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 7 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 3 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 intake and a high production level and at the same time maintain the sow’s BCS 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 BCS, 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), whereas 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 BCS after weaning of first litter (BCS\textsubscript{w}), 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 3 wk (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 FI 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 Recording

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) 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 to 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 Inc., Natick, MA) 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, BCS, 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 d and sows are loose housed through all stages of production (Thingnes, 2013). Hence, the data are collected in herds that do 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 BCS\textsubscript{w}, 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 3 wk of age in the first litter. The piglets are weighed between 17 and 25 d of age, and their weight is adjusted to 3 wk of age (21 d). The total number of piglets born in the 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 farmers follow national guidelines for body condition scoring of sows provided by TN and Norwegian Meat and Poultry Research Centre (Oslo, Norway) 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 d or older than 730 d at farrowing, and sows weaning piglets older than 70 d were discarded. Only sows with at least 2 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 back 10 generations 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 $h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_e^2)$, in which $\sigma_a^2$ is the genetic variance and $\sigma_e^2$ 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:

$$FI_{ijklmnopq} = HY_i + BM_j + ST_k + SEC_n + \beta_{lm} \times LMEAT_o + \beta_{fat} \times FAT_q + \beta_{amw} \times AMW_r + a_i + pen_t + a_{q} \times lmeat_o + a_{q} \times fat_q + e_{ijklmnopq}$$  \[1\]

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 BW (AMW) were included as fixed regression covariates. As a measure of feed efficiency, random regressions on amount of lean meat (lmeat) and fat (fat, respectively) were included in the model as in Martinsen et al. (2015). As each boar has only 1 measure each for lean meat and fat content (kg), the random regression model is fitted through the genetic relationships between boars with records of lean meat and fat. Therefore, the model can use a situation with only 1 record per animal. The animals’ additive genetic effect ($a_i$) and pen were included as random effects. In this model, $a_i$ 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, $a_i$ is referred to as lean meat efficiency (LME) and $a_{q}$ 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 1 kg of lean meat or fat. It should be noted that increased levels are unfavorable as this indicates a greater demand for feed per kilogram 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 AMW and the fixed random regressions on carcass LMEAT and fat.

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

The fixed effects are the same as in model [1], whereas the random effect ($a_m$) is the genetic effect of the animal on FI. 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:

$$BCSw_{ijklmnopq} = M_{LNO_i} + HY_j + SEA_k + BRYEAR_l + WEAN_m + p \times AGEM_n + q \times AGEW_o + \text{animal}_{p} + \text{litter}_{q} + e_{ijklmnopq}$$  \[3\]

---

**Table 1.** Average (mean), 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 BCS after weaning of first litter (BCSw), stayability up to insemination for a second litter (STAY), total litter weight of first litter at 3 wk (TLW), and total number of piglets born in first litter (TNB) registered on sows off test

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>FI, kg</td>
<td>152.1</td>
<td>29.4</td>
<td>97.2</td>
<td>270.6</td>
</tr>
<tr>
<td>Lean meat, kg</td>
<td>52.3</td>
<td>3.6</td>
<td>40.5</td>
<td>68.2</td>
</tr>
<tr>
<td>Fat, kg</td>
<td>15.9</td>
<td>4.3</td>
<td>7.2</td>
<td>33.0</td>
</tr>
<tr>
<td>BCSw, points</td>
<td>4.2</td>
<td>0.9</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>STAY, points</td>
<td>0.7</td>
<td>0.5</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>TLW, kg</td>
<td>66.8</td>
<td>19.7</td>
<td>1.5</td>
<td>193.1</td>
</tr>
<tr>
<td>TNB, no.</td>
<td>12.9</td>
<td>3.6</td>
<td>2</td>
<td>29</td>
</tr>
</tbody>
</table>
The fixed effects in the model was dam’s litter number (\(M_{LNO}\), \(i = 1\) to \(3\), in which all \(M_{LNO} > 3\) was assigned as \(3\)), 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). 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 \(66.8 \pm 19.7\) 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 the 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 0. Significance was tested based on the estimate \(\pm 1.96 \times SE\), 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, respectively). 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 nonsignificant. Significant correlations were found between RFI and both efficiency measures (LME and FE), suggesting that animals with a high overall feed intake had a lower efficiency (higher feed intake per kilogram 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 were close to 0 and nonsignificant between all traits.

**The Sow Traits and Residual Feed Intake of the Animal**

The correlations between RFI and the sow traits were positive but low and mostly not significantly different from 0. Still, a positive and significant correlation was found between RFI and BCSw, which implies that animals with an overall high feed intake
Boar feed efficiency and sow performance

Table 2. Distribution of observations between total feed intake in the test period (FI), BCS after weaning of first litter (BCSw), stayability up to insemination for a second litter (STAY), total litter weight of first litter at 3 wk (TLW), and total number of piglets born in first litter (TNB).

<table>
<thead>
<tr>
<th>Trait</th>
<th>FI</th>
<th>BCSw</th>
<th>STAY</th>
<th>TLW</th>
<th>TNB</th>
</tr>
</thead>
<tbody>
<tr>
<td>FI</td>
<td>8,161</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>BCSw</td>
<td>–</td>
<td>38,251</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>STAY</td>
<td>–</td>
<td>36,257</td>
<td>88,453</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>TLW</td>
<td>–</td>
<td>34,128</td>
<td>68,319</td>
<td>70,321</td>
<td>–</td>
</tr>
<tr>
<td>TNB</td>
<td>–</td>
<td>38,251</td>
<td>88,453</td>
<td>70,321</td>
<td>90,945</td>
</tr>
</tbody>
</table>

(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 nonsignificant, 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, 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, unless the trait is 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 included only 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. Primiparous sows have a lower uterus capacity than multiparous 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 BW at 3 wk (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 and therefore 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, 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.,

Table 3. Genetic variance components (\(\sigma^2\)) for total feed intake in the test period (FI) for boars, BCS after weaning of first litter (BCSw), stayability up to insemination for a second litter (STAY), total litter weight of first litter at 3 wk (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 (residual feed intake of the animal [RFI]), lean meat efficiency (LME), and fat efficiency (FE).

<table>
<thead>
<tr>
<th>Trait</th>
<th>(\sigma^2_e)</th>
<th>(\sigma^2_a)</th>
<th>(h^2)</th>
<th>(\sigma^2_e)</th>
<th>(\sigma^2_a)</th>
<th>(h^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FI</td>
<td>25.58</td>
<td>17.50 (0.95)</td>
<td>0.59</td>
<td>23.34 (3.26)</td>
<td>83.22 (2.79)</td>
<td>0.22</td>
</tr>
<tr>
<td>RFI ((a_e))</td>
<td>18.16 (1.47)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>LME ((a_e))</td>
<td>0.27 (0.04)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>BCSw ((a_e))</td>
<td>0.07 (0.00)</td>
<td>0.46 (0.00)</td>
<td>0.14</td>
<td>0.07 (0.00)</td>
<td>0.46 (0.00)</td>
<td>0.13</td>
</tr>
<tr>
<td>STAY ((a_e))</td>
<td>0.02 (0.00)</td>
<td>0.14 (0.00)</td>
<td>0.10</td>
<td>0.02 (0.00)</td>
<td>0.13 (0.00)</td>
<td>0.10</td>
</tr>
<tr>
<td>TLW ((a_e))</td>
<td>12.10 (0.66)</td>
<td>63.37 (0.59)</td>
<td>0.16</td>
<td>11.91 (0.63)</td>
<td>63.28 (0.59)</td>
<td>0.16</td>
</tr>
<tr>
<td>TNB ((a_e))</td>
<td>0.80 (0.06)</td>
<td>11.08 (0.07)</td>
<td>0.07</td>
<td>0.81 (0.06)</td>
<td>11.07 (0.07)</td>
<td>0.07</td>
</tr>
</tbody>
</table>

DISCUSSION

This genetic analysis showed nonexisting 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, unless the trait is actively selected for.
Table 4. Genetic correlations (SE) between feed intake in the test period not explained by genetics of lean meat and fat efficiency, named residual feed intake of the animal (RFI), lean meat efficiency (LME), fat efficiency (FE), BCS after weaning of first litter (BCSω), stayability up to insemination for a second litter (STAY), total litter weight of first litter at 3 wk (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 BCSω, STAY, TLW and TNB (Model [2])

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td></td>
<td>RFI</td>
<td>LME</td>
</tr>
<tr>
<td>LME</td>
<td>0.25 (0.07)</td>
<td>–</td>
</tr>
<tr>
<td>FE</td>
<td>0.71 (0.05)</td>
<td>−0.19 (0.12)</td>
</tr>
<tr>
<td>BCSω</td>
<td>0.16 (0.07)</td>
<td>−0.03 (0.13)</td>
</tr>
<tr>
<td>STAY</td>
<td>0.12 (0.07)</td>
<td>−0.14 (0.12)</td>
</tr>
<tr>
<td>TLW</td>
<td>0.09 (0.06)</td>
<td>−0.16 (0.11)</td>
</tr>
<tr>
<td>TNB</td>
<td>0.03 (0.08)</td>
<td>0.14 (0.14)</td>
</tr>
</tbody>
</table>

1FI = total feed intake in the test period.

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 with that of a linear model. An ordinal threshold model may be beneficial for analysis of both BCSω 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 with 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 judgment from the farmer.

The sows in the herds in this data set 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 EBV at the time of insemination or culling. This means that sows with poor EBV 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 $\sigma_a^2$ 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 FI 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 modeled with more flexibility than the error variance. This may have resulted in the genetic factor capturing some of the residual heterogeneity. Therefore, 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 nonsignificant 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 with lean meat and fat (Norwegian Meat and Poultry Research Centre, 2012). Therefore, more fat at a given BW 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 1 kg fat may be similar.

**The Sow Traits and Residual Feed Intake of the Animal.** 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 with 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, 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 DMI in cows. Dunnington and Siegel (1996) showed that chicken lines selected for high BW had a significantly greater feed intake than the line selected for low BW. In addition, animals selected for low residual feed intake tended to have a higher BW 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 nonsignificant correlations between residual feed intake and total number of piglets born and litter weight at 3 wk. In contrast, Young et al. (2010) investigated animals selected for reduced residual feed intake over 6 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 as if 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 1 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 were 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 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 FAT exists (D. Olsen, Topigs Norsvin, Hamar, Norway, personal communication). It is, therefore, 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 on 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 1 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 0 for Norwegian Landrace. Significant genetic correlations were found between FE and STAY and between FE and TLW (0.21 and 0.21, respectively), 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.

LITERATURE CITED


