

Genetic parameters of *in vivo* primal cuts and body composition (PigAtlas) in pigs measured by computed tomography (CT)¹

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ABSTRACT: Genetic parameters of *in vivo* primal cuts in breeding pigs using computed tomography were estimated. A total of 2,439 Duroc and 1998 Landrace boars from the Topigs Norsvin boar testing station in Norway were CT scanned as part of the genetic program. *In vivo* primal cuts were derived from the CT images using atlas segmentation; the method called the Pig Atlas. The (co)variance estimates were obtained from univariate (heritabilities) and multivariate (correlations) animal genetic models using DMU software. The heritabilities for all primal cuts proportions (%) were intermediate to large for both breeds, h^2 ranging from 0.15 to 0.50. Negative genetic correlations were found between

most of the other primal cuts, and the strongest correlation was between belly and ham. Carcass lean meat percentage showed a positive correlation to shoulder and ham, but was negatively correlated to belly. In this study, *in vivo* primal cuts from atlas segmentation are used for genetic parameter calculations for the first time. Computed Tomography (CT) makes it possible to measure *in vivo* body or carcass composition. This will aid the selection response by measuring on the candidates themselves instead of using relatives. Primal cut proportion and composition measured *in vivo* by computed tomography and atlas segmentation show heritable variation comparable to previous post mortem studies.

Key words: body composition, computed tomography, genetic parameters, pigs, PigAtlas, primal cuts

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Transl. Anim. Sci. 2017.1:599–606
doi:10.2527/tas2017.0072

INTRODUCTION

The most important traits in pig breeding have for decades been related to efficient lean meat production, i.e., selection for increased growth rate, feed efficiency and low fat carcass composition (Cameron, 1990). However, breeding goals have been changing from focus on cost reduction toward retail carcass yield and meat quality (Miar et al., 2014), and recently including sustainability (Rydhmer et al., 2014), social breeding values (Reimert et al., 2014) and robustness (Herrero-Medrano et al., 2015). Carcass yield is still highly valid in breeding goals, but to give more space to the more recent traits, we need to find more efficient

ways of measuring carcass traits *in vivo*, bypass the use of sibs or half-sibs to measure these traits on the selection candidates themselves. *In vivo* or non-invasive measures of carcass composition can be derived either indirectly by ultrasound and other anthropometric measures like body conformation score, or more directly by Computed Tomography (CT), Magnetic Resonance Imaging and dual-energy X-ray absorptiometry (Scholz et al., 2015). Heritability, h^2 , is defined as the genetic contributions to a population's phenotypic variance. Heritabilities of the primal cuts ham, loin, belly, and shoulder, based on dissected carcasses, are found to be medium to large. For example, the ham, belly and loin have been reported to range from 0.29 to 0.57 in previous studies, and for deboned cuts, the heritabilities were even greater ($h^2 > 0.70$; Newcom et al., 2002; Van Wijk et al., 2005). Previous studies have shown that primal cut traits are highly heritable on the carcass level (post mortem), however the genetic parameters for *in vivo* primal cuts and carcass composition remain elusive.

¹The Norwegian Research Council is acknowledged for funding this project with grant #256316.

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Received October 9, 2017.

Accepted October 23, 2017.

Today, CT is used in pig breeding, and to handle large amounts of data and animals, more automation is needed in the process of virtually dissect the pig based on CT. To aid the automated process, the authors have recently looked at developing a pig atlas based on CT (Gangsei et al., 2016a; Gangsei and Kongsro, 2016). The Pig Atlas is a digital map based on computed tomography body scans of a subset of ~500 pigs from the population of purebred Landrace and Duroc pigs in Norway. The Pig Atlas is an average pig based on that particular subset. Volumes of CT scanned pigs are continuously fitted onto the pig atlas and deformed to transfer information from the atlas to the new animal. The primal cuts are identified using the already established “landmarks”, and the pig is brought back to its original shape. This has proven to be an effective way of recording primal cut data from a large number of animals in an automated way (Gangsei et al., 2016a). This is, to our knowledge, the first attempt to study in vivo carcass and primal cut composition using CT in a commercial breeding program. Study of genetic parameters for in vivo carcass and primal cut composition is necessary to implement these traits in a commercial breeding program for pigs. Thus, the aim of this study was to estimate genetic parameters of in vivo primal cuts and carcass composition in breeding pigs measured by atlas segmented images from CT.

MATERIALS AND METHODS

All animals were cared for according to the laws and regulations for keeping pigs in Norway (Regulation for the keeping of pigs in Norway 2003–02–18–175, 2003; Animal Welfare Act 2009–06–19–97, 2009).

Animals

A total of 2,439 purebred Duroc and 1998 Landrace boars from the boar testing station, Norsvin Delta in Norway, were CT scanned as part of the Topigs Norsvin genetic program as described more in detail by Aasmundstad et al. (2013). The purebred boars were born and raised to 25 to 30 kg in different nucleus herds located in Norway. As part of the test program, the pigs are sent to the boar testing station, Norsvin Delta, when reaching 25 to 30 kg. The test includes feed and weight recordings, score of exterior traits and CT scanning at the end of test when they reach 120 kg as described more in detail by Gjerlaug-Enger et al. (2012).

CT Scanning

The pigs were CT scanned using a GE Healthcare VCT 32 scanner at 120 kg body weight. The protocol used was optimized for soft tissue using a slice thick-

ness of 1.25 mm, 120 kV and dynamic mA based on the thickness of the slice. Prior to CT scanning, the boars were sedated using Azaperone, 8 mg/kg live weight (Stresnil Vet, Janssen-Cilag Ltd, Buckinghamshire, UK) administered intramuscularly. Boars were scanned approximately 45 min after injection, as the sedation was given to keep the boars calm during scanning.

Image Analysis and Atlas Segmentation

Atlas segmentation (Gangsei et al., 2016a; Gangsei et al., 2016b) was the means for obtaining new and better phenotypes in vivo to improve accuracy and potentially increase heritabilities for the traits of interest. By atlas segmentation every voxel was assigned to one of the primal cuts, i.e., ham, belly, loin (including tenderloin) or shoulder, or as non-commercial parts, i.e., internal organs, testicles etc. The labeled atlas was based on expert segmentation of CT images (Gangsei et al., 2016a). After atlas segmentation all voxels in the primal cuts were classified into the tissue classes; lean meat, fat or bone. Voxels with HU > 200 were classified as bone. Thereafter, to reduce noise, a simple filter was applied to the soft tissue (HU < 200). HU values used for tissue classification of soft tissue voxels were set to the minimum HU value of a 2 × 2 sliding frame within each 2D image slice. Soft tissue voxels with filtered HU > 0 were classified as lean meat and the rest were classified as fat. The weight of each voxel in the primal cuts was calculated as the product of its volume and density, where the density was set based on a simple linear relationship ($1.0062 + 0.0016 \times \text{HU}$; Campbell et al., 2003). Thereafter, the total weights of meat, fat and bone within each primal cut were easily calculated as the sum of weights of voxels were classified to the actual cut and tissue. These weights constitute the basis for all genetic parameter calculations in this study.

Traits

Carcass weight was defined as the sum of primal cuts (ham, belly, loin, and shoulder), excluding the head. The primal cuts ham, belly, loin, and shoulder were obtained as described above, and were expressed as primal cut weights (absolute weights in kg) or as relative primal yield (relative proportions of carcass weight in %). Lean meat in each of the primal cuts was also expressed as a percentage of lean meat (LMP) in the specific primal cut. Carcass lean meat was expressed as carcass lean meat percentage (CLMP). Carcass yield was defined as a ratio of carcass weight (sum of all primal cuts) over live weight estimated from the entire CT volume of the pig. Loin depth was defined as muscle (*m. longissimus*) depth in cm at the last rib measured on CT images. Backfat

depth was defined as subcutaneous fat layer over loin depth at the last rib measured on CT. Both backfat and loin depth was measured by ruler on the images across the widest part of the *m. longissimus* muscle approximately 7 cm off the midline of the animal.

Statistical Analysis

The difference in phenotypic means between Duroc and Landrace was analyzed by a student *t* test in SAS (SAS Inst. Inc., Cary, NC). Duroc and Landrace were analyzed separately as there is no common pedigree. The (co)variance estimates were obtained from univariate (heritabilities) and multivariate (correlations) animal genetic models. The DMU software (Madsen P and Jensen J, 2013) was used. The model for each trait was defined as:

$$y_{ijklmno} = PARITY_i + HY_j + MONTH_k + SECTION_l + \beta_1 \times LW_{ijklmno} + \beta_2 \times LW_{ijklmno}^2 + pen_m + litter_n + animal_o + error_{ijklmno}$$

Where Y is the studied trait(s). For all y, PARITY (parity of dam) included four levels (*i* = 1, 2, 3, or a later parity, unknown parity), HY (herd of origin and year of birth) included *j* = 35 levels for Duroc and 108 levels for Landrace. Mmonth born in (MONTH) included *k* = 12 levels. The section in the barn at the testing station (SECTION) included *l* = 74 levels for Duroc and 77 for Landrace. The live body weight in kg from CT scanning of each animal was fitted as a fixed linear (β_1) and quadratic (β_2) regression coefficients. The effects of PARITY, HY, MONTH and SECTION were treated as fixed effects. Pen (at the testing station), litter (common

environmental effect for full sibs), animal and error were treated as random effects. The additive genetic effects were expected and both the pen, litter, and residual effect were expected where A is the additive relationship matrix, G is the additive genetic (co) variance matrix, I is an identity matrix of dimension equal to the number of animals with phenotypic records and R is the residual (co)variance matrix. Heritability estimates were obtained from univariate analysis, and heritability was defined as additive genetic variance divided by the phenotypic variance (sum of additive genetic-, pen-, litter and residual variance). Genetic and residual correlations were obtained from multivariate analysis using the same model as for univariate analysis. For the random effects of the pen and litter no co-variance was assumed between traits. Due to convergence problems, some traits for Landrace had to be split into 4 blocks with the following traits: 1) percentage primal cuts, 2) percent primal cuts with LMP and carcass yield, 3) percent primal cuts with muscle and backfat, 4) LMP, carcass yield, muscle and backfat.

RESULTS

Descriptive Statistics of Primal Cuts and Carcass Traits

Descriptive statistics are shown in Table 1 and 2. Ham was the greatest primal cut for both breeds, and loin was the smallest. Loin and ham were also the primal cuts with the greatest differences between breeds where Duroc had the greatest ham, and Landrace the greatest loin. Duroc had also a slightly smaller belly and a greater shoulder compared to Landrace. Landrace showed the greatest variance in primal cut proportions. Duroc had a smaller CLMP compared to Landrace, and this was reflected in the LMP within each primal cut where the greatest differences were

Table 1. Summary statistics for traits. Duroc, *n* = 2,439

Trait	Mean	SD	Min	Max	CV ¹
Shoulder, %	31.05	0.85	28.18	34.33	2.74 %
Belly, %	20.09	1.26	13.72	27.05	6.26 %
Loin, %	13.40	0.69	10.27	22.42	5.17 %
Ham, %	35.00	1.32	22.31	46.47	3.77 %
Shoulder lean, %	59.55	3.32	44.57	71.48	5.57 %
Belly lean, %	50.37	4.20	35.66	64.78	8.34 %
Loin lean, %	61.99	3.03	50.85	71.96	4.89 %
Ham lean, %	63.96	2.53	53.99	73.52	3.95 %
Carcass lean, %	59.66	2.99	48.25	69.68	5.02 %
Carcass yield ² , %	74.29	1.10	69.33	80.55	1.49 %
Backfat ³ , mm	6.23	1.68	3	13	27.23 %
Loin ² , mm	61.20	4.24	49	78	6.77 %

¹Coefficient of variation (CV) = SD/mean.

²Carcass (kg)/Live animal (kg) × 100%.

³Backfat and loin depth over last rib.

Table 2. Summary statistics for traits. Landrace, $n = 1,998$

Trait	Mean	SD	Min	Max	CV ¹
Shoulder, %	30.46	1.02	26.83	34.54	3.36 %
Belly, %	20.50	1.34	15.88	26.27	6.56 %
Loin, %	14.47	0.79	7.90	20.65	5.43 %
Ham, %	34.07	1.35	26.84	45.63	3.97 %
Shoulder lean, %	61.93	3.25	47.09	73.88	5.25 %
Belly lean, %	55.04	4.46	38.46	69.98	8.11 %
Loin lean, %	68.16	2.62	55.03	77.19	3.85 %
Ham lean, %	69.27	2.74	50.42	77.97	3.95 %
Carcass lean, %	63.32	2.95	47.04	73.53	4.66 %
Carcass yield ² , %	75.41	1.14	71.00	79.56	1.51 %
Backfat ³ , mm	5.25	1.79	2	20	34.23 %
Loin ² , mm	65.34	4.38	49	79	6.70 %

¹Coefficient of variation (CV) = SD/mean.

²Carcass (kg)/Live animal (kg) × 100%.

³Backfat and loin depth over last rib.

seen for LMP within loin and ham. Duroc had greater variation in lean content (%) in loin, shoulder and belly compared to Landrace. Further, Duroc had a smaller measure of loin depth and a greater measure of backfat compared to Landrace. Duroc gave a smaller carcass yield compared to Landrace. The mean live weight was 120 kg deviating with 2.14 kg and 2.79 for Duroc and Landrace, respectively. The average number of days from 40 to 120 kg was 76.54 and 72.96, for Duroc and Landrace, respectively.

Heritability Estimates

The heritability estimates (+ standard errors) are presented in Table 3 through 6 (diagonal elements). The heritabilities for all primal cuts were intermediate to large for both breeds, h^2 ranging from 0.15 to 0.50 (Table 3 and Table 4). The smallest and largest heritabilities were found in Landrace for shoulder and belly, respectively. The standard errors were relatively small (0.05 to 0.07) and similar across cuts and breeds. Lean meat percentage had a large-intermediate heritability, whereas carcass

yield showed a smaller heritability. Loin depth and backfat was also intermediate heritable (Table 3 and Table 4). The heritability of LMP within each primal cut was similar to the CLMP, although somewhat smaller for shoulder in Landrace (Table 5 and Table 6).

Genetic Correlations

Genetic correlations close to zero were found for shoulder and ham (both breeds) and shoulder and loin (Duroc; Table 3 and Table 4). Negative genetic correlations were found between most of the other primal cuts, and the strongest correlation was between belly and ham. However, a weak, positive genetic correlation was found between ham and loin in Landrace (Table 4). The carcass lean meat percentage showed a positive correlation to shoulder and ham, but was negatively correlated to belly. Loin showed no genetic correlation to CLMP. Carcass yield was positively correlated to ham and shoulder, but the correlation to loin was close to zero. Correlation between carcass yield and belly was close to zero in Duroc and negative in Landrace. Loin

Table 3. Duroc Heritabilities (diagonal, bold) and genetic (below diagonal) and residual (above diagonal) correlations (with SE). Primal cuts, lean meat percentage carcass (CLMP) and carcass yield in (%), backfat and loin depth in millimeters

Trait	Shoulder	Belly	Loin	Ham	CLMP	YIELD	BF	LD
Shoulder	0.26 (0.06)	-0.28 (0.04)	0.08 (0.05)	-0.45 (0.04)	-0.07 (0.07)	0.24 (0.04)	0.10 (0.05)	0.00 (0.06)
Belly	-0.50(0.10)	0.39 (0.06)	-0.15 (0.05)	-0.58 (0.03)	-0.12 (0.07)	-0.45 (0.04)	0.25 (0.05)	0.01 (0.07)
Loin	-0.02 (0.13)	-0.24 (0.11)	0.34 (0.06)	-0.44 (0.04)	-0.02 (0.07)	-0.10 (0.05)	0.03 (0.05)	0.21 (0.06)
Ham	-0.04 (0.14)	-0.68 (0.07)	-0.32 (0.11)	0.27 (0.05)	0.15 (0.06)	0.28 (0.04)	-0.28 (0.04)	-0.10 (0.06)
CMLP	0.38 (0.11)	-0.46 (0.09)	-0.05 (0.10)	0.31 (0.11)	0.58 (0.07)	-0.03 (0.06)	-0.23 (0.07)	0.17 (0.09)
YIELD	0.11 (0.17)	0.02 (0.13)	0.02 (0.15)	0.34 (0.15)	0.05 (0.14)	0.14 (0.04)	0.08 (0.05)	0.27 (0.05)
BF	-0.18 (0.14)	0.38 (0.11)	0.26 (0.12)	-0.47 (0.11)	-0.67 (0.08)	0.10 (0.16)	0.33 (0.06)	0.09 (0.06)
LD	-0.18 (0.14)	-0.23 (0.11)	0.26 (0.11)	0.22 (0.13)	0.21 (0.10)	0.50 (0.13)	0.05 (0.12)	0.49 (0.07)

Table 4. Landrace Heritabilities (diagonal, bold) and genetic (below diagonal) and residual (above diagonal) correlations (with SE). Primal cuts, lean meat percentage carcass (CLMP) and carcass yield in (%), backfat and loin depth in millimeters

Trait	Shoulder	Belly	Loin	Ham	CLMP	YIELD	BF	LD
Shoulder	0.15 (0.05)	-0.39 (0.05)	-0.16 (0.04)	-0.41 (0.04)	0.06 (0.07)	0.34 (0.05)	-0.08 (0.07)	-0.12 (0.06)
Belly	-0.32 (0.15)	0.51 (0.07)	-0.07 (0.06)	-0.43 (0.05)	-0.15 (0.10)	-0.40 (0.07)	0.25 (0.09)	0.07 (0.08)
Loin	-0.29 (0.19)	-0.35 (0.14)	0.21 (0.06)	-0.46 (0.05)	0.05 (0.07)	-0.26 (0.05)	0.15 (0.07)	0.23 (0.06)
Ham	-0.02 (0.19)	-0.87 (0.05)	0.12 (0.17)	0.32 (0.07)	0.04 (0.08)	0.22 (0.06)	-0.23 (0.07)	-0.10 (0.07)
CMLP	0.30 (0.16)	-0.42 (0.10)	0.05 (0.15)	0.32 (0.13)	0.50 (0.07)	-0.07 (0.09)	-0.10 (0.11)	0.05 (0.10)
YIELD	0.14 (0.19)	-0.25 (0.13)	-0.05 (0.17)	0.26 (0.15)	0.43 (0.12)	0.27 (0.06)	0.21 (0.07)	0.25 (0.05)
BF	-0.35 (0.16)	0.66 (0.08)	0.04 (0.16)	-0.57 (0.11)	-0.73 (0.07)	-0.30 (0.14)	0.41 (0.07)	0.35 (0.10)
LD	-0.21 (0.19)	-0.03 (0.14)	0.40 (0.15)	-0.02 (0.15)	0.61 (0.11)	0.61 (0.11)	-0.27 (0.14)	0.33 (0.07)

Table 5. Duroc Heritabilities (diagonal, bold) and genetic (below diagonal) and residual (above diagonal) correlations (with SE). Primal cut lean meat composition (%), CLMP and carcass yield in (%), backfat and loin depth in millimeters

Trait	Shoulder LMP	Belly LMP	Loin LMP	Ham LMP	CLMP	YIELD	BF	LD
Shoulder LMP	0.53 (0.05)	0.74 (0.04)	0.66 (0.04)	0.66 (0.04)	0.91 (0.01)	-0.09 (0.01)	-0.23 (0.07)	0.09 (0.08)
Belly LMP	0.89 (0.02)	0.55 (0.07)	0.79 (0.03)	0.67 (0.04)	0.91 (0.01)	-0.12 (0.06)	-0.20 (0.07)	0.08 (0.09)
Loin LMP	0.90 (0.02)	0.90 (0.02)	0.53 (0.07)	0.55 (0.05)	0.82 (0.03)	0.08 (0.06)	-0.27 (0.07)	0.29 (0.08)
Ham LMP	0.91 (0.02)	0.89 (0.02)	0.91 (0.02)	0.51 (0.07)	0.82 (0.02)	-0.07 (0.06)	-0.04 (0.07)	0.24 (0.08)
CMLP	0.97 (0.01)	0.96 (0.01)	0.95 (0.01)	0.96 (0.01)	0.58 (0.07)	-0.03 (0.06)	-0.23 (0.07)	0.17 (0.09)
YIELD	0.03 (0.13)	-0.03 (0.13)	0.19 (0.13)	0.05 (0.13)	0.06 (0.14)	0.14 (0.04)	0.08 (0.05)	0.27 (0.05)
BF	-0.63 (0.08)	-0.70 (0.07)	-0.62 (0.08)	-0.57 (0.09)	-0.66 (0.08)	0.11 (0.16)	0.33 (0.06)	0.07 (0.07)
LD	0.13 (0.10)	0.18 (0.10)	0.32 (0.09)	0.17 (0.10)	0.19 (0.10)	0.48 (0.15)	0.05 (0.12)	0.49 (0.07)

Table 6. Landrace Heritabilities (diagonal, bold) and genetic (below diagonal) and residual (above diagonal) correlations (with SE). Primal cut lean meat composition (%), CLMP and carcass yield in (%), backfat and loin depth in millimeters

Trait	Shoulder LMP	Belly LMP	Loin LMP	Ham LMP	CLMP	YIELD	BF	LD
Shoulder LMP	0.38 (0.07)	0.68 (0.04)	0.60 (0.05)	0.60 (0.04)	0.88 (0.02)	-0.06 (0.07)	-0.09 (0.08)	-0.04 (0.08)
Belly LMP	0.89 (0.03)	0.54 (0.07)	0.81 (0.03)	0.67 (0.04)	0.91 (0.02)	-0.04 (0.08)	-0.17 (0.10)	-0.04 (0.10)
Loin LMP	0.89 (0.04)	0.91 (0.02)	0.58 (0.08)	0.59 (0.05)	0.82 (0.03)	0.05 (0.09)	-0.19 (0.10)	0.13 (0.10)
Ham LMP	0.89 (0.04)	0.83 (0.04)	0.84 (0.04)	0.41 (0.07)	0.83 (0.02)	-0.15 (0.07)	-0.07 (0.09)	0.10 (0.08)
CMLP	0.97 (0.01)	0.96 (0.01)	0.94 (0.02)	0.93 (0.02)	0.58 (0.07)	-0.05 (0.08)	-0.10 (0.10)	0.02 (0.09)
YIELD	0.36 (0.13)	0.40 (0.11)	0.47 (0.11)	0.40 (0.13)	0.42 (0.12)	0.14 (0.04)	0.24 (0.07)	0.18 (0.08)
BF	-0.63 (0.09)	-0.75 (0.07)	-0.71 (0.07)	-0.56 (0.10)	-0.72 (0.07)	-0.29 (0.14)	0.33 (0.06)	0.31 (0.09)
LD	0.59 (0.12)	0.55 (0.11)	0.71 (0.09)	0.69 (0.10)	0.64 (0.10)	0.59 (0.12)	-0.25 (0.14)	0.49 (0.07)

depth and loin was positively correlated in both breeds, but there was a negative correlation between loin depth and shoulder. Belly and ham did not correlate to loin depth in Landrace, but Duroc showed weak negative (belly) and positive (ham) correlations. Backfat showed a positive correlation with belly, but a negative correlation with shoulder and ham. For Duroc, there was a positive correlation between backfat and loin but this was not seen in Landrace (Table 3 and Table 4).

The lean meat percentage within each primal cut were strongly correlated to each other (0.83 to 0.91) and even more so to CLMP (Table 5 and Table 6). Carcass

yield showed intermediate genetic correlations to LMP within all primal cuts for Landrace, but the same correlations were weak for Duroc. Loin depth showed intermediate-strong genetic correlations to the LMP within each primal for Landrace, but again, weaker correlations for Duroc. Backfat was negatively correlated to LMP in each primal cut in both breeds (Table 3 through 6).

DISCUSSION

The objective of the study was to identify and measure genetic parameters of primal cuts and carcass com-

position measured in vivo by CT, to implement these traits in a commercial breeding program for pigs. The focus of this study is the new phenotypes obtained from atlas segmentation, and results for the other traits will only be discussed when relevant for the new atlas based traits. The results show that the traits measured in vivo using CT and atlas segmentation are intermediate to highly heritable.

To the best of our knowledge, this is the first attempt to apply the use of atlas segmentation based on CT scans of boars in vivo in a commercial genetic program. In this study, in vivo primal cuts from atlas segmentation are used for genetic parameter calculations for the first time. The primal cuts have different market values and their value varies also considerably between markets (European vs. Asian and North American). The relative value change; i.e., belly becoming increasingly more valuable relative to loin and ham, particularly in the US markets. Primal cuts from in vivo measurements implemented in the breeding goal could more efficiently breed for or sort lines with the most profitable carcasses to different markets. In vivo measurements mean that selection candidates will have own phenotype which is more efficient than post mortem measurements where data is available only to relatives of the AI boars.

Moreover, the total phenotypic variance is for the calculation of heritability decomposed into 2 parts; genetic and environmental variation. Variation caused by erroneous segmentation, atlas or manual, will add to the environmental part. Consequently, precise segmentation is important to improve heritability estimates. Correlation within the residuals like side effects (left/right) are not regarded in this study as a source of error since we use both sides or whole in vivo carcasses, not half carcasses like in other post mortem studies. As reported by Nissen et al. (2006) substantial errors might also occur by manual segmentation. Recently, Olsen et al. (2017) points out that the precision of CLMP obtained by CT has the potential of outperforming the precision obtained by manual dissection. Under the assumption of flawless atlas segmentation, these arguments should also be valid for primal cuts.

Furthermore, when calculating the weight of each voxel as a product of its volume and density, a formula by Campbell et al. (2003) was used. This formula was tested for sheep, and there is no such formula for specifically for pigs. There might be unexplained variation, especially in pig fat tissue, due to variable lipid content, saturation and water in fat. A validation of the equation might be needed to improve the accuracy. However, the authors made an approximation that this formula was valid also for pigs, since the variation is picked up by the variation in HU. However, further studies is recommended to validate the relationship

between HU and density for a wide range of species, in particular farmed animals, and HU levels.

The results of the present study provide indirect support for the validity of atlas segmentation. If the atlas segmentation offered no information, the heritability estimates should be results of random noise. Heritability for ham was 0.27 for Duroc and 0.32 for Landrace which is a bit lower than reported by other studies based on manual segmentation Newcom et al. (2002) and van Wijk et al. (2005; $h^2 = 0.57$ and 0.40 , respectively). Further, Newcom et al. (2002) and van Wijk et al. (2005) found heritability of 0.29 and 0.51 for loin, and our results are in between for Landrace ($h^2 = 0.34$) and a bit smaller for Duroc ($h^2 = 0.21$). For belly, Newcom et al. (2002) reported heritability of 0.51 which is same as we found for Landrace, but again the heritability for Duroc was a bit smaller ($h^2 = 0.39$). With respect to the composition of cuts, Hermes and O'Shea (2005) found a heritability of 0.34 on predicted fat percentage of the belly by image analysis of a belly image of the anterior side (Hermes and O'Shea, 2005; Hermes, 2008). This is slightly lower than the heritability of Belly LMP found in this paper (0.55), which might be related to the accuracy of methods, since Hermes (2008) stated that it might difficult to take quality images of bellies from lean carcasses. As we get heritability results in line with, or slightly inferior to, heritability results obtained by manual segmentation, the precision of atlas segmentation are indicated to be in line with, or at least close to the precision of manual segmentation. The only comparison with manual primal cuts from other studies have been possible so far, however, in another study results will be validated by comparing results from in vivo segmented boars with results from manual segmentation.

In this paper, it was decided to use primal cuts as the relative proportions (%) of carcass weight, to avoid confounding between carcass weight and primal cut yields. This contrasts with previous studies on traits related to primal cuts, where the focus has been on primal cut weights, with carcass weight included as a covariate in the models. The authors find it more relevant to use proportions directly as a response in the models, as emphasis on the proportion of valuable primal cuts in breeding goals will facilitate more valuable carcasses and not just bigger carcasses (Moore et al., 2017).

The results for both breeds strongly indicate that selection for increased LMP will decrease the percent belly, which is natural as the belly is the fattest primal cut, and per definition the pig gets leaner when LMP increase. The loin is minimally affected by selection for LMP, and the percent of shoulder and ham will increase when selecting for increased LMP.

Nevertheless, a large CLMP means a carcass with high muscle to fat ratio. Belly is a primal cut with large fat content, and the negative correlation between belly and CLMP is therefore not surprising. Backfat and CLMP were negatively correlated which is natural as the backfat measure is expected to be smaller in pigs with high CLMP (lean pigs). The positive correlation of backfat with the belly is therefore expected. The positive correlation of loin and backfat in Duroc is a bit unexpected, and is not seen in Landrace. Correlations for backfat with shoulder and ham showed the same pattern as CLMP indicating that pigs with large backfat and/or large CLMP (lean pigs) have greater proportions of shoulder and ham compared to fatter pigs. Carcass yield was the least heritable of the studied traits, and show that environmental factors (e.g., measuring technique, trait definition) plays a major role for this trait. Ham was the trait with the strongest correlation to carcass yield in both breeds suggesting that selection for increased yield primarily leads to increased proportion of ham. The negative correlation of carcass yield and belly reported for Landrace suggests that increased yield will lead to a smaller proportion of belly in Landrace. The correlations for CLMP and carcass yield with the primal cuts were generally intermediate to small, and this indicates that these 2 measures does not accurately capture the variation in primal cut composition. Loin depth was measured at one point of the loin, and the positive genetic correlation to loin as a primal cut is therefore expected. The genetic and residual correlations are however only intermediate (0.21 to 0.40) showing that loin depth may not be an optimal indicator of the proportion loin in a carcass. Loin depth is an important predictor of carcass value and composition in the industry today, and the results in this study show the need for a revision of the use of loin depth to predict carcass value and composition. The carcass lean meat percentage seems to be a good indicator of lean meat percentage within each primal as the genetic and residual correlations were very strong. The genetic correlations between the primal cuts with respect to LMP were around 0.9 which is very strong, but it will still be possible to change the lean content more in some parts than in others. Some primal cuts like shoulder and belly might also be used as predictors of carcass lean meat if a whole carcass is difficult to obtain or to reduce costs of dissection.

On the other hand, the percentages of primal cuts change as the animals mature, i.e., the weights of the cuts have different allometric growths. Less mature animal will consequently have more ham and leaner hams, and lower percent and leaner bellies. The genetic correlations may to some extent reflect variation in the degree of maturity of pigs within the genetic population. However, since we do not have performed this study over the entire

growth period of the pig, only using a fixed target weight of 120 kg, the effect of maturity remains elusive.

Implications

Computed Tomography (CT) makes it possible to measure in vivo body or carcass composition. This will aid the selection response by measuring on the candidates themselves instead of using relatives. Primal cut proportion and composition measured in vivo by computed tomography and atlas segmentation show heritable variation comparable to previous post mortem studies. The detailed information on carcass composition can be used to improve carcass value through selection using in vivo information. It can also be used to sort i.e., boars used for artificial insemination, based on different markets worldwide. Future studies should include the value of cuts in relation to different markets and regions, and in vivo primal cut yields in relation to growth, feed intake and meat quality. Hopefully, the PigAtlas will give us new insight on the relationship between in vivo body composition and other traits in the breeding goal for pigs in the future.

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