regarding unfavorable genetic relationships to important sow traits and for improved feed efficiency and economy in pork production. The new efficiency traits, LME and FE would further improve the selective breeding for feed efficiency. Lean meat efficiency had a high economic importance in the breeding goal and did not have unfavorable relationships to any of the sow traits included in the genetic analysis in this thesis. Lean meat efficiency would therefore be a suitable trait for selection for feed efficient boars with an efficient deposition of lean meat in the carcass. This thesis did not investigate its genetic relationship to other important traits in the breeding goal such as growth or LMP. These genetic relationships should be accounted for when including LME in the breeding goal.

7. Conclusions

This thesis defined two new traits for efficiency to deposit lean meat and fat through an extended residual feed intake model for Norwegian Landrace and Norwegian Duroc. Genetic variation existed in both traits and the genetic analyses found no significant correlations between lean meat efficiency and the sow traits, while fat efficiency had low but unfavorable genetic correlations to stayability and total litter weight at three weeks. Selection for improved lean meat efficiency would be possible without having a deleterious effect on economical important sow traits. Selection for fat efficiency on the other hand would require supervision of piglet production and stayability in sows. Both traits had an economic value in a pork production system and contributed with new information to the genetic evaluation of the boars. The new traits developed in this thesis may be important for future genetic improvement of feed efficiency in pigs and resulted in valuable extension of the breeding goal i.e. the increase in genetic gains in economic terms. In the total merit index, all relationships between the new traits and existing traits should be accounted for.

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