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Genetic parameters between slaughter pig efficiency and growth rate of different body tissues estimated by computed tomography in live boars of Landrace and Duroc

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In this study, computed tomography (CT) technology was used to measure body composition on live pigs for breeding purposes. Norwegian Landrace (L; n *= 3835) and Duroc (D;* n *= 3139) boars, selection candidates to be elite boars in a breeding programme, were CT-scanned between August 2008 and August 2010 as part of an ongoing testing programme at Norsvin's boar test station. Genetic parameters in the growth rate of muscle (MG), carcass fat (FG), bone (BG) and non-carcass tissue (NCG), from birth to ~100 kg live weight, were calculated from CT data. Genetic correlations between growth of different body tissues scanned using CT, lean meat percentage (LMP) calculated from CT and more traditional production traits such as the average daily gain (ADG) from birth to 25 kg (ADG1), the ADG from 25 kg to 100 kg (ADG2) and the feed conversion ratio (FCR) from 25 kg to 100 kg were also estimated from data on the same boars. Genetic parameters were estimated based on multi-trait animal models using the average information–restricted maximum likelihood (AI-REML) methodology. The heritability estimates (s.e. = 0.04 to 0.05) for the various traits for Landrace and Duroc were as follows: MG (0.19 and 0.43), FG (0.53 and 0.59), BG (0.37 and 0.58), NCG (0.38 and 0.50), LMP (0.50 and 0.57), ADG1 (0.25 and 0.48), ADG2 (0.41 and 0.42) and FCR (0.29 and 0.42). Genetic correlations for MG with LMP were 0.55 and 0.68, and genetic correlations between MG and ADG2 were −0.06 and 0.07 for Landrace and Duroc, respectively. LMP and ADG2 were clearly unfavourably genetically correlated (L: −0.75 and D: −0.54). These results showed the difficulty in jointly improving LMP and ADG2. ADG2 was unfavourably correlated with FG (L: 0.84 and D: 0.72), thus indicating to a large extent that selection for increased growth implies selection for fatness under an* ad libitum *feeding regime. Selection for MG is not expected to increase ADG2, but will yield faster growth of the desired tissues and a better carcass quality. Hence, we consider MG to be a better biological trait in selection for improved productivity and carcass quality. CT is a powerful instrument in conjunction with breeding, as it combines the high accuracy of CT data with measurements taken from the selection candidates. CT also allows the selection of new traits such as real body composition, and in particular, the actual MG on living animals.*

Keywords: computed tomography, body composition, lean meat growth, muscle growth, genetic parameters

Implications

The use of computed tomography (CT) makes it possible to obtain accurate body composition from live pigs. As these pigs are selection candidates for elite boars, this information is expected to substantially improve the accuracy of selection for carcass traits and growth of different body tissues. The CT image analysis is automated, so that the records on each boar are available for breeding value estimation shortly after scanning. This makes it possible for Norsvin (the Norwegian Pig Breeders Association) to breed for actual muscle growth.

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Introduction

In the 1950s, systematic breeding for leaner pig meat became an important breeding goal, and as the leanness of the pigs is very heritable (ranging from 0.12 to 0.74 for 16 studies; Clutter and Brascamp, 1998), the Western modern breeds have become much leaner. Selection has been performed based on measurements of ultrasound backfat and loin measurements taken from live selection candidates or experimental dissection for carcass composition of full-sibs, half-sibs and offspring of the selection candidates (Clutter and Brascamp, 1998). The Norwegian dissection procedure has changed from the weighing of trimmed ham and loin, in addition to manual

measurement of the loin eye area, to the dissection of the shoulder, loin and ham into different tissues for the prediction of lean meat percentage (LMP; Gjerlaug-Enger *et al*., 2010a).

A third option to determine body composition is the computed tomography (CT) technology, which is commonly used for human diagnostic purposes, and can also be used for detailed measurements of different tissues in sheep (Afonso, 1992; Vangen and Thompson, 1992), intact iced halibut (Kolstad *et al*., 2004) and different pig breeds (Luiting *et al*., 1995; Kolstad, 2001). The advantage with CT is that it can be used as a non-destructive method without killing the animal. Phenotypes on many animals are required for genetic analyses. A few studies on sheep have used CT data for the estimation of genetic parameters (Jones *et al*., 2004; Kvame and Vangen, 2007), but to the best of the authors' knowledge, similar work has not been carried out previously on pigs.

Norsvin is running a boar-testing station with routine CT scanning of live pigs in a breeding programme, with an annual scanning capacity of 3500 live purebred boars. The image analysis at this boar test is completely automated and features specially designed software for the removal of non-carcass tissues to obtain a virtual carcass and for the calculation of several traits, for example, determination of body composition: kilograms of lean muscle, carcass fat, bone and non-carcass tissues. The LMP calculated from CT could, with only small adaptations, replace the LMP taken from dissection in the estimated breeding values (EBVs).

Determination of leanness is not straightforward, and unfavourable genetic correlations between growth and leanness (Mcphee *et al*., 1979; Cleveland *et al*., 1982) make joint improvement of these traits a challenge. Fowler *et al*. (1976) showed that lean meat growth can be selected by using an economic selection index that combines lean meat content and growth or by using lean meat growth, which is measured as lean gain per day. Clutter and Brascamp (1998) proposed that lean meat growth is the most appropriate expression of the industry's objective for market pigs, whereas Chen *et al*. (2002) indicated that direct selection of EBV for lean meat growth with a multi-trait model yielded higher lean meat growth than a linear index of EBV for growth, backfat and the loin eye area.

The aims of this study were to calculate genetic parameters for the growth rate of muscle (MG), carcass fat (FG), bone (BG) and non-carcass tissues (NCG) based on CT data. The genetic correlations between these traits and more traditional production traits for slaughter pig efficiency, such as LMP, average daily gain (ADG) in early life and in the boar test period, and feed conversion ratio (FCR) in the boar test, will also be examined.

Material and methods

Animals

Data for this study were collected from August 2008 to August 2010 in Norsvin's boar testing station in southeastern Norway, and Norwegian Landrace ($n = 3835$) and Duroc ($n = 3139$) boars were included. Boars were kept in single-breed groups of 12 pigs/pen, and fed *ad libitum* on conventional concentrates containing 161 and 136 g digestible protein and 9.68 and 9.50 MJ net energy/kg before and after 50 kg, respectively, with 1 month of mixing the two feeds to facilitate the feed change. Major feedstuff compounds were barley, oats, peas, soya meal extract and rendering (animal) fat. The full-sib group size of tested boars was 1.1 for Landrace and 1.3 for Duroc, and the average half-sib group size was 35. The average start and end weight for the test was 25 and 100 kg live weight. The pigs started the test 2 days after entering the test station (average age was 67 days), and ended the test on the day they reached 100 kg with CT scanning a few days later. The boars are all selection candidates to be elite boars based on EBV and genetic uniqueness. More detailed information about the populations has been provided in Gjerlaug-Enger *et al*. (2010b). Herd of origin were 37 L and nine D nucleus farms.

CT technology

A General Electric (GE) multi-slice VCT LightSpeed scanner (PO Box 4220, Nydalen, 0401 Oslo, Norway) was used for the CT analysis. The protocol used is a helical scan with a 1.25-mm slice thickness and a soft tissue algorithm for reconstruction of the X-ray signal to image. The scanning of a pig takes 15 s and yields 1100 images (Figure 1). The scan starts and stops at the same anatomical position on each pig, as the entire body is scanned. Different tissues have different CT values, and a Hounsfield unit (HU) defines fat as having HU values from −200 to 0, muscle as HU values from 0 to 200 and bone as HU values from 200 and higher (www.medcyclopaedia.com). The images were analysed using an in-house developed MATLAB (The MathWorks Inc., 3 Apple Hill Drive, Natick, MA, USA) programme. The non-carcass tissues were removed to obtain a virtual carcass using distance measurements in the images relative to skin and internal fat. Previous carcass studies have shown that the volume and weight of different tissues (fat, muscle and bone) can be estimated directly from a stack of images with a constant slice thickness (Kongsro *et al*., 2008).

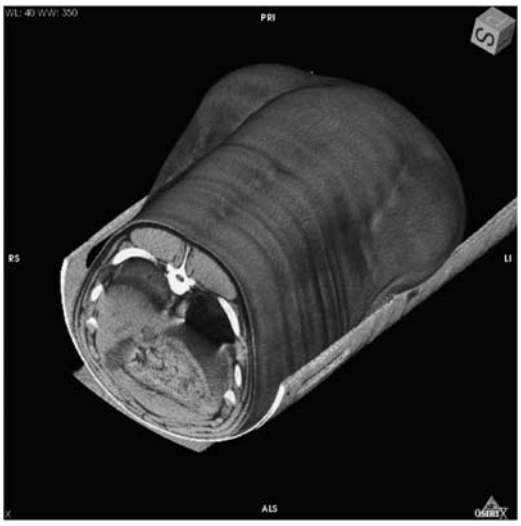

Figure 1 Spiral scan of a boar, 1100 slices. The images start from the middle of the pig, lying on the belly. The black area in the middle shows the air in the lungs, above the stomach.

The volume of different tissues was estimated using the number of pixels classified as muscle, fat and bone, multiplied by slice thickness (volume) and the average density of muscle, fat and bone tissue to obtain the mass of the different tissues. The average densities of muscle, fat and bone tissue were 1.04, 0.95 and 1.36, respectively. The pixels were classified using a pixel value and column-wise neighbourhood operation classifier (The MathWorks Inc.) to classify pixels relative to 'real' tissues. The final parameters used in this study were the weight of lean muscle, carcass fat, bone and non-carcass tissues (the sum of internal organs and fat).

The traits analysed were as follows:

(i) MG – average daily growth of muscle measured using CT from birth to the date of scanning, ~100 kg live weight. The trait was defined as (kg muscle from CT)/($age_{100\,kg}$).
(ii) FG – average daily growth of carcass fat measured usingh CT from birth to the date of scanning. The trait was defined as (kg carcass−fat from CT)/($age_{100\,kg}$).
(iii) BG – average daily growth of bone measured using CT from birth to the date of scanning. The trait was defined as (kg bone from CT)/($age_{100\,kg}$).
(iv) NCG – average daily growth of non-carcass tissue measured usingh CT from birth to the date of scanning. The trait was defined as (kg non-carcass tissue from CT)/($age_{100\,kg}$).
(v) LMP – the mass of muscle tissue was divided by the total mass of the carcass, and all the variables were measured using CT. The trait was defined as (kg muscle from CT × 100)/(kg muscle + carcass−fat + bone from CT).
(vi) ADG from birth to 25 kg (ADG1) – young boars start the test a couple of days after entering the testing station, and the pigs' age at test start is corrected to age at 25 kg. Individual weights are automatically recorded by the Feed Intake Recording Equipment (FIRE) system (Osborne Industries Inc., Osborne, KS, USA). The trait was defined as (25 kg)/($age_{25\,kg}$).
(vii) ADG from 25 kg to 100 kg (ADG2) – the boar test ends when the pigs reach 100 kg, as measured through the FIRE system. The pig's final test weight is ~100 kg, and is corrected to 100 kg. The trait was defined as 75 kg/($age_{100\,kg}$−$age_{25\,kg}$).
(viii) FCR from 25 to 100 kg – using the FIRE system under an *ad libitum* feeding regime, the individual daily feed intake is recorded for the boars. All visits to the feeding dispensers are logged, which is the basis for the individual feed consumption daily and for the entire testing period. The pigs are fed two types of feed in a distribution of ~1 : 2, and the feed energy consumed is estimated assuming 9.56 MJ net energy/kg feed. The trait was defined as feed intake (MJ)/(75 kg).

Statistical analyses

Least square means for breed. SAS Proc GLM with the least square means procedure (SAS Institute Inc., Cary, NC, USA) was used to estimate the effect of breed. An analysis was performed with both breeds in one analysis, but without herd of origin effect, due to confounding between herd and breed. The fixed effects were breed, year × month of birth, mother's parity number and number of live born in the litter the boar originated from.

Quantitative genetic analyses. Initial computations were performed on each breed separately using SAS Proc GLM to evaluate the non-genetic factors to be included in the model. For the traits analysed, the tested fixed effects were herd × year, year × month, parity number and the number of live born. Only significant effects were included in the final models, and various sub-models of the full model were used for further genetic analyses.

The significant effect of pen was included as a random effect in models for all traits. The significance of the random effects of pen was tested using a likelihood ratio test. A random effect of litter was not included due to small full-sib groups. In the quantitative genetic analyses, each breed was analysed separately. The traits (MG, FG, BG, NCG, LMP, ADG1, ADG2 and FCR) were analysed in sub-groups as described below, using a general multi-trait animal model for the genetic analyses:

$$\mathbf{Y} = \mathbf{X\beta} + \mathbf{Zu} + \mathbf{Qp} + \mathbf{e}$$

where **Y** is a vector of observations, **β**, **u**, **p** and **e** are vectors of fixed, random additive genetic, random pen and residual effects, respectively, and **X**, **Z** and **Q** are known incidence matrices. An estimation of (co)variance components was performed using multi-trait animal models and analysed using the restricted maximum likelihood methodology. The DMU 6.7 software package (Madsen and Jensen, 2008) and the average information (AI) algorithm were used in the estimation. Asymptotic standard errors of (co)variance components were computed from the inverse AI matrix.

Owing to computational constraints because of linear dependency between the growth traits, all traits could not be analysed simultaneously using multi-trait analysis. To obtain the correlations between MG, FG, BG and NCG, these four traits were analysed based on a multi-trait model and presented in a first matrix. The second set of analysed traits (MG, FG, BG, NCG, LMP, ADG1, ADG2 and FCR) was examined in four analyses. Each analysis consists of LMP, ADG1, ADG2 and FCR, with MG, FG, BG or NCG added to each of the four analyses.

The pedigree file contained all tested animals and their ancestors traced back to 2002. The final pedigree files included 9336 Landrace and 6403 Duroc pigs.

Results

Fixed effects

Descriptive statistics of the traits studied are presented in Table 1. Initial analyses on fixed effects for the traits produced the sub-models presented in Table 2, and the significant effects were included in the final models. Among the fixed effects,

Table 1 *Numbers of animals per trait, mean, s.d., minimum and maximum values for Landrace and Duroc*

Trait	Abbreviation	Breed	*n*	Mean	s.d.	Minimum	Maximum
Muscle growth from birth to 100 kg (g/day)	MG	Landrace	3835	278	21	168	360
		Duroc	3139	233	21	160	304
Carcass fat growth from birth to 100 kg (g/day)	FG	Landrace	3835	98	17	47	172
		Duroc	3139	112	20	47	190
Bone growth from birth to 100 kg (g/day)	BG	Landrace	3835	50	5	36	70
		Duroc	3139	53	4	39	73
Non-carcass tissue growth from birth to 100 kg (g/day)	NCG	Landrace	3830	219	22	142	319
		Duroc	3136	214	22	142	311
Lean meat percentage at 100 kg (%)	LMP	Landrace	3835	65.3	3.4	51.6	75.7
		Duroc	3139	58.6	4.2	44.4	73.9
Average daily gain from birth to 25 kg (g/day)	ADG1	Landrace	3832	390	44	223	635
		Duroc	3125	365	38	241	543
Average daily gain from 25 kg to 100 kg (g/day)	ADG2	Landrace	3835	905	74	631	1174
		Duroc	3139	874	73	613	1361
Feed conversion ratio from 25 kg to 100 kg (MJ/day)	FCR	Landrace	3604	20.1	1.2	14.2	27.9
		Duroc	2956	20.6	1.4	13.0	27.8

Table 2 *Hypothesis test of fixed effects of the models for the analysed traits[a] in Landrace and Duroc*

Trait	Year × month	Herd × year	Parity number[b]	Live born[c]	R^2 (Landrace)	R^2 (Duroc)
MG	xz	xz	xz	xz	0.21	0.19
FG	xz	xz	z	xz	0.20	0.16
BG	xz	xz	xz	xz	0.29	0.18
NCG	xz	xz	xz	xz	0.30	0.21
LMP	xz	xz	ns	ns	0.20	0.16
ADG1	xz	xz	xz	xz	0.31	0.18
ADG2	xz	xz	z	x	0.17	0.12
FCR	xz	xz	z	x	0.22	0.19

x = significant effect ($P < 0.05$) for Landrace; z = significant effect ($P < 0.05$) for Duroc; ns = non-significant ($P < 0.05$).
[a]See Table 1 for definitions of trait abbreviations.
[b]Parity number of the litter the pig originated from, ranged from 1 to 3.
[c]Number of live born of the litter the pig originated from, ranged from 1 to 23.

year × month had a significant effect on all the traits analysed. The herd of origin showed a large effect on the growth traits analysed. On average, the fixed effects account for 20.5% of the total variation (R^2) of the traits analysed here.

Breed effects

Least square means of the effect for breed are presented in Table 3. Landrace had higher MG and NCG and lower BG and FG than D. Landrace was the most efficient breed, with the highest LMP, ADG1 and ADG2, and the lowest FCR.

Heritability estimates

The CT and FIRE technology used to measure production efficiency yielded moderate-to-high heritability estimates for all traits in both breeds (Tables 4a and 4b). In general, Duroc had a higher additive genetic variation for the traits analysed than Landrace, in addition to higher estimated heritabilities. The estimated heritabilities for MG, FG, BG, NCG, LMP, ADG1, ADG2 and FCR ranged from 0.19 to 0.53 in Landrace and from 0.42 to 0.59 in Duroc.

Table 3 *Least square means[a] and s.e. (in brackets) of the breed effects for the analysed traits[b] in Landrace and Duroc*

Trait	Landrace	Duroc	Significance
MG	281.3 (0.3)	234.1 (0.3)	***
FG	99.5 (0.3)	113.1 (0.3)	***
BG	50.9 (0.1)	53.0 (0.1)	***
NCG	221.4 (0.3)	214.7 (0.3)	***
LMP	65.2 (0.05)	58.5 (0.05)	***
ADG1	401.5 (0.7)	369.1 (0.8)	***
ADG2	907.4 (1.0)	874.0 (1.1)	***
FCR	20.1 (0.02)	20.7 (0.02)	***

[a]The fixed effects in GLM models were: breed, year × month, mother's parity number and number of live born.
[b]See Table 1 for definitions of trait abbreviations.
*** = $P < 0.001$.

Genetic correlations

The genetic correlations between the growth of different tissues for the live pigs are shown in Table 5. MG is negatively correlated with FG and uncorrelated with NCG with

Table 4a *Heritabilities (h^2) for the analysed traits[a] with s.e., genetic and phenotypic s.d. (σ_a and σ_p, respectively) in Landrace*

Trait	h^2	s.e.	σ_a	σ_p
MG	0.19	0.04	8.49	19.51
FG	0.53	0.05	11.78	16.24
BG	0.37	0.05	2.43	3.99
NCG	0.38	0.05	12.19	19.67
LMP	0.50	0.05	2.26	3.20
ADG1	0.25	0.04	19.08	37.79
ADG2	0.41	0.05	45.67	71.07
FCR	0.29	0.04	0.63	1.17

[a]See Table 1 for definitions of trait abbreviations.

Table 4b *Heritabilities (h^2) for the analysed traits[a] with s.e., genetic and phenotypic s.d. (σ_a and σ_p, respectively) in Duroc*

Trait	h^2	s.e.	σ_a	σ_p
MG	0.43	0.05	12.88	19.65
FG	0.59	0.05	14.74	19.23
BG	0.58	0.05	3.10	4.08
NCG	0.50	0.05	14.65	20.72
LMP	0.57	0.05	3.02	4.00
ADG1	0.48	0.05	25.08	36.13
ADG2	0.42	0.05	45.91	70.51
FCR	0.42	0.05	0.88	1.36

[a]See Table 1 for trait abbreviation definitions.

Table 5 *Genetic correlations and s.e. (in brackets) among traits[a] of growth of body composition for Landrace (above diagonal) and Duroc (below diagonal)*

Trait	MG	FG	BG	NCG
MG	1	−0.37 (0.11)	0.21 (0.12)	−0.02 (0.12)
FG	−0.35 (0.08)	1	0.34 (0.09)	0.87 (0.03)
BG	0.33 (0.08)	0.37 (0.07)	1	0.44 (0.08)
NCG	0.17 (0.09)	0.77 (0.04)	0.60 (0.06)	1

[a]See Table 1 for definitions of trait abbreviations.

both breeds. FG and NCG are highly correlated. BG is positively correlated with all other traits (MG, FG and FG).

The estimated genetic correlations between traditional production traits and the growth rate of different tissues for the live pigs at 100 kg are shown in Tables 6a and 6b. With only a few exceptions, the sign and magnitude of the parameters were similar for both breeds. The genetic correlations between FCR and the other traits seem to differ most between the two breeds. On the basis of current analyses, LMP is positively correlated with MG and negatively correlated with FG, BG and NCG. ADG1 is positively correlated with MG, FG, BG and NCG and ADG2 is almost uncorrelated with MG. The ADG2 is highly unfavourable and positively correlated with FG and NCG and moderately to positively correlated with BG. FCR showed a moderate-to-high favourable correlation to MG in Duroc.

Table 6a *Genetic correlations and s.e. (in brackets) among traits[a] of slaughter pig efficiency and growth rate of different body tissues for Landrace*

	LMP	ADG1	ADG2	FCR
LMP	*1*			
ADG1	*−0.25 (0.10)*	*1*		
ADG2	*−0.75 (0.05)*	*0.15 (0.11)*	*1*	
FCR	*0.14 (0.10)*	*0.27 (0.11)*	*−0.53 (0.07)*	*1*
MG	0.55 (0.08)	0.40 (0.11)	−0.06 (0.12)	−0.11 (0.12)
FG	−0.97 (0.01)	0.35 (0.09)	0.84 (0.03)	−0.21 (0.09)
BG	−0.38 (0.08)	0.52 (0.08)	0.38 (0.09)	−0.06 (0.11)
NCG	−0.78 (0.05)	0.54 (0.08)	0.87 (0.03)	−0.29 (0.09)

[a]See Table 1 for definitions of trait abbreviations.
Correlations in italic are average values from different analyses.

Table 6b *Genetic correlations and s.e. (in brackets) among traits[a] of slaughter pig efficiency and growth rate of different body tissues for Duroc*

	LMP	ADG1	ADG2	FCR
LMP	*1*			
ADG1	*−0.27 (0.08)*	*1*		
ADG2	*−0.54 (0.07)*	*0.40 (0.09)*	*1*	
FCR	*−0.31 (0.08)*	*−0.08 (0.09)*	*−0.34 (0.08)*	*1*
MG	0.68 (0.05)	0.45 (0.07)	0.07 (0.10)	−0.53 (0.07)
FG	−0.92 (0.01)	0.52 (0.07)	0.72 (0.05)	0.09 (0.09)
BG	−0.25 (0.08)	0.71 (0.05)	0.39 (0.08)	−0.03 (0.09)
NCG	−0.56 (0.06)	0.75 (0.05)	0.87 (0.03)	−0.22 (0.08)

[a]See Table 1 for definitions of trait abbreviations.
Correlations in italic are average values from different analyses.

Discussion

Breed differences

Landrace is a highly efficient breed, and Norwegian Landrace is bred today as a dam line. Owing to high efficiency of the breed (ADG1, ADG2 and FCR) and leanness (Table 3), further genetic gain for increased leanness is not desirable. The Norwegian Duroc is bred as a sire line, but due to the high weighting on meat quality traits and shorter selection history for this breed, the efficiency and leanness are not at the same level as Landrace.

Heritability estimates

This study showed that the CT technology yielded medium-to-high estimated heritabilities for MG, FG, BG, NCG and LMP, and medium high heritabilities for ADG1, ADG2 and FCR. There were no studies with genetic parameters in the literature on FG, BG or NCG, but in this study, all these traits showed higher heritabilities than MG in both breeds. MG is less heritable than LMP. This may be due to the higher heritability for FG, which seems to explain the majority of the genetic variation in LMP. The lower heritability for MG than FG shows that fat tissue growth has a higher heritability than muscle tissue growth.

To the authors' knowledge, MG, calculated from CT images, has not been analysed previously. Nevertheless, the lean meat content can be predicted from ultrasound measurements of backfat and loin, which can then be used for the prediction of lean meat growth (PLMG). In studies of PLMG, heritability estimates range from 0.37 to 0.47 (Stern *et al*., 1993; Cameron, 1994; Chen *et al*., 2002). These estimates are in the range of our estimate for Duroc, whereas Cameron and Curran (1994) found a lower heritability (0.25) at the same magnitude as our estimate for Landrace. All those parameters for PLMG originate from ultrasound measurements of backfat and loin. This indicates that the heritability of MG from CT in our study does not yield any higher heritability than the PLMG from ultrasound measurements in other studies. However, the CT measures the muscle directly and might yield the true variation of the trait more correctly. The high heritability for PLMG from ultrasound measurements might be a result of the less unfavourable genetic correlation between ADG and ultrasound-predicted LMP in these studies.

This is the first study to present heritabilities for LMP estimated from CT scanning of live pigs. A similar size in heritability has been reported by Kvame and Vangen (2007), who studied genetic variation in a Norwegian sheep population with CT. Duroc exhibited a larger genetic variation for LMP than Landrace. The heritabilities for LMP in this study are slightly higher than those estimated for these two breeds with the previous method used in Norsvin: an experimental dissection for carcass composition of half-sibs tested females and castrates (Gjerlaug-Enger *et al*., 2010a). However, the genetic standard deviation of LMP has increased from 1.50 to 2.26 for Landrace and from 1.67 to 3.02 for Duroc, which means that there is a considerably larger genetic variation for LMP measured with CT than measured with dissection. Estimated heritabilities for LMP in our study were consistent with the corresponding estimates (ranging from 0.41 to 0.68) reported by Ducos *et al*. (1993), Sonesson *et al*. (1998) and Gilbert *et al*. (2007). All studies calculated an LMP based on a cutting procedure and the weight of lean meat for different premium cuts expressed as a percentage of the half carcass weight. Traits associated with fatness generally have high heritability and estimated heritabilities for ultrasonic backfat ranged from 0.35 to 0.72 in some studies by Ducos *et al*. (1993), Hoque *et al*. (2007) and Solanes *et al*. (2009).

Heritability estimates were higher for ADG1 in Duroc than in Landrace, and these heritabilities were higher than or comparable to those obtained for the ADG from birth to weaning and the ADG from weaning to 12 weeks (0.15 and 0.27, respectively) as reported by Chimonyo and Dzama (2007). Hermesch *et al*. (2000) tested pigs from 3 to 18 weeks, thereby overlapping our ADG1 and ADG2 periods, and the heritability estimates were 0.10 in Large White and 0.48 in Landrace. This study also demonstrated the importance of the litter effect (random effect of the litter that the piglet came from). In our study, we did not include any litter effect, due to the small full-sib group and problems with computational constraints. This might have yielded overestimated heritability for ADG1 in Duroc, as this breed had a full-sib group size of 1.3 and also higher heritability for this trait than Landrace, which had a full-sib group size of 1.1. The heritabilities for growth in the testing station period (ADG2) were of the same magnitude (ranging from 0.30 to 0.52) as those reported by Ducos *et al*. (1993), de Vries *et al*. (1994) and Suzuki *et al*. (2005).

The estimated heritabilities for FCR, particularly for Duroc, were larger than those (ranging from 0.15 to 0.27) reported by Hoque *et al*. (2007), Hermesch *et al*. (2000) and Ducos *et al*. (1993). The FCR in our study was adjusted to a fixed growth period from 25 to 100 kg live weight, which might have had a positive effect on the size of the estimated heritabilities. The data are also routinely used in the breeding programme and both automated and manual cleaning of these data can be carried out; hence, the quality of data was good.

Relationship among growth of different tissues and slaughter pig efficiency

Genetic correlation between MG, FG, BG and NCG. In general, we expected positive correlations between the growth of different body tissues. Animals with a high growth rate will necessarily need a high growth for all their body components. However, MG was little correlated with the other traits, especially NCG, whereas FG and NCG were highly positively correlated in both breeds. The only negative correlation was estimated for the genetic correlation between MG and FG; thus, an antagonistic relationship exists between the growth of carcass fat and muscles.

Genetic correlation between LMP and MG, FG, BG and NCG. As expected, only MG was positively correlated with LMP. However, the highest genetic correlation was estimated between FG and LMP. This correlation was close to -1. Therefore, selection for increased LMP reduces FG to a high degree and affects the growth of the other body tissues to a smaller degree.

A genetic correlation between FG and LMP of close to -1 means that these traits are almost identical. One explanation for this is that carcasses consist of muscle, fat and bone. As the variation in bone percentage is very small, it can be expected that the correlation between LMP and fat percentage in carcasses is high, at close to -1. Thus, having a high negative correlation between FG and LMP is the same as having a high positive correlation between FG and fat percentage. A high FG is either due to a high ADG, a high fat percentage or a combination of a high ADG and fat percentage. ADG, particularly ADG2, is highly positively correlated with fat percentage. Therefore, the overall correlation between FG and fat percentage has to be high. On the other hand, a high MG is due to a high ADG, a high LMP or a combination of a high ADG and LMP. ADG, however, is negatively correlated with LMP, which means that the correlation between MG is much lower than LMP. This explains why FG is more correlated with LMP than MG.

Genetic correlation between ADG1 and MG. Selection for growth has different effects on the different tissues of the

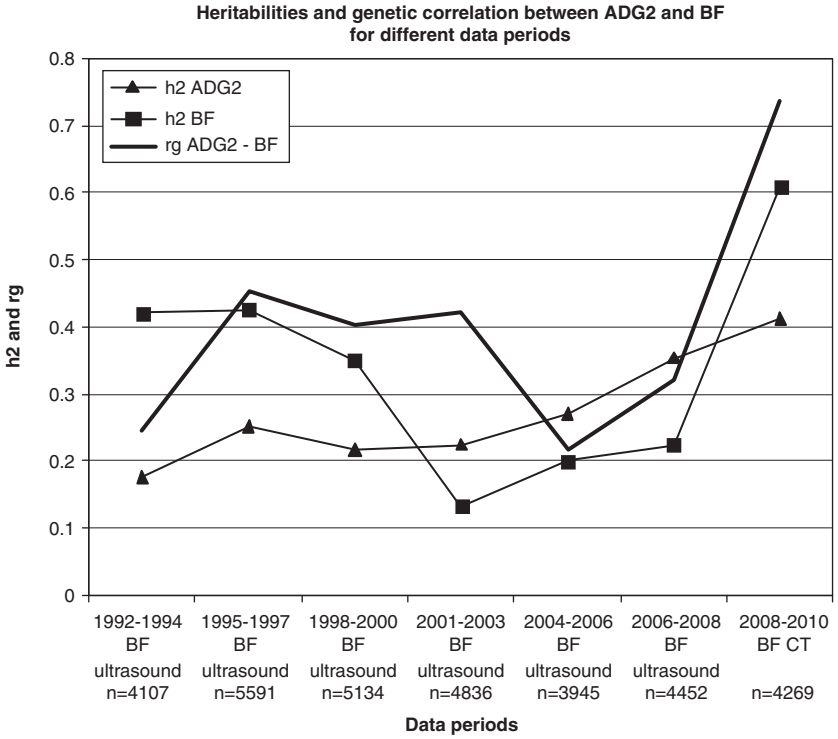

Figure 2 Different levels of heritabilities for ADG2 and BF, and genetic correlations between ADG2 and BF at different data recording periods with different measurement methods (ultrasound *v.* CT) for Norwegian Landrace; ADG2 = average daily gain from 25 kg to 100 kg; BF = back fat; CT = computed tomography).

pig. ADG1 is positively correlated with all different types of tissue in the small pig, which indicates a general response in body size when selecting ADG1. Kolstad (2001) found no differences in leanness early in life (10 to 25 kg) between three lines that were very different in fatness as finished slaughter pigs. The three lines, the Norwegian Landrace, Duroc and a 'backfat-line cross', were CT-scanned several times from 10 to 105 kg. The 'backfat-line cross' was a crossbreed between Norwegian Landrace and a line from a selection experiment in which pigs were selected for high backfat and a low growth rate (Vangen, 1977). This 'backfat-line cross' had twice the amount of total fat compared with ordinary Norwegian Landrace at 105 kg (Kolstad, 2001). Consequently, the high degrees of uniform distribution of different tissues in small pigs of different lines and breeds are obvious, and support our results with moderate genetic correlations between ADG1 and growth of all the different tissues.

Genetic correlation between ADG2 and FG. When looking at the parameters for Norwegian Landrace in earlier periods, the genetic correlation between backfat and ADG2 was less unfavourable with ultrasonic backfat measurements than with CT backfat measurements. This is shown in Figure 2, and all the analyses from earlier periods were performed simultaneously in 2010, so that the statistical analyses (models and methods) were the same for all periods. An extra generation for pedigree, in addition to the generations with data, was used for all periods. The backfat from CT was measured in the CT image, and the backfat measurement from ultrasound was real-time measured. Position was at the last rib on the live boars. The genetic correlations between backfat and ADG2 were in the range from 0.21 to 0.45 between 1992 and 2008 with ultrasound measurements. The heritabilities for backfat were in the range from 0.13 to 0.42 during this period. The largest part of fat reduction in Norwegian Landrace was achieved from 1958 to 1992, ranging from ~30 to 8.1 mm backfat on Landrace boars at 90 to 100 kg. Only a few millimetres of fat reduction, ranging from 8.1 to 5.9 mm backfat on Landrace boars at 100 kg, was achieved from 1992 to 2010. There is a reduction in the phenotypic variation of backfat thickness for this selection period, and a reduction in heritability for backfat for the period of ultrasound measurements from 1992 to 2008. For the period of CT measurements from 2008 to 2010, we observed an increased heritability for backfat. CT uncovers new genetic variation due to the higher accuracy of estimation, and this new part of genetic variation has a stronger covariation with ADG2, yielding an increased genetic correlation between backfat and ADG2. Estimated heritabilities for ADG2 increased for this period (1992 to 2010) despite reduced phenotypic variance. A change from manual to electronic (FIRE) weighing was made in the data period, which positively affected the quality of the data.

One theory of growth has been that selection for growth will produce leaner animals because a selection for growth is a selection for animals with steeper growth curves (Krieter and Kalm, 1989; Kohn *et al.*, 2007). For this reason, selection for growth is expected to result in a higher adult weight and in less mature, leaner animals at a fixed weight, as fat growth is expected to increase around puberty. Estimated

genetic correlations between backfat and growth were close to zero in a selection experiment with Landrace selected for increased fatness and reduced growth rate (Vangen, 1979). In a study by Hetzer and Miller (1972), also on relatively fat pigs, the results indicated that a selection for lower fatness should improve the growth rate in Duroc, whereas in Yorkshire, a higher leanness would result in slower growing pigs. A favourable or a small correlation between growth and leanness is, however, far from what we can interpret from our results. Modern, fast-growing, lean pigs such as the Norwegian Landrace and Duroc have a highly unfavourable genetic correlation between ADG2 and FG or LMP, which is in agreement with the results reviewed in a paper by Cleveland *et al*. (1982). The mean correlation between the ADG and backfat was 0.12, ranging from 0.26 to 0.55 for 11 studies from 1962 to 1994 (Clutter and Brascamp, 1998).

Early dissection studies on farm animals at different ages have made it possible to produce growth curves of different tissues, and the maximum growth rate for bone is reached before that of muscle, whereas fat is the last to be developed (Hammond, 1950). Modern pigs are fast-growing animals, and in our study, FG increased in the ADG2 period from 25 to 100 kg live weight. In addition, a pig is different from other farm animals, because of its high volume of subcutaneous fat in the carcass, whereas ruminants have more internal fat. Hammond (1950) compared pigs with high/low *v.* low/high growth, both early (before 16 weeks) and late (from 16 to 34 weeks), in a growth period to 200 lb live weight (90.7 kg). He found very different frames (body composition), despite having an equal final weight for the two tested groups. The pigs that had grown high/low had more bone and muscles, whereas the pigs that had grown low/high had a higher fat content. Although this was a feeding experiment, it supports our findings that pigs that grow fast in the beginning (ADG1) have higher MG, whereas pigs that grow fast in the later period (ADG2) have a higher FG. Despite the very high age in this study (100 days longer than for our pigs), the final weight was almost similar (10 kg higher in the present study).

Genetic correlation between MG and ADG2. Bennett (1992) stresses the difference between predicted and actual measurements. If lean meat growth could be measured directly, then selecting for lean meat growth would be straightforward. However, composition is often predicted by indirect means. The relationship between PLMG and other traits can be different from the relationship of actual lean meat growth (ALMG) for the same traits. Hence, a selection for ALMG may be desirable, whereas a selection for PLMG may be undesirable. Therefore, ALMG is distinguished from PLMG, partly because fat affects PLMG more than ALMG.

Chen *et al*. (2002) estimated very high favourable genetic correlations (ranging from −0.80 to −0.86) between growth (number of days to 113.5 kg, not ADG, and therefore the opposite sign) and PLMG in Yorkshire, Duroc, Hampshire and Landrace. Mrode and Kennedy (1993) also found a high genetic correlation (0.96) between growth (ADG from 30 to 90 kg) and PLMG in Yorkshire, Duroc and Landrace. This is very different from the parameters estimated in our study, with genetic correlations close to 0 between ADG2 and MG for both breeds. Some preliminary analyses attempted to determine the effect of trial (breed and environment) and the effect of the method and technology, as correlations between ADG2 and MG in our study are so different from similar parameters (i.e. PLMG) from other studies. The equation for PLMG (National Pork Producers Council (NPPC, 2000) from a study by Chen *et al*. (2002) was used to generate NPPC's PLMG for our Norwegian Landrace and Duroc pigs. Measurements for backfat and loin area were then taken from analyses of CT images. The NPPC's PLMG equation yielded similar results for the Norwegian breeds in terms of similar means and standard deviations as MG, but with different genetic correlations to other traits. Estimated genetic correlations between NPPC's PLMG and ADG2 were 0.32 (Landrace) and 0.21 (Duroc) points higher and more positive than the corresponding correlations between MG and ADG2, whereas genetic correlations between NPPC's PLMG and LMP were 0.35 (Landrace) and 0.27 (Duroc) points lower and less positive than the corresponding correlations between MG and LMP. Higher genetic correlations between MG and LMP than between NPPC's PLMG and LMP are expected as LMP originate from weight of different tissues measured with CT, but the high genetic correlations between NPPC's PLMG and ADG2 are more problematic. Therefore, the higher correlation between ADG2 and PLMG using ultrasound compared with CT might be overestimated as a result of the technology used. Lower genetic correlations between ultrasound-predicted LMP and ADG2 than between CT-predicted LMP and ADG2 might be one explanation. The growth period used in the studies was not identical, and growth early in life is more positively correlated with MG; nonetheless, this does not explain the differences between the correlations discussed here.

The size of genetic standard deviations (Table 4a and 4b) indicates that FG has a higher genetic variation than MG. Animals with high MG often have low FG, and therefore, not higher ADG2 in total. This is one explanation for the low genetic correlation between ADG2 and MG. A positive correlation between MG and ADG2 can only be estimated if there are less antagonistic relationship between FG and MG.

Genetic correlation between FCR and MG v. FG. Webster (1977) compared the energy required for protein deposition and fat deposition, and concluded that the same amount of metabolic energy is deposited in 1 kg of fat as in ~8 kg of fat-free muscle. This supports the favourable genetic correlations between FCR and MG, especially in Duroc, as also reported by Hoque *et al*. (2007). In contrast, more energy is required to maintain muscle tissue due to the higher metabolism in that tissue, whereas fat has a low metabolic activity. Webster (1981) found the energy demand for maintenance to be less per kg metabolic body weight in obese than in lean rats, but the differences disappeared when the maintenance was expressed as a function of lean mass. Kolstad and Vangen (1996) found a higher maintenance requirement in Landrace, which was a faster growing breed, than in Duroc. This indicates

that a selection for improved MG may increase the maintenance requirement. In our study, genetic correlations between FCR and growth of different tissues were small, except for FCR and MG in Duroc, which showed medium growth. There are small genetic correlations between FCR and the different body tissues in Landrace, and this might be because the low energy demand required for MG is outweighed by the greater need for maintenance for muscles than for fat. FG, on the other hand, costs more to grow but requires less energy to maintain.

There are opposite signs of the genetic correlation between FCR and LMP for Landrace and Duroc, and increased LMP is not positive for FCR in Landrace. This yields a low correlation between MG and FCR for this breed. In Duroc, both ADG2 and LMP are positive for FCR, yielding the positive correlation between MG and FCR.

The high genetic correlation between FCR and MG in Duroc is favourable, but only to a certain level. In the long term, a reduced FCR can reduce the ability of MG due to reduced appetite and feed intake. The minimum feed intake capacity should not be lower than the feed intake that maximises the potential for protein deposition and therefore MG, which was thoroughly discussed in papers by Hermesch *et al*. (2003) and Hermesch (2004).

Genetic correlation between ADG2 and NCG. A large volume of non-carcass tissues is undesirable, as there is no value for this tissue at slaughtering. The high genetic correlations between ADG2 and NCG, particularly in Landrace, may indicate that the pigs need larger internal organs to achieve fast growth. The estimated parameters in this study clearly show the unfavourable connection between ADG2 and NCG. NCG has not been discussed in earlier studies, but our results are in accordance with Bidanel and Ducos (1996) and Norsvin's selection parameters, in which unfavourable genetic correlations between growth and dressing percentage were estimated. Dressing percentage is almost the inverse trait to the percentage of non-carcass tissues. However, a high ADG2 is highly influenced by FG, and the high genetic correlation between NCG and FG may thus point towards a connection between subcutaneous fat and internal fat. Therefore, large non-carcass tissues may consist of a high amount of internal fat and a lesser degree of internal organs such as the lungs, heart, stomach, intestines and liver, as these vary less between animals (J. Kongsro, personal communication). A selection against NCG or for a higher dressing percentage is controversial as the internal organs are needed to achieve a high production. Nevertheless, the amount of internal fat should be controlled, as this fat has low value. To maintain the dressing percentage unchanged, a balanced selection may be one strategy for this biological challenge.

Selection strategies

In an integrated pig industry, high MG of good quality meat is the main objective. MG combines requirements from both the pig producers and the meat industry. MG has a lower heritability than LMP and ADG2, but a selection for MG yields higher genetic gain than a selection for two unfavourably correlated traits. The estimated genetic correlations between MG and FG, NCG and BG are favourable or small, which makes it possible to select modern pigs for MG without compromising other traits such as FG, NCG and BG. In addition, ADG1, ADG2, LMP and slaughter percentage are not crucial for the breeding goal. Exclusion of so many traits from the breeding goal provides reduced information about the genetic gain in these traits, although it makes the variance component structure less complex. This allows for new possibilities to obtain estimated genetic parameters and breeding values for other traits such as meat quality, maternal ability, reproduction and health traits, together with the slaughter pig efficiency trait MG.

The high negative correlation between LMP and ADG2 makes it a challenge to find the optimal weighting of these traits in a total merit index. The challenge with a selection for only MG is to control the genetic progress for the component traits LMP, ADG1 and ADG2. The estimated genetic correlations indicate that a selection for an increased MG does not result in increased ADG2, whereas ADG1 will show a positive change. In view of maintenance costs, pig producers are aware that ADG2 is a more important trait than ADG1. In view of the estimated parameters, it is difficult to improve ADG2 without increasing FG, whereas animals with a high ADG1 and moderate ADG2 often have high MG and provide a more desirable carcass quality.

The genetic development of other traits is not affected by the choice of the selection strategy of MG *v.* LMP and ADG2. To illustrate this, the favourable correlation between MG and FCR in Duroc makes selection for both traits easy to obtain, although this is also the case with a selection for LMP and ADG2, with both traits being favourably genetically correlated with FCR.

Conclusions

CT technology has the unique ability to measure body composition in the live animals. Dissection methods of pigs for breeding purpose are often based on the composition of only a few cuts and ultrasound measurements recording leanness and muscle depth only at a few positions. Hence, the CT data provide more knowledge about the actual content of lean muscle in a carcass. This yields a larger variation in lean meat content and different genetic correlations to several traits.

The genetic parameters of the growth of different tissues measured with CT in this study provide new understanding of traditional slaughter pig efficiency traits, such as the antagonistic relationship between LMP and ADG2 in modern pigs.

MG seems to be a suitable trait for carcass quality and slaughter pig efficiency, in addition to being a biologically robust trait. MG is favourably correlated with FG, which simplifies the breeding. In cases in which LMP, ADG1 and ADG2 are optimally combined in a total merit index, the results are almost the same as those in the selection for MG.

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References

Afonso JJM 1992. Factors affecting growth and body composition in sheep. PhD, University of New England.

Bennett GL 1992. Predicting lean growth while accounting for correlated traits. Journal of Animal Science 70, 51–56.

Bidanel JP and Ducos A 1996. Genetic correlations between test station and on-farm performance traits in Large White and French Landrace pig breeds. Livestock Production Science 45, 55–62.

Cameron ND 1994. Selection for components of efficient lean growth-rate in pigs. 1. Selection pressure applied and direct responses in a Large White Herd. Animal Production 59, 251–262.

Cameron ND and Curran MK 1994. Selection for components of efficient lean growth-rate in pigs. 2. Selection pressure applied and direct responses in a Landrace Herd. Animal Production 59, 263–269.

Chen P, Baas TJ, Mabry JW, Dekkers JCM and Koehler KJ 2002. Genetic parameters and trends for lean growth rate and its components in US Yorkshire, Duroc, Hampshire, and Landrace pigs. Journal of Animal Science 80, 2062–2070.

Chimonyo M and Dzama K 2007. Estimation of genetic parameters for growth performance and carcass traits in Mukota pigs. Animal 1, 317–323.

Cleveland ER, Cunningham PJ and Peo ER 1982. Selection for Lean Growth in Swine. Journal of Animal Science 54, 719–727.

Clutter AC and Brascamp EW 1998. Genetics of performance traits. In The genetics of the pig (ed. MF Rothschild and A Ruvinsky), pp. 427–462. CAB International, Wallingford, UK.

de Vries AG, van der Wal PG, Long T, Eikelenboom G and Merks JWM 1994. Genetic parameters of pork quality and production traits in Yorkshire populations. Livestock Production Science 40, 277–289.

Ducos A, Bidanel JP, Ducrocq V, Boichard D and Groeneveld E 1993. Multivariate restricted maximum-likelihood-estimation of genetic-parameters for growth, carcass and meat quality traits in French Large White and French Landrace pigs. Genetics Selection Evolution 25, 475–493.

Fowler VR, Bichard M and Pease A 1976. Objectives in pig breeding. Animal Production 23, 365–387.

Gilbert H, Bidanel JP, Gruand J, Caritez JC, Billon Y, Guillouet P, Lagant H, Noblet J and Sellier P 2007. Genetic parameters for residual feed intake in growing pigs, with emphasis on genetic relationships with carcass and meat quality traits. Journal of Animal Science 85, 3182–3188.

Gjerlaug-Enger E, Aass L, Ødegård J, Kongsro J and Vangen O 2010a. Genetic parameters of fat quality in pig measured by near infrared spectroscopy. Animal, in press; doi:10.1017/S1751731111000528.

Gjerlaug-Enger E, Aass L, Ødegård J and Vangen O 2010b. Genetic parameters of meat quality traits in two pig breeds measured by rapid methods. Animal 4, 1832–1843.

Hammond J 1950. Measuring growth in farm animals. Proceedings of the Royal Society of London Series B-Biological Sciences 137, 452–461.

Hermesch S 2004. Genetic improvement of lean meat growth and feed efficiency in pigs. Australian Journal of Experimental Agriculture 44, 383–391.

Hermesch S, Luxford BG and Graser HU 2000. Genetic parameters for lean meat yield, meat quality, reproduction and feed efficiency traits for Australian pigs 1. Description of traits and heritability estimates. Livestock Production Science 65, 239–248.

Hermesch S, Kanis E and Eissen JJ 2003. Economic weights for feed intake in the growing pig derived from a growth model and an economic model. Journal of Animal Science 81, 895–903.

Hetzer HO and Miller RH 1972. Rate of growth as influenced by selection for high and low fatness in Swine. Journal of Animal Science 35, 730–742.

Hoque MA, Suzuki K, Kadowaki H, Shibata T and Oikawa T 2007. Genetic parameters for feed efficiency traits and their relationships with growth and carcass traits in Duroc pigs. Journal of Animal Breeding and Genetics 124, 108–116.

Jones HE, Lewis RM, Young MJ and Simm G 2004. Genetic parameters for carcass composition and muscularity in sheep measured by X-ray computer tomography, ultrasound and dissection. Livestock Production Science 90, 167–179.

Kohn F, Sharifi AR and Simianer H 2007. Modeling the growth of the Goettingen minipig. Journal of Animal Science 85, 84–92.

Kolstad K 2001. Fat deposition and distribution measured by computer tomography in three genetic groups of pigs. Livestock Production Science 67, 281–292.

Kolstad K and Vangen O 1996. Breed differences in maintenance requirements of growing pigs when accounting for changes in body composition. Livestock Production Science 47, 23–32.

Kolstad K, Vegusdal A, Baeverfjord G and Einen O 2004. Quantification of fat deposits and fat distribution in Atlantic halibut (Hippoglossus hippoglossus L.) using computerised X-ray tomography (CT). Aquaculture 229, 255–264.

Kongsro J, Roe M, Aastveit AH, Kvaal K and Egelandsdal B 2008. Virtual dissection of lamb carcasses using computer tomography (CT) and its correlation to manual dissection. Journal of Food Engineering 88, 86–93.

Krieter J and Kalm E 1989. Growth, feed-intake and mature size in Large White and Pietrain pigs. Journal of Animal Breeding and Genetics-Zeitschrift Fur Tierzuchtung Und Zuchtungsbiologie 106, 300–311.

Kvame T and Vangen O 2007. Selection for lean weight based on ultrasound and CT in a meat line of sheep. Livestock Science 106, 232–242.

Luiting P, Kolstad K, Enting H and Vangen O 1995. Pig breed comparison for body-composition at maintenance – analysis of computerized-tomography data by mixture distributions. Livestock Production Science 43, 225–234.

Madsen P and Jensen J 2008. A user's guide to DMU. A package for analysing multivariate mixed models. Version 6, release 4.7. Danish Institute of Agricutural Sciences (DIAS), Department of Animal Breeding and Genetics, Research Center Foulum, Tjele, Denmark.

Mcphee CP, Brennan PJ and Duncalfe F 1979. Genetic and phenotypic parameters of Australian Large White and Landrace Boars performance-tested when offered food ad-libitum. Animal Production 28, 79–85.

Mrode RA and Kennedy BW 1993. Genetic-variation in measures of food efficiency in pigs and their genetic-relationships with growth-rate and backfat. Animal Production 56, 225–232.

Solanes FX, Reixach J, Tor M, Tibau J and Estany J 2009. Genetic correlations and expected response for intramuscular fat content in a Duroc pig line. Livestock Science 123, 63–69.

Sonesson AK, de Greef KH and Meuwissen THE 1998. Genetic parameters and trends of meat quality, carcass composition and performance traits in two selected lines of large white pigs. Livestock Production Science 57, 23–32.

Stern S, Johansson K, Rydhmer L and Andersson K 1993. Performance testing of pigs for lean tissue-growth rate in a selection experiment with low and high-protein diets.1. Experimental-design and efficiency of selection. Acta Agriculturae Scandinavica Section A – Animal Science 43, 136–143.

Suzuki K, Irie M, Kadowaki H, Shibata T, Kumagai M and Nishida A 2005. Genetic parameter estimates of meat quality traits in Duroc pigs selected for average daily gain, longissimus muscle area, backfat thickness, and intramuscular fat content. Journal of Animal Science 83, 2058–2065.

Vangen O 1977. Studies on A 2 trait selection experiment in pigs. 1. Growth, feed consumption and feed conversion ratio after 10 years of selection for growth-rate and backfat thickness. Acta Agriculturae Scandinavica 27, 331–340.

Vangen O 1979. Studies on A 2 trait selection experiment in pigs. 2. Genetic changes and realized genetic-parameters in the traits under selection. Acta Agriculturae Scandinavica 29, 305–319.

Vangen O and Thompson J 1992. The use of CAT-scanning to measure maintenance efficiency in genetic lines of sheep. In: Spain, 43rd Meeting of the European Association for Animal Production.

Webster AJF 1977. Selection for leanness and energetic efficiency of growth in meat animals. Proceedings of the Nutrition Society 36, 53–59.

Webster AJF 1981. The energetic efficiency of metabolism. Proceedings of the Nutrition Society 40, 121–128.