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Genetic analyses of novel traits derived from CT scanning for implementation in terminal sire sheep breeding programmes

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Abstract

This study used archived CT scanning images from Texel (n = 3534), Suffolk (n = 2357) and Charollais (n = 2013) ram lambs, scanned between 1997 and 2016 as part of the national UK terminal sire breeding programmes, to measure new, previously unexploited, CT phenotypes for product quality. The new CT phenotypes included 12 traits relating to eye muscle dimensions, spine region lengths and vertebrae numbers, and intramuscular fat (IMF), as a predictor of meat quality. The aim was to estimate genetic parameters for these new traits, confirm genetic parameters for existing growth and carcass traits, and investigate relationships amongst traits, when adjusted for either age or live weight. The new CT traits were generally moderately heritable (h^2 ranging from 0.23-0.54 when adjusted for age) within each breed.

Notable exceptions were: vertebrae counts, which had lower heritabilities (0.11-0.18) in the Suffolk and Texel; lumbar region spine length and vertebrae count in the Charollais, (0.04); and CT-predicted IMF in the Charollais (0.88). Generally, genetic variation decreased, but heritabilities increased, when traits were adjusted for live-weight rather than age, ranging from h^2 0.21-0.74 for the new CT traits, except for the Charollias lumbar spine length (0.01) and CT-predicted IMF (0.87). Within-breed genetic correlations between new CT traits and current CT traits (carcass fat and muscle weights, muscularity), ultrasound tissue depths, or scan weight (at ~21 weeks), were low to moderate. High genetic correlations were observed between ultrasound and CT measured eye muscle depth (r = 0.77-0.85). Genetic correlations between CT-predicted IMF and total carcass fat estimates, however, were unfavourable (large and positive; r = 0.66-0.96), especially in the Suffolk and Charollais, suggesting little scope for divergent selection between fat depots. Some unfavourable genetic correlations of spine length with CT muscle weight or eye muscle depth were also estimated, after live weight adjustment. Possibilities therefore exist for genetic selection on additional product quality traits that can be routinely measured by CT scanning. Adjusting new and existing carcass traits for live weight, rather than age, should increase heritabilities and provide a more relevant industry end-point. These findings could contribute to the production of a new selection index, with optimal weightings on growth, carcass and product quality traits, for a sustainable UK terminal sire sheep breeding programme.

Keywords:

Computer tomography; Carcass; Genetic parameters; Ultrasound; Intramuscular fat; Spine

1. Introduction

Computer tomography (CT) scanning, a non-invasive technique that allows measurements to be collected in vivo, has been incorporated into terminal sire sheep breeding programmes in the UK for the past few decades. This is most effective as part of a two-stage selection strategy, where all lambs are scanned on-farm using ultrasound, to measure subcutaneous fat and muscle depths, then the top 15 - 20% of ram lambs, based on growth and ultrasound data, are sent for CT scanning (Macfarlane and Simm, 2008). This process has been shown to be economically beneficial within terminal sire breeding programmes for improving carcass composition (Jopson et al., 1997; Bunger et al., 2014). Indeed, when using age adjusted data from ram breeding flocks across the UK, it has been shown that response to selection is 7% (CT–measured muscle weight), 10% (CT-measured fat weight) and 20% (CT measured muscularity) higher when CT scanning is used together with ultrasound scanning compared to ultrasound alone (Moore et al., 2011).

The ability to measure other valuable traits from the resulting CT derived images would potentially add further value to the CT scanning process. Variation in spine related traits, in both pure and crossbred sheep, has been observed in images routinely collected during CT scanning (Donaldson, 2015). It has also been found that information on tissue densities collected during the CT scanning process provide good in vivo estimates of intramuscular fat (IMF) in the loin of Texel sheep (Clelland et al., 2015a). The prediction equations developed in that work were shown to be transferable across different breeds and crosses, providing an objective proxy trait to predict meat eating quality in live animals (Clelland, 2015). To date, preliminary genetic parameters for these new CT traits have only been estimated in one breed, the Texel, using a relatively small number of records which were available at that time. Moderate heritabilities were estimated for spine lengths and IMF, but low heritabilities for vertebrae number in the different spinal regions (Lambe et al., 2015; Clelland et al., 2015b).

Genetic correlations with current breeding goal traits suggested that these new CT traits may have potential to be incorporated into breeding programmes without having detrimental effects on current breeding objectives. However, further analyses were suggested across the wider Texel population, and other terminal sire breeds, before recommendations could be made as to how to incorporate these traits into breeding programmes (Lambe et al., 2015; Clelland et al., 2015b).

In addition to the introduction of new CT traits, it would also be worthy to assess the difference between carcass traits (measured by either ultrasound or CT) that have been adjusted to a fixed live weight, compared to those adjusted to a fixed age. These carcass traits have previously been adjusted for age in UK terminal sire breeding programmes. However, bearing in mind that lambs in the UK tend to be killed at a fixed weight (and level of fat cover), rather than age, by fitting live weight as a covariate the breeding goals could become more commercially focused. This would potentially lead to higher rates of genetic gain in carcass composition at a fixed carcass weight, as observed in previous studies of both ultrasound and CT traits (Kvame and Vangen, 2007; Roden 2016).

The main objectives of this study were therefore to a) investigate new, previously unexploited, CT phenotypes in Charollais, Suffolk and Texel sheep and estimate their genetic parameters; b) assess the difference between the genetic parameters associated with carcass composition once adjusted for age or live weight, and c) consider the potential impact of including these traits alongside current breeding goal traits in a genetic selection programme.

2. Materials and methods

2.1. Animals and Data Collection

All procedures involving animals were approved by an animal ethics committee at Scotland's Rural College (SRUC) and were performed under the United Kingdom Home Office licence following the regulations of the Animals Act 1986.

The data available for the three terminal sire breeds used in this study (Texel, Suffolk and Charollais) were from entire ram lambs, reared in ram breeding flocks and performance recorded as part of the Signet Sheepbreeder scheme in the UK (www.signetdata.com). The data used were from lambs CT scanned between 1997 and 2016 (Texel n = 3534 lambs, from 102 flocks; Suffolk n = 2357 lambs, from 75 flocks) and between 2003 and 2016 (Charollais n = 2013 lambs, from 56 flocks).

Additional data, relating to existing growth and carcass traits recorded on both male and female lambs between 1997 and 2016 (between 2007 and 2016 for Texels), were also available (Texel n = 89948 lambs; Suffolk n = 125506 lambs; Charollais n = 61747 lambs). These traits were recorded at approximately 21 weeks of age as part of the normal recording process all flocks within each recording scheme follow and included: live weight at ultrasound scanning (USWT), ultrasound fat depth (UFD) and ultrasound muscle depth (UMD) depths, both of which were measured at the third lumbar vertebra of the lambs. Summaries of all data, for each breed, are given in Table 1.

2.2. CT measurements and image analysis

Lambs were scanned using one of 2 CT scanners; a Siemans Somatom Esprit single slice fixed scanner (Scanner A) or a mobile GE LightSpeed 16 slice scanner (Scanner B). During the CT scanning process, all lambs were lightly sedated (Rompun^{TM}) at a dose of 0.1-0.2 mg xylazine hydrochloride/kg body weight and were secured on their backs in a cradle before being scanned. The process is described in more detail by Jones *et al.* (2002) and Bunger *et al.* (2011). Two-dimensional (2D) cross-sectional images were taken at three defined anatomical landmarks,

through the top of the leg at the ischium bone (ISC), the loin at the fifth lumbar vertebra (LV5) and through the chest at the eighth thoracic vertebra (TV8); all identified using a longitudal full body scan (topogram). Image analyses were then performed to separate carcass from non-carcass tissues, based on the method described by Glasbey and Young (2002). The density of each pixel in the carcass portion of each reference scan image was measured in Hounsfield units (HU). Each pixel was then allocated to fat, muscle or bone, according to different density thresholds, using Sheep Tomogram Analysis Routines (STAR) software (Mann et al., 2003). By using this method, areas and average densities of carcass fat, muscle and bone were calculated for each reference scan. Visual assessment of the longitudinal topogram images of the body allowed vertebrae to be identified and counted and the lengths of the spinal regions to be measured.

The CT measurements collected included total carcass fat weight (CTFWT; kg) and muscle weight (CTMWT; kg), which were estimated using previously-derived breed-specific prediction equations, based on tissue areas and live weight (Lambe et al. 2003) and gigot muscularity (CTMusc; ratio), defined as a ratio of the gigot muscle depth to width in the cross-sectional ISC scan (Jones et al. 2002; Lambe et al, 2007). These traits are existing CT traits routinely measured to produce commercially available estimated breeding values (EBVs).

Additional CT traits included eye muscle area (CTEMA; cm^2) and eye muscle depth (CTEMD; mm), based on measurements from the LV5 scan, which were collected as described by Jones et al. (2002) and Lambe et al. (2007). Intramuscular fat content in the *M. longissimus lumborum* (CTIMF; %) was estimated using prediction equations developed by Clelland et al. (2015), based on average fat and muscle densities, and their standard deviations, across the three reference scans (ISC, LV5 and TV8). Because there can be a scanner effect on the density

values estimated within soft tissues (Bunger et al., 2010) two different equations (one for each scanner) were used to predict CTIMF (Clelland et al., 2015b).

The spine traits recorded were the lengths of the thoracic (SLTh; mm) and lumbar (SLLum; mm) regions and the overall thoracolumbar region (SLTL; mm), calculated as the sum of the SLTh + SLLum. Similarly, for the number of vertebrae in each region, the counts of thoracic vertebrae (VNTh), lumber vertebrae (VNLum) and the overall thoracolumbar vertebrae (VNTL; calculated as the sum of the VNTh + VNLum) were taken (Donaldson et al., 2013). More detailed descriptions of the image analyses involved in assessing the spine characteristics and predicted intramuscular fat percentage are outlined by Donaldson et al. (2013) and Clelland et al. (2015a) respectively.

2.3. Genetic parameter analysis

Genetic analyses were run within breed. The three pedigree files used in the analyses contained sire and dam information for a total of 164,969 Texels (14888 sires and 73170 dams), 196,282 Suffolks (12825 sires and 79584 dams) and 137,774 Charollais (5200 sires and 35702 dams) animals. The RelaX2 programme (Stranden and Vuori, 2006) was used to prune the larger Texel and Suffolk pedigrees to retain only the information necessary for estimating variance components. Variance components were estimated using within-breed univariate analyses in ASReml 3.0 (Gilmour et al., 2009), using the following model:

$$y = Xb + Za + e$$

where y is the vector of phenotypic observations; b is the vector of fixed effects, consisting of the litter size reared, dam age, contemporary group and either age or liveweight at CT scanning as a covariate; a is the vector of random animal effects; e is the vector of random residual effects, and X and Z are incidence matrices relating observations to their respective effects.

Litter size reared was the number of lambs reared together by the same ewe (3 levels; 1 to 3) and dam age was the age of the dam at lambing in years (5 levels; 1 to $\geq$5). The contemporary group fitted consisted of the flock, year of birth, season of birth, management group and sex of the animal. CT scan covariate was either age or live weight at CT scanning. Age at CT scanning was defined as the number of days between birth and CT scanning. Summary statistics for age and live weight at CT scanning are given in Table 1. A quadratic term associated with lamb age or live weight, was also tested in the fixed effects model for key traits. The addition of the quadratic term did not improve the accuracy of the predictions, therefore the quadratic term was dropped from the final models and the lambs were assumed to be in the linear growth phase. Each fixed effect was significant for the majority of traits and to remain consistent, the same models were fitted across the different traits. The only exceptions to this were the inclusion of dam breed at weaning in the Texel models (2 levels; Texel or any another breed) and in the vertebrae count traits for each breed, where litter size at birth was fitted (4 levels; 1 to 4), instead of litter size reared. There was also no covariate fitted for the vertebrae count traits, as these were determined during pre-natal development, so should not be affected by post-natal growth. Spearman's Rank and Pearson correlations were estimated, for each breed separately, between all breeding values produced from the live weight and age adjusted analyses, to determine what effect the change of covariate had on breeding values.

Genetic and phenotypic correlations were then estimated between each CT trait and existing growth and carcass traits, recorded at ultrasound scanning (USWT, UFD and UMD), using within-breed bivariate models in ASReml 3.0 (Gilmour et al., 2009). The animal model fitted for the CT traits was the same as described above. The animal model used for USWT, UFD and UMD included a direct genetic random effect and the following fixed effects model:

$$y = Xb + Za + e$$

where y is the vector of phenotypic observations; b is the vector of fixed effects, consisting of the litter size reared, dam age, contemporary group, age or liveweight at ultrasound scanning as a covariate and an interaction term between the covariate and contemporary group; a is the vector of random animal effects; e is the vector of random residual effects, and X and Z are incidence matrices relating observations to their respective effects. The effects fitted were the same as those described previously for the CT traits. Ultrasound scan covariate was either age or live weight at ultrasound scanning. Age was defined as the number of days between birth and ultrasound scanning. Summary statistics for age and live weight at ultrasound scanning are given in Table 1. Each fixed effect was significant for the majority of traits and to remain consistent, the same models were fitted across the different ultrasound traits. The only exception to this was the addition of dam breed at weaning in the Texel US trait models.

The covariance structure for the bivariate analyses was

$$Var\begin{bmatrix} a_1 \\ a_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{g1}^2 & \mathbf{A}\sigma_{g12} & 0 & 0 \\ & \mathbf{A}\sigma_{g2}^2 & 0 & 0 \\ & & \mathbf{I}\sigma_{e1}^2 & \mathbf{I}\sigma_{e12} \\ symm & & & \mathbf{I}\sigma_{e2}^2 \end{bmatrix}$$

where indices 1 and 2 indicate the 2 traits in each analyses. The first trait was one of the new CT traits and the second trait was one of the existing ultrasound or CT breeding goal traits, **A** is the additive genetic relationship matrix, **I** are identity matrices, and σ_g^2 and σ_e^2 are the genetic and residual variances, respectively. The differences between the correlations estimated between the same traits, when adjusted for age and for live weight, were compared using a *t*-test to test for significance.

3. Results

3.1. Data summaries

Summaries of the data analysed, and the relevant covariates fitted in the models, are given in Table 1.

The frequency distributions for the total number of thoracolumbar vertebrae in each breed are given in Figure 1. The overall counts ranged from 18 to 21 for all breeds, with a very low percentage of extreme values (18 and 21) observed in each breed (all below 1.4%). The Suffolk and Charollais lambs had a similar distribution, with the highest percentage of lambs having a total of 20 vertebrae (78.33% and 74.39% for Suffolk and Charollais respectively). The distribution for the Texel lambs differed, with 65.34% of lambs having a total of 19 vertebrae and only 33.12% having 20 vertebrae.

3.2. Genetic parameters

The univariate heritabilities for the CT traits estimated using animal models, either adjusted for lamb age at CT scanning or lamb live weight at CT scanning, are given in Tables 2 and 3, respectively. In the Texel, all heritabilities (both age and live weight adjusted) were low to moderate, in the range 0.11-0.43. Adjusting for live weight, rather than age, reduced the genetic variation and phenotypic variation in most traits, but resulted in increased heritability estimates for CTFWT, CTMWT and CTIMF. Heritabilities for the muscularity traits (CTMusc, CTEMD, CTEMA) remained similar, whereas spine length heritabilities were lower after adjusting for live weight. The Suffolk heritability estimates were similar to the Texel results for age-adjusted CT traits. However, following the adjustment of the Suffolk data for live weight, the genetic and phenotypic variation in CTFWT, CTMWT and SLTL was reduced, resulting in markedly higher heritability estimates associated with these traits. The only Suffolk heritability estimate that went down following the live weight adjustment was for CTMusc. The Charollais heritability estimates tended to be higher than those estimated in the other breeds for most CT traits. Fat traits in particular (CTFWT, CTIMF) had high heritabilities (>0.5). As with the other breeds, adjusting for live weight increased the heritabilities for

CTFWT and CTMWT, as well as for CTMusc and CTEMA, with most other traits showing similar heritabilities after age or live weight adjustment. There was very little genetic variation observed for SLLum in the Charollais lambs resulting in very low heritability estimates, when adjusted for either age or live weight. The lowest heritability estimates (<0.12), for both the Texel and Suffolk breeds, were associated with the vertebrae number traits, however, of these traits, only VNLum in the Charollais was low. Moderate heritability estimates were observed for all ultrasound traits, across the three breeds. The estimates associated with UFD and UMD increased slightly when adjusted for live weight.

3.3. Breeding value correlations

The correlations estimated between the breeding values calculated in the univariate analyses adjusted for age and live weight, for each trait, are given in Table 4. The Spearman's Rank and Pearson correlations ranged from 0.33-0.98 and 0.39-0.99 respectively. The lowest correlations were generally associated with CTFWT (0.37-0.55) and CTMWT (0.33-0.76).

3.4. Within-breed correlations amongst growth, carcass and CT traits

Genetic relationships, across all three breeds, between USWT and both CTMWT and CTFWT were moderate to high when all traits were adjusted for age (0.63-0.82) and when the CT traits were adjusted for live weight (0.46-0.67) (Tables 5, 6 and 7). Moderate to high positive genetic correlations were also observed between USWT and most spine length traits, when age adjusted. The strength of these correlations fell when adjusted for live weight, with only those associated with SLTh and SLTL, in the Texel and Charollais animals, remaining significantly different to zero ($P<0.05$; Tables 5, 6 and 7). The relationships observed between UMD and both CTEMA and CTEMD, across all three breeds, were moderate to highly positive and did not differ significantly between the age (0.66-0.85) and live weight (0.67-0.84) adjusted analyses, with the highest correlations estimated with CTEMD. Most genetic correlations between UMD and spine length or vertebrae number traits were negative and often associated with high standard errors. Few correlations with UMD changed significantly ($P<0.05$) when adjusted for either age or live weight, with the exception of SLTh and SLTL in the Texels, which became stronger (more negative) when live weight adjusted. Moderate to highly positive genetic correlations were estimated between UFD and both CTFWT and CTIMF. The age adjusted genetic correlations between UFD and CTFWT ranged from 0.69-0.79, across the three breeds. When adjusted for live weight, the genetic correlations estimated for this association in both the Suffolk and Charollais were reduced, with the largest drop in the Suffolk (0.72 for age adjusted and 0.57 for live weight adjusted). The moderate to highly positive genetic correlations between UFD and CTIMF were not significantly different ($P<0.05$) between age or live weight adjusted estimates, with the highest correlations found in the Texels.

The genetic correlations estimated between CTFWT and CTMWT for the Texel and Suffolk in the age adjusted analyses were moderate (0.36-0.39). When adjusted for live weight, the Texel

correlation fell, although not significantly, whereas the Suffolk correlation increased in strength, from 0.36 to 0.59. The age adjusted correlation estimated for the Charollais between these two CT tissue weight traits was low and positive, but when adjusted for live weight, the correlation became highly negative (-0.82). The correlations estimated between CTMusc and CTFWT or CTMWT did not change significantly ($P<0.05$) between the age and live weight adjusted analyses within any of the breeds.

4. Discussion

4.1. New traits measured using computed tomography (CT) scanning

The results from this study have confirmed that the majority of new CT traits investigated displayed genetic variation within each breed and that the implementation of routinely measuring these traits, in future terminal sire breeding programmes, would be of benefit. Although previous studies have already assessed these traits using preliminary datasets available for Texel lambs (Clelland et al., 2015; Donaldson et al., 2013; Lambe et al., 2015), this is the first time that the genetic component of many of them have been investigated in Suffolk and Charollais lambs. It is important to note that the process of collecting data for these new traits does not involve any additional scanning, as the measurements can be made from existing scan images collected to assess carcass composition. There is currently some additional time taken for image analysis to derive phenotypes for the new traits, but now that these traits look worthwhile to continue recording, it is anticipated that the image analysis process will become more automated in the future.

4.2. Genetic parameters

When considering genetic parameters for the new CT traits, adjusted for age (as has been the norm in UK genetic evaluations pre-2018) and for live weight, most traits were moderately

heritable in each breed. Notable exceptions to this included CTIMF in the Charollais, which showed a surprisingly high heritability (0.88 and 0.87 when adjusted for age and live-weight, respectively) and SLLum, also in the Charollais, which had a very low heritability estimates (0.04 and 0.01, respectively).

Previous heritability estimates for IMF in lamb have been moderate (ranging from ~0.3 to 0.5) when estimated by CT on smaller data sets from UK Texel lambs (Clelland et al., 2015; Lambe et al., 2015) and when measured using laboratory tests, across different lamb breeds and countries (Karamichou et al., 2006; Lorentzen and Vangen, 2012; Mortimer et al., 2014). Both the Texel and Suffolk estimates observed in this study fell within, or slightly below, this range (0.21-0.40) when adjusted for age or live weight, suggesting general agreement with previous literature. The genetic parameters estimated for CTIMF, in all three breeds, suggest that genetic improvements could be made in the future by selecting upon this trait, leading to improvements in product quality due to the fact IMF is a good, *in-vivo*, predictor of meat-eating quality (Clelland et al., 2014; Lambe et al., 2017). The heritability estimates observed for the eye muscle traits, CTEMA and CTEMD were also moderate, and very similar to the heritability estimates for UMD in the Texel and Suffolk, although in the Charollais, the heritability estimates for the CT eye muscle traits (ranging from 0.46 to 0.57) were higher than for UMD (0.30-0.37).

With the exception of SLLum in the Charollais, which showed little genetic variation but was in line with a similar observation by Maximini et al. (2012), the remaining spine traits, across all breeds, were moderately heritable. In pigs, thoracolumbar vertebrae number has been reported to be highly heritable (e.g. $h^2 = 0.62$, Borchers et al., 2004). However, there is limited published information on the genetic control of variation in spine traits in sheep. Previous estimates observed by Lambe et al. (2015), using a smaller data set from UK Texel lambs and

a model adjusting for live weight, rather than age, estimated heritabilities for SLThor and SLTotal only slightly higher than those estimated in the current study. Maximini et al. (2012) observed a heritability of 0.24 for SLThor in Austrian meat sheep, when adjusted for live weight, similar to the Texel estimate observed in the current study. The vertebrae counts had lower heritabilities than the length traits overall, similar to those observed by Lambe et al. (2015), although heritability estimates for VNThor and VNTotal in the Charollais were moderate in magnitude. Similar to the spine length results, VNLum also showed little genetic variation in the Charollais. These results indicate that genetic selection to change traits associated with the spine may be more successful by selecting upon spine region lengths rather than vertebrae numbers. However, change could still be achieved in terms of vertebrae numbers, albeit at a slower rate due to the lower hertiabilties estimated, particularly for the Texel and Suffolk lambs.

In general, higher heritabilities for CT traits were estimated for the Charollais than the Suffolk and Texel, except for the lumbar spine traits, largely due to higher genetic variances. Heritabilities for ultrasound traits, however, were similar across all three breeds. Heritabilities estimated for CTIMF were particularly high in the Charollais (0.88 and 0.87, with age and live weight adjustments, respectively). The reasons for these breed differences in genetic control of CT traits are unclear. Differences in the frequency of major genes influencing muscle or fat distribution may be a contributing factor. In particular, the c.*1232G>A mutation in the myostatin gene on chromosome 2 is associated with increased muscle and decreased fat at a fixed carcass weight (Johnson et al., 2009). Previous studies have found this allele to be approaching fixation in the UK Texel breed, but segregating at intermediate frequencies in UK Charollais sheep (Hadjipavlou et al., 2008), whilst there is no evidence of this mutation in UK Suffolk sheep. It cannot be ruled out that differences may also be related to the selection process of ram lambs for CT scanning, which could alter genetic or phenotypic variation within the

348 population of lambs CT scanned. Although it is recommended that all lambs within the breeding
349 programme are ultrasound scanned and the top 15-20% of ram lambs then go forward for CT
350 scanning (Macfarlane and Simm, 2008), in reality, not all breeders CT scan their top ram lambs.
351 Therefore, there may be differences in the range of genetic merit in CT scanned lambs.
352 Differences may also exist in the degree of genetic connectedness arising between flocks that
353 CT scan.

354 The heritabilities observed for the current traits relating to growth and ultrasound muscle and
355 fat measurements, were similar across the three breeds, ranging from 0.29 to 0.34 when adjusted
356 for age, and from 0.36 to 0.39 when adjusted for live weight. Fitzmaurice et al. (2020) looked
357 at the same three breeds in the Republic of Ireland sheep population (after adjusting for age)
358 and observed more variation between the breeds than was seen in the current study. In general,
359 the Irish study found that Texel lambs had higher heritabilities than both the Suffolk and
360 Charollais, with the difference particularly evident for Post-weaning weight (similar to USWT
361 in the current study). There was little difference observed between the Suffolk and Charollais
362 estimates. Additionally, when assessing genetic parameters for similar traits in Meatlinc and
363 Lleyn lambs, Roden (2016) observed differences between breeds, with the Lleyn (maternal
364 breed) having higher heritability estimates compared to the Meatlinc (terminal sire breed).
365 These differences could be due to a number of reasons, including the different populations and
366 models used, but they demonstrate nonetheless that genetic progress can be made, although the
367 rate of progress may vary.

368 *4.3. Could new CT traits be included in terminal sire breeding programmes?*

369 When assessing the relationships amongst the new and existing traits, adjusting for age at
370 measurement for each breed, the correlations estimated indicated that selecting for longer spine
371 length or more vertebrae would not be antagonistic with the breeding goal of increased growth

to 21 weeks. There is some indication of unfavourable, negative genetic relationships between UMD and spine traits, but these correlations tended to be low, and were not observed with CTMWT, where significant correlations with spine traits tended to be positive. There were few significant trends seen between spine traits and fat measurements (UFD and CTFWT). An increase in thoracolumbar vertebra in the pig spine was found to be linked to a favourable increase in meat to fat ratio (Borchers et al., 2004).

CTEMA and CTEMD were favourably genetically correlated with scan weight, muscling and muscularity traits, where significant genetic correlations were observed. Particularly high correlations were observed between UMD and CTEMD ($\geq$0.77). Additionally, when this relationship was further examined, strong relationships were observed between CTEMA and CTEMD across all three breeds (0.73-0.80, s.e. 0.05-0.08, when adjusting for age or live weight; results not shown in tables). Correlations of eye muscle traits with fat measured by ultrasound or CT tended to be low and not significantly different from zero, with the exception of CTEMA in the Texel, which was moderately positively correlated with CTFWT. Overall, these relationships suggest few antagonistic effects on current breeding goals of selecting for eye muscle area. The results also highlight the usefulness of ultrasound muscle depth as a rapid and accurate measure that can lead to an increase in eye muscle area through indirect selection.

Selection for CTIMF is likely to be favourable for increasing 21-week weight, but antagonistic with selection for increased muscle depth or muscle weight, and reduced fat in the carcass, in each of the three breeds. The genetic correlation of 0.66 in Texel suggests CTIMF and total carcass fat are partially under different genetic control, and that selection could be applied to increase IMF, whilst decreasing total carcass fat at a given age. However, these correlations in Suffolk and Charollais were 0.90 and 0.89, respectively, suggesting less scope for divergent selection.

4.4. Effects of adjusting CT and ultrasound traits for live weight, rather than age

Overall, adjusting ultrasound and CT traits for live weight, rather than age, lead to a reduction in genetic variation in most traits. However, for ultrasound tissue depths and CT tissue weights (including CTIMF), heritabilities tended to increase due to a larger increase in phenotypic variation. Similar or higher heritabilities were also observed for muscularity traits (CTmusc, CTEMD, CTEMA), whilst the effect on the spine traits differed between breeds. The tendency for heritabilities to increase, when adjusting measurements for live weight, suggest the rate of genetic change could be increased. However, within individual traits, this would be balanced against any observed reductions in genetic variation, which also contributes to the rate of response to selection. Kvame and Vangen (2007) and Roden (2016) observed similar results in terms of the changes in genetic variation and heritability estimates between age and live weight adjustments.

The results from the breeding value correlation analyses indicate that although all traits will be affected to some extent by re-ranking, CTMWT and CTFWT traits would be the most affected by the change from age to live weight adjustment. Adjusting ultrasound and CT traits for live weight, rather than age, will allow breeders to assess genetic merit for proportions of different tissues in the carcass at a given live weight. This is potentially more relevant to breed slaughter lambs that are killed at a given live weight, rather than age, end-point. When adjusting for age, tissue depths and CT tissue weights are somewhat confounded with growth rate (faster growing lambs that are heavier at scanning will also tend to have more fat and muscle). These messages will have to be clearly presented to breeders to explain why some animals may re-rank with the change of covariate, although live weight adjusted traits should be easier to interpret and incorporate into a selection index, as they are more independent from growth.

Genetic correlations between CT traits and 21-week weight tended to decrease following adjustment for live weight, whereas genetic correlations of CT traits with ultrasound muscle depth tended to remain similar for most traits. Especially in Suffolks and Charollais, live weight adjustment led to a decrease in the genetic correlations between ultrasound predictors of fat and muscle and their CT weight equivalents, suggesting that ultrasound tissue depths become poorer predictors of total carcass tissue weights. However, the relationship between UMD and both CTEMD and CTEMA remained strong, particularly those associated with CTEMD (correlations of 0.77-0.84 across the three breeds), similar to the correlation of 0.84 observed by Maximini et al. (2012).

Genetic correlations between CT tissue weights and spine lengths became negative, in some cases, following adjustment for live weight, which may be due to the fact that bone is contributing to live weight. With an age adjustment, increased fat and muscle weights are associated with increased spine length. However, adjusting for live weight considers fat and muscle as proportions of body weight, so an increase in these proportions is associated with a decrease in bone proportion, potentially through reduced spine length. Likewise, CT eye muscle depth and total spine length became more strongly negatively correlated, suggesting that as spine length increases, the loin muscle becomes shallower at the same live weight.

Total carcass fat weight and IMF became more strongly correlated after an adjustment for live weight, which would be antagonistic for divergent selection, especially in the Suffolk and Charollais where these correlations were not significantly different from one. Genetic correlations between live weight adjusted CTFWT and CTMWT were markedly different between breeds – the Charollais showing a high negative correlation, the Suffolk and Texel showing positive correlations. This breed difference is difficult to explain. There may be differences between breeds in the proportion of variation in live weight due to fat, muscle, bone,

and other non-carcass parts, in the range of weights observed here. Major genes that can influence carcass composition, such as mutations within the myostatin gene that were highlighted earlier, could also be having an effect. There will also be breed differences in terms of mature size and we may be observing lambs from different breeds at a different stage in their growth curves.

5. Conclusion

In conclusion, these results suggest that newly-derived CT traits, relating to eye muscle dimensions, spine traits and intramuscular fat (as a predictor of meat quality) are under low to moderate genetic control and have potential for incorporation into breeding programmes for UK terminal sire sheep. Live-weight adjusted CT and ultrasound traits are more heritable than age-adjusted traits and could help select for desired carcass characteristics at commercial slaughter weights. However, the combined effects of the new and existing CT traits, ultrasound traits and weight traits within an index for improved growth, carcass composition and product quality have not yet been assessed, which will be an important step before recommendations can be made on the most effective use of these traits for genetic improvement of terminal sire sheep. It would also be beneficial to assess how these traits could be combined most effectively with other economically important traits, such as maternal characteristics, within future indices. These findings can also help to inform strategies that aim to combine information across terminal sire breeds in genetic evaluations.

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Figures

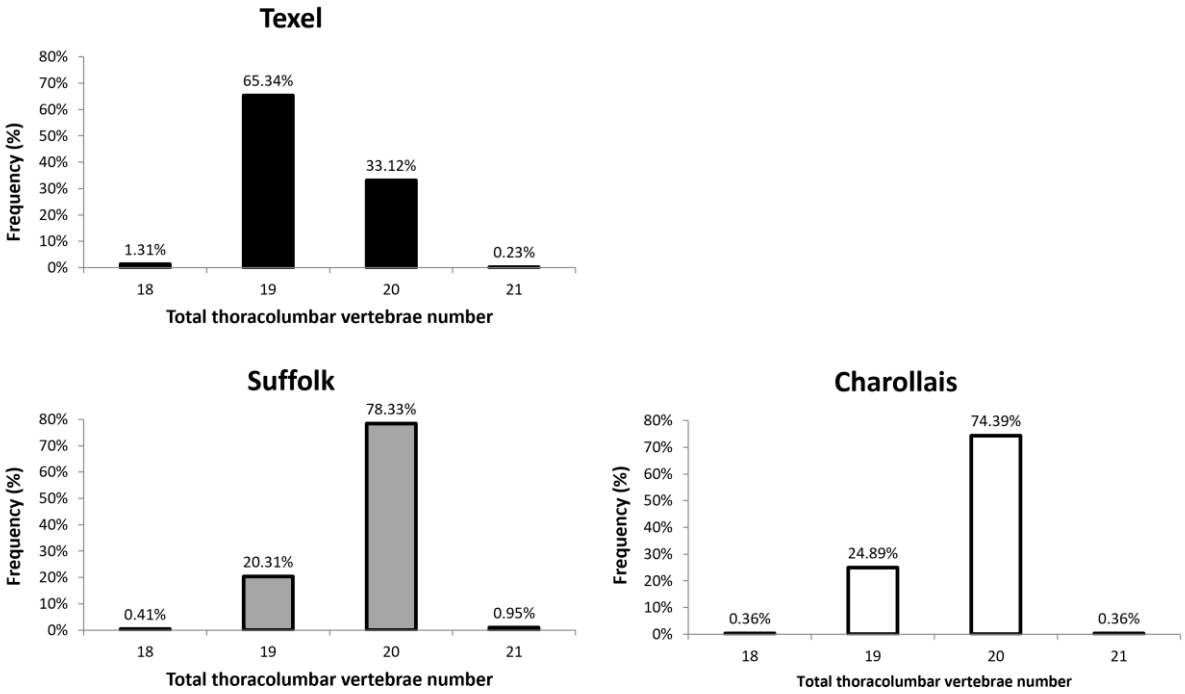

Figure 1. Frequency of lambs (by breed) in each class for total thoracolumbar vertebrae number.

574 **Table 1.** *Summary of the computer tomography (CT) and ultrasound traits, for each breed, included in the analyses*

	Texel					Suffolk					Charollais				
Trait	Count	Min.	Max.	Mean	SD	Count	Min.	Max.	Mean	SD	Count	Min.	Max.	Mean	SD
CTFWT	3 525	1.0	15.2	5.1	1.8	2 357	1.3	14.2	6.7	2.3	2 012	1.6	14.4	7.6	2.1
CTMWT	3 534	7.1	27.8	16.9	2.9	2 353	5.1	23.5	16.7	2.8	2 013	6.3	23.6	17.5	2.3
CTMusc	3 529	38.2	86.1	67.2	7.0	2 357	37.7	78.4	61.0	6.6	2 013	45.1	83.5	66.6	6.2
CTEMD	3 049	24.5	54.5	37.9	2.3	1 880	23.5	53.0	38.0	4.8	1 456	26.5	52.5	38.6	3.5
CTEMA	3 049	14.4	47.1	27.6	4.4	1 880	14.4	42.6	27.4	4.6	1 456	19.3	42.9	29.6	3.6
CTIMF	2 640	0.3	3.6	1.8	0.5	1 534	0.6	3.8	2.5	0.5	1 456	0.7	3.9	2.6	0.5
SLThor	2 986	226.0	405.0	298.9	23.4	1 462	228.0	406.0	337.0	21.0	1 434	266.0	396.0	337.2	18.7
SLLum	2 986	164.0	288.0	208.5	16.6	1 462	180.0	27.4.0	229.2	14.5	1 434	176.0	268.0	236.6	15.0
SLTotal	2 986	414.0	638.0	507.4	31.6	1 462	452.0	670.0	566.2	28.0	1 434	475.0	651.0	574.0	25.9
VNThor	2 986	12.0	14.0	13.0	0.3	1 462	12.0	14.0	13.0	0.4	1 434	12.0	14.0	12.9	0.4
VNLum	2 986	6.0	7.0	6.4	0.5	1 462	6.0	8.0	6.8	0.4	1 434	6.0	8.0	6.8	0.4
VNTotal	2 986	18.0	21.0	19.3	0.5	1 462	18.0	21.0	19.8	0.4	1 434	18.0	21.0	19.7	0.5
CTWT	3 049	31.5	97.8	54.9	8.3	1 880	32.0	87.2	59.4	9.6	1456	38.1	88.4	63.4	7.7
CTAge	3 534	89.0	222.0	150.5	18.9	2 357	95.0	220.0	148.6	20.9	2 013	91.0	208.0	155.4	11.6
USWT	89944	11.5	90.0	47.5	9.9	125506	15.0	92.0	53.6	12.5	61747	16.5	82.0	52.1	10.0
UFD	89930	0.1	13.4	2.5	1.3	125500	0.1	17.0	3.7	2.0	61742	0.1	17.3	4.1	2.0
UMD	89948	9.0	45.2	28.7	4.0	125478	9.7	49.5	30.2	4.6	61747	11.6	44.5	29.2	3.7
USAge	89948	85.0	208.0	145.4	19.8	125506	85.0	206.0	145.3	18.3	61747	85.0	214.0	148.0	18.9

575 CTFWT = CT fat weight (kg); CTMWT = CT muscle weight (kg); CTMusc = CT muscularity (ratio); CTEMD = CT eye muscle depth (mm); CTEMA = CT eye muscle area (cm^2); CTIMF = CT
576 intramuscular fat (%); SLThor = Thoracic spine length (mm); SLLum = Lumbar spine length (mm); SLTotal = Total spine length (mm); VNThor = Thoracic vertebrae number; VNLum = Lumbar vertebrae
577 number; VNTotal = Total vertebrae number; CTWT = Weight at CT scanning (kg); CTAge = Age at CT scanning (days); USWT = Ultrasound scan weight (kg); UFD = Ultrasound fat depth (mm); UMD =
578 Ultrasound muscle depth (mm); USAge = Age at Ultrasound scanning (days)
579

Table 2 *Univariate genetic variances (σ^2_g), phenotypic variances (σ^2_p) and heritabilities (h^2) for age-adjusted computer tomography (CT) and ultrasound traits, for each breed (SE in parentheses)*

	Texel			Suffolk			Charollais		
Trait	σ^2_g	σ^2_p	h^2	σ^2_g	σ^2_p	h^2	σ^2_g	σ^2_p	h^2
CTFWT	0.31	1.13 (0.03)	0.28 (0.06)	0.47	1.56 (0.06)	0.30 (0.07)	0.95	1.76 (0.07)	0.54 (0.08)
CTMWT	0.49	1.84 (0.05)	0.27 (0.05)	0.53	1.56 (0.06)	0.34 (0.06)	0.70	1.69 (0.07)	0.41 (0.08)
CTMusc	7.88	25.15 (0.73)	0.31 (0.06)	10.50	27.15 (0.99)	0.39 (0.07)	8.27	24.77 (0.94)	0.33 (0.07)
CTEMD	3.34	10.06 (0.32)	0.33 (0.06)	2.40	8.78 (0.35)	0.27 (0.07)	4.47	8.50 (0.40)	0.53 (0.09)
CTEMA	2.81	9.31 (0.29)	0.30 (0.06)	2.33	6.84 (0.27)	0.34 (0.07)	3.51	7.48 (0.35)	0.47 (0.08)
CTIMF	0.04	0.13 (0.004)	0.28 (0.07)	0.03	0.13 (0.01)	0.23 (0.09)	0.11	0.13 (0.01)	0.88 (0.08)
SLThor	58.98	199.90 (6.32)	0.30 (0.06)	56.37	232.40 (10.51)	0.24 (0.08)	118.00	239.00 (11.40)	0.49 (0.09)
SLLum	68.12	221.20 (7.07)	0.31 (0.06)	59.65	178.00 (8.41)	0.36 (0.09)	7.80	177.90 (7.39)	0.04 (0.06)
SLTotal	141.83	394.00 (12.70)	0.36 (0.06)	131.44	411.60 (19.34)	0.32 (0.09)	162.58	409.50 (18.91)	0.40 (0.09)
VNThor*	0.01	0.08 (0.002)	0.11 (0.05)	0.01	0.12 (0.01)	0.11 (0.08)	0.04	0.12 (0.01)	0.33 (0.09)
VNLum*	0.03	0.21 (0.01)	0.15 (0.06)	0.02	0.13 (0.01)	0.13 (0.08)	0.01	0.14 (0.01)	0.04 (0.06)
VNTotal*	0.04	0.24 (0.01)	0.18 (0.06)	0.03	0.18 (0.01)	0.16 (0.08)	0.05	0.20 (0.01)	0.27 (0.08)
USWT	10.59	31.39 (0.20)	0.34 (0.01)	10.47	35.2 (0.19)	0.29 (0.01)	9.05	29.72 (0.22)	0.30 (0.01)
UFD	0.32	0.97 (0.01)	0.33 (0.01)	0.50	1.50 (0.01)	0.33 (0.01)	0.62	1.92 (0.01)	0.32 (0.01)
UMD	2.44	8.17 (0.05)	0.30 (0.01)	2.25	7.58 (0.04)	0.30 (0.01)	1.94	6.55 (0.05)	0.30 (0.01)

* No covariate was fitted. CTFWT = CT fat weight; CTMWT = CT muscle weight; CTMusc = CT muscularity; CTEMD = CT eye muscle depth; CTEMA = CT eye muscle area; CTIMF = CT intramuscular fat; SLThor = Thoracic spine length; SLLum = Lumbar spine length; SLTotal = Total spine length; VNThor = Thoracic vertebrae number; VNLum = Lumbar vertebrae number; VNTotal = Total vertebrae number; USWT = Ultrasound scan weight (kg); UFD = Ultrasound fat depth (mm); UMD = Ultrasound muscle depth (mm)

Table 3 *Univariate genetic variances (σ^2_g), phenotypic variances (σ^2_p) and heritabilities (h^2) for live weight-adjusted computer tomography (CT) traits, for each breed (SE in parentheses)*

	Texel			Suffolk			Charollais		
Trait	σ^2_g	σ^2_p	h^2	σ^2_g	σ^2_p	h^2	σ^2_g	σ^2_p	h^2
CTFWT	0.14	0.42 (0.01)	0.35 (0.06)	0.38	0.61 (0.03)	0.61 (0.09)	0.54	0.73 (0.04)	0.74 (0.09)
CTMWT	0.23	0.53 (0.02)	0.43 (0.06)	0.18	0.42 (0.02)	0.43 (0.07)	0.35	0.54 (0.03)	0.65 (0.08)
CTMusc	8.06	23.12 (0.73)	0.35 (0.06)	7.59	25.06 (1.01)	0.30 (0.08)	10.50	24.46 (1.15)	0.43 (0.08)
CTEMD	3.04	8.90 (0.28)	0.34 (0.06)	2.69	7.68 (0.31)	0.35 (0.08)	4.43	8.20 (0.39)	0.54 (0.09)
CTEMA	2.20	7.45 (0.23)	0.30 (0.06)	2.41	5.30 (0.22)	0.45 (0.07)	3.77	6.71 (0.32)	0.56 (0.08)
CTIMF	0.04	0.11 (0.003)	0.40 (0.07)	0.03	0.12 (0.01)	0.21 (0.08)	0.10	0.11 (0.01)	0.87 (0.08)
SLThor	37.29	155.20 (4.81)	0.24 (0.06)	62.06	194.40 (9.11)	0.32 (0.09)	79.80	178.20 (8.35)	0.44 (0.09)
SLLum	52.01	201.70 (6.31)	0.26 (0.06)	55.88	157.20 (7.42)	0.36 (0.09)	2.10	156.80 (6.46)	0.01 (0.06)
SLTotal	76.47	274.60 (8.62)	0.28 (0.06)	140.61	300.40 (14.85)	0.47 (0.09)	90.14	257.00 (11.63)	0.35 (0.08)
VNThor	-	-	-	-	-	-	-	-	-
VNLum	-	-	-	-	-	-	-	-	-
VNTotal	-	-	-	-	-	-	-	-	-
USWT	-	-	-	-	-	-	-	-	-
UFD	0.26	0.69 (0.004)	0.37 (0.01)	0.44	1.11 (0.01)	0.39 (0.01)	0.58	1.49 (0.01)	0.39 (0.01)
UMD	1.90	5.29 (0.03)	0.36 (0.01)	1.80	4.85 (0.03)	0.37 (0.01)	1.87	5.06 (0.04)	0.37 (0.01)

CTFWT = CT fat weight; CTMWT = CT muscle weight; CTMusc = CT muscularity; CTEMD = CT eye muscle depth; CTEMA = CT eye muscle area; CTIMF = CT intramuscular fat; SLThor = Thoracic spine length; SLLum = Lumbar spine length; SLTotal = Total spine length; VNThor = Thoracic vertebrae number; VNLum = Lumbar vertebrae number; VNTotal = Total vertebrae number; USWT = Ultrasound scan weight (kg); UFD = Ultrasound fat depth (mm); UMD = Ultrasound muscle depth (mm)

Table 4. *Spearman's Rank and Pearson correlations between age and live weight adjusted analyses.*

	Texel		Suffolk		Charollais	
Trait	Spearman's	Pearson	Spearman's	Pearson	Spearman's	Pearson
CTMWT	0.33	0.53	0.42	0.76	0.69	0.73
CTFWT	0.37	0.39	0.49	0.49	0.50	0.55
CTMusc	0.81	0.89	0.81	0.86	0.93	0.95
CTEMD	0.90	0.94	0.85	0.94	0.98	0.99
CTEMA	0.89	0.92	0.85	0.93	0.93	0.96
CTIMF	0.75	0.87	0.91	0.94	0.94	0.95
SLThor	0.93	0.91	0.91	0.92	0.87	0.92
SLLum	0.89	0.92	0.93	0.95	0.90	0.93
SLTotal	0.87	0.86	0.74	0.83	0.82	0.89
UFD	0.73	0.76	0.72	0.75	0.80	0.83
UMD	0.66	0.71	0.81	0.83	0.88	0.89

CTFWT = CT fat weight (kg); CTMWT = CT muscle weight (kg); CTMusc = CT muscularity (ratio); CTEMD = CT eye muscle depth (mm); CTEMA = CT eye muscle area (cm^2); CTIMF = CT intramuscular fat (%); SLThor = Thoracic spine length (mm); SLLum = Lumbar spine length (mm); SLTotal = Total spine length (mm); UFD = Ultrasound fat depth (mm); UMD = Ultrasound muscle depth (mm)

Table 5 Genetic correlations estimated between current growth and carcass traits and traits measured by computer tomography (CT), for both age adjusted and live weight adjusted analyses of Texel lambs. Standard errors in parenthesis.

	Age-adjusted						Live weight adjusted					
	USWT	UMD	UFD	CTMWT	CTFWT	CTMusc	USWT	UMD	UFD	CTMWT	CTFWT	CTMusc
CTMWT	0.82 (0.03)	0.50 (0.06)	-0.07 (0.08)				0.67 (0.04)	0.46 (0.06)	-0.44 (0.07)			
CTFWT	0.78 (0.03)	0.24 (0.08)	0.69 (0.04)	0.39 (0.10)			0.67 (0.04)	0.06 (0.07)	0.70 (0.04)	0.28 (0.10)		
CTMusc	0.13 (0.08)	0.28 (0.07)	-0.10 (0.08)	0.18 (0.12)	-0.07 (0.13)		0.11 (0.08)	0.28 (0.07)	-0.09 (0.08)	0.15 (0.11)	-0.11 (0.12)	
CTEMD	0.26 (0.08)	0.85 (0.05)	0.04 (0.08)	0.49 (0.10)	0.24 (0.13)	0.25 (0.12)	-0.14 (0.09)	0.84 (0.05)	0.02 (0.08)	0.62 (0.08)	0.13 (0.14)	0.25 (0.12)
CTEMA	0.45 (0.08)	0.79 (0.06)	0.03 (0.09)	0.59 (0.09)	0.36 (0.13)	0.24 (0.13)	-0.06 (0.09)	0.77 (0.06)	-0.03 (0.09)	0.63 (0.08)	0.09 (0.15)	0.23 (0.13)
SLThor	0.68 (0.07)	-0.01 (0.09)	-0.08 (0.09)	0.39 (0.13)	0.29 (0.14)	-0.01 (0.15)	0.25 (0.10)	-0.26 (0.09)	-0.30 (0.09)	-0.02 (0.16)	-0.25 (0.16)	-0.06 (0.16)
VNThor	-0.08 (0.14)	0.003 (0.14)	-0.18 (0.14)	0.10 (0.22)	-0.21 (0.22)	0.20 (0.23)	-0.08 (0.14)	-0.02 (0.13)	-0.17 (0.14)	0.44 (0.22)	-0.14 (0.23)	0.23 (0.23)
SLLum	0.42 (0.09)	-0.21 (0.09)	-0.05 (0.09)	0.14 (0.14)	0.31 (0.14)	0.06 (0.15)	0.05 (0.10)	-0.29 (0.09)	-0.16 (0.09)	-0.49 (0.13)	-0.17 (0.16)	0.04 (0.16)
VNLum	-0.06 (0.12)	-0.32 (0.12)	-0.14 (0.12)	-0.12 (0.19)	0.05 (0.20)	-0.02 (0.19)	-0.06 (0.12)	-0.25 (0.11)	-0.12 (0.12)	-0.39 (0.18)	-0.11 (0.20)	-0.04 (0.19)
SLTotal	0.73 (0.06)	-0.16 (0.08)	-0.09 (0.08)	0.34 (0.12)	0.39 (0.12)	0.03 (0.14)	0.21 (0.09)	-0.43 (0.09)	-0.34 (0.09)	-0.42 (0.14)	-0.30 (0.14)	-0.02 (0.15)
VNTotal	-0.09 (0.12)	-0.29 (0.11)	-0.21 (0.12)	-0.07 (0.18)	-0.06 (0.18)	0.05 (0.18)	-0.09 (0.12)	-0.23 (0.11)	-0.19 (0.11)	-0.18 (0.18)	-0.16 (0.19)	0.04 (0.18)
CTIMF	0.32 (0.08)	-0.17 (0.10)	0.73 (0.06)	-0.25 (0.17)	0.66 (0.08)	-0.18 (0.16)	-0.06 (0.08)	-0.15 (0.08)	0.67 (0.07)	-0.69 (0.08)	0.85 (0.04)	-0.18 (0.14)

CTFWT = CT fat weight (kg); CTMWT = CT muscle weight (kg); CTMusc = CT muscularity (ratio); CTEMD = CT eye muscle depth (mm); CTEMA = CT eye muscle area (cm^2); CTIMF = CT intramuscular fat (%); SLThor = Thoracic spine length (mm); SLLum = Lumbar spine length (mm); SLTotal = Total spine length (mm); VNThor = Thoracic vertebrae number; VNLum = Lumbar vertebrae number; VNTotal = Total vertebrae number; USWT = Ultrasound scan weight (kg); UFD = Ultrasound fat depth (mm); UMD = Ultrasound muscle depth (mm)

Table 6 Genetic correlations estimated between current growth and carcass traits and traits measured by computer tomography (CT), for both age adjusted and live weight adjusted analyses of Suffolk lambs. Standard errors in parenthesis.

	Age-adjusted						Live weight adjusted					
	USWT	UMD	UFD	CTMWT	CTFWT	CTMusc	USWT	UMD	UFD	CTMWT	CTFWT	CTMusc
CTMWT	0.81 (0.03)	0.44 (0.06)	0.03 (0.07)				0.65 (0.04)	0.20 (0.06)	-0.23 (0.06)			
CTFWT	0.69 (0.04)	0.21 (0.07)	0.72 (0.05)	0.36 (0.11)			0.46 (0.05)	0.08 (0.05)	0.57 (0.04)	0.59 (0.05)		
CTMusc	0.20 (0.08)	0.30 (0.07)	0.06 (0.08)	0.36 (0.12)	0.04 (0.13)		0.20 (0.08)	0.25 (0.07)	-0.01 (0.08)	0.35 (0.10)	0.05 (0.10)	
CTEMD	0.15 (0.10)	0.81 (0.07)	0.17 (0.10)	0.49 (0.12)	0.02 (0.18)	0.41 (0.15)	-0.23 (0.10)	0.80 (0.06)	0.18 (0.09)	0.65 (0.09)	0.16 (0.13)	0.31 (0.15)
CTEMA	0.23 (0.09)	0.68 (0.06)	0.16 (0.09)	0.57 (0.09)	0.13 (0.15)	0.37 (0.15)	-0.21 (0.08)	0.67 (0.06)	0.13 (0.08)	0.72 (0.06)	0.22 (0.11)	0.25 (0.14)
SLThor	0.41 (0.12)	-0.31 (0.15)	-0.13 (0.14)	0.15 (0.19)	-0.06 (0.23)	-0.21 (0.21)	-0.04 (0.13)	-0.25 (0.11)	-0.23 (0.12)	0.09 (0.17)	-0.04 (0.17)	-0.43 (0.18)
VNThor	-0.02 (0.20)	-0.24 (0.20)	-0.30 (0.23)	0.16 (0.29)	-0.58 (0.27)	0.02 (0.29)	-0.02 (0.20)	-0.21 (0.20)	-0.45 (0.26)	0.40 (0.28)	-0.53 (0.30)	0.05 (0.30)
SLLum	0.42 (0.10)	-0.17 (0.11)	0.28 (0.12)	-0.10 (0.19)	0.43 (0.18)	-0.31 (0.19)	0.10 (0.12)	-0.25 (0.10)	0.12 (0.11)	-0.38 (0.16)	0.30 (0.16)	-0.53 (0.17)
VNLum	-0.09 (0.18)	0.01 (0.17)	0.35 (0.20)	-0.23 (0.26)	0.27 (0.31)	-0.06 (0.28)	-0.09 (0.18)	0.02 (0.16)	0.36 (0.19)	-0.55 (0.22)	-0.11 (0.24)	-0.11 (0.28)
SLTotal	0.52 (0.09)	-0.30 (0.13)	0.17 (0.10)	0.07 (0.18)	0.23 (0.19)	-0.35 (0.19)	0.05 (0.10)	-0.32 (0.09)	-0.07 (0.09)	-0.11 (0.15)	0.14 (0.14)	-0.61 (0.14)
VNTotal	-0.08 (0.17)	-0.15 (0.15)	0.07 (0.16)	-0.09 (0.24)	-0.29 (0.26)	-0.04 (0.25)	-0.08 (0.17)	-0.15 (0.15)	0.01 (0.15)	-0.20 (0.22)	-0.39 (0.21)	-0.05 (0.26)
CTIMF	0.20 (0.15)	-0.09 (0.13)	0.61 (0.13)	0.02 (0.20)	0.90 (0.10)	0.26 (0.22)	-0.16 (0.14)	-0.05 (0.12)	0.60 (0.13)	-0.09 (0.20)	0.95 (0.06)	0.15 (0.22)

CTFWT = CT fat weight (kg); CTMWT = CT muscle weight (kg); CTMusc = CT muscularity (ratio); CTEMD = CT eye muscle depth (mm); CTEMA = CT eye muscle area (cm^2); CTIMF = CT intramuscular fat (%); SLThor = Thoracic spine length (mm); SLLum = Lumbar spine length (mm); SLTotal = Total spine length (mm); VNThor = Thoracic vertebrae number; VNLum = Lumbar vertebrae number; VNTotal = Total vertebrae number; USWT = Ultrasound scan weight (kg); UFD = Ultrasound fat depth (mm); UMD = Ultrasound muscle depth (mm)

Table 7 Genetic correlations estimated between current growth and carcass traits and traits measured by computer tomography (CT), for both age adjusted and live weight adjusted analyses of Charollais lambs. Standard errors in parenthesis.

	Age-adjusted						Live weight adjusted					
	USWT	UMD	UFD	CTMWT	CTFWT	CTMusc	USWT	UMD	UFD	CTMWT	CTFWT	CTMusc
CTMWT	0.65 (0.04)	0.44 (0.07)	-0.17 (0.08)				0.52 (0.05)	0.27 (0.07)	0.09 (0.02)			
CTFWT	0.63 (0.04)	-0.04 (0.08)	0.79 (0.04)	0.15 (0.13)			0.56 (0.05)	-0.25 (0.07)	0.69 (0.05)	-0.82 (0.06)		
CTMusc	-0.30 (0.09)	0.49 (0.08)	-0.24 (0.09)	0.37 (0.12)	-0.17 (0.14)		-0.31 (0.09)	0.56 (0.08)	-0.12 (0.08)	0.39 (0.11)	-0.17 (0.13)	
CTEMD	-0.08 (0.09)	0.79 (0.06)	-0.12 (0.09)	0.34 (0.12)	0.03 (0.15)	0.57 (0.13)	-0.35 (0.08)	0.77 (0.06)	-0.07 (0.08)	0.39 (0.12)	-0.13 (0.16)	0.59 (0.12)
CTEMA	-0.07 (0.09)	0.66 (0.07)	-0.21 (0.09)	0.52 (0.10)	-0.25 (0.16)	0.72 (0.11)	-0.41 (0.08)	0.67 (0.06)	-0.13 (0.08)	0.72 (0.07)	-0.47 (0.14)	0.73 (0.10)
SLThor	0.61 (0.07)	-0.14 (0.09)	0.38 (0.11)	0.24 (0.14)	0.41 (0.13)	-0.26 (0.16)	0.31 (0.10)	-0.22 (0.09)	0.08 (0.09)	-0.30 (0.15)	0.04 (0.17)	-0.29 (0.16)
VNThor	0.12 (0.12)	-0.07 (0.11)	-0.005 (0.11)	0.02 (0.18)	0.42 (0.17)	-0.12 (0.20)	0.12 (0.12)	-0.06 (0.10)	-0.05 (0.11)	-0.20 (0.19)	0.47 (0.17)	-0.15 (0.20)
SLLum	0.99 (0.29)	-0.84 (1.22)	0.23 (0.09)	0.46 (0.31)	0.96 (1.13)	-0.37 (0.58)	0.73 (0.73)	N/E	-0.75 (0.29)	0.55 (0.90)	0.60 (1.47)	-0.31 (0.89)
VNLum	0.23 (0.33)	-0.44 (0.55)	-0.73 (0.30)	-0.22 (0.63)	-0.55 (0.43)	-0.11 (0.52)	0.23 (0.33)	-0.48 (0.40)	-0.69 (0.23)	0.23 (0.42)	-0.41 (0.41)	-0.06 (0.51)
SLTotal	0.76 (0.05)	-0.22 (0.10)	-0.38 (0.35)	0.39 (0.13)	0.41 (0.14)	-0.24 (0.17)	0.45 (0.10)	-0.40 (0.09)	-0.23 (0.10)	-0.07 (0.18)	-0.02 (0.19)	-0.27 (0.17)
VNTotal	0.18 (0.13)	-0.18 (0.12)	-0.34 (0.12)	0.06 (0.19)	0.06 (0.20)	-0.13 (0.21)	0.18 (0.13)	-0.23 (0.11)	-0.41 (0.11)	0.06 (0.20)	0.07 (0.21)	-0.13 (0.21)
CTIMF	0.26 (0.07)	-0.21 (0.07)	0.66 (0.06)	-0.45 (0.13)	0.89 (0.04)	-0.43 (0.13)	0.09 (0.07)	-0.24 (0.07)	0.61 (0.05)	-0.95 (0.03)	0.96 (0.02)	-0.42 (0.13)

CTFWT = CT fat weight (kg); CTMWT = CT muscle weight (kg); CTMusc = CT muscularity (ratio); CTEMD = CT eye muscle depth (mm); CTEMA = CT eye muscle area (cm^2); CTIMF = CT intramuscular fat (%); SLThor = Thoracic spine length (mm); SLLum = Lumbar spine length (mm); SLTotal = Total spine length (mm); VNThor = Thoracic vertebrae number; VNLum = Lumbar vertebrae number; VNTotal = Total vertebrae number; USWT = Ultrasound scan weight (kg); UFD = Ultrasound fat depth (mm); UMD = Ultrasound muscle depth (mm)