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Between- and within-breed variations of spine characteristics in sheep[1]

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ABSTRACT: Implementing the use of spine traits in a commercial breeding program has been seen to improve meat production from the carcass of larger-bodied pigs. The aim of this study was to assess the extent of variation in spine characteristics within and between breeds of sheep and to investigate the association with body length and tissues traits to deliberate if a similar approach could be applicable in the sheep sector. Spine traits (vertebrae number, VN; spine region length, SPL; individual vertebra length, VL) of the thoracic ($_{\text{THOR}}$) lumbar ($_{\text{LUM}}$) and thoracolumbar ($_{\text{T+L}}$) spine regions were measured using x-ray computed tomography (CT) on 254 Texel (TEX), 1100 Scottish Blackface (SBF), 326 Texel cross Mule (TEX × MULE), and 178 Poll Dorset cross Mule (PD × MULE) lambs. Simple descriptive statistics inform that variation in thoracolumbar VN exists within all breeds and crosses; TEX animals showed the largest range of variation in thoracolumbar VN (17 to 21) and the TEX × MULE the smallest (18 to 20). Significant differences were not observed between sexes, but did occur between breeds ($P < 0.05$), which is indicative of a genetic basis for these traits. Least-squares means identified that TEX had the least thoracolumbar VN (19.24) and SBF possessed the most (19.63); similarly the lowest measures for SPL and VL for each spine region were observed in TEX, but the greatest values for these traits were expressed predominantly in the crosses (TEX × MULE and PD × MULE). Correlation coefficients (r) within each breed or cross support the interpretation of additional vertebrae contributing to a longer length of the spine region in which they occur ($P < 0.001$; e.g., for PD × MULE lambs), r between traits VN_{THOR} and SPL_{THOR} ($r = 0.59$), VN_{LUM} and SPL_{LUM} ($r = 0.94$) and $\text{VN}_{\text{T+L}}$ and $\text{SPL}_{\text{T+L}}$ ($r = 0.65$) all reach moderate to very high values. In all breeds and crosses, this relationship is particularly strong for the lumbar region. The few significant ($P < 0.05$) correlations observed between spine and tissue traits [CT-predicted quantities of carcass fat and muscle (kg) and area of the LM (mm^2)] indicated no substantial relationships, r was small (ranging from –0.25 to 0.19) in each case. To conclude, significant vertebral variation exists within and between sheep breeds and crosses, which can contribute to an increase in body (and carcass) length. Including measurements taken for other primal cuts will further aid in assessing any potential increase in meat production from these longer-bodied sheep.

Key words: body length, sheep, spine, thoracolumbar, vertebrae variation

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INTRODUCTION

The vertebrate spinal column comprises a series of repeating bones called vertebrae. These bones are variable in size, and their morphological differences subdivide the vertebrae series into 5 functionally distinct spinal regions: cervical, thoracic, lumbar, sacral, and caudal. Counting the number of vertebrae that comprise each spinal region provides the vertebral formulae [e.g., for the majority of humans, this is cervical 7 thoracic 12 lumbar 5 sacral 5 and caudal 4; Willis (1923); Treuting and Dintzis (2011)]. In mammals, the cervical component of these formulae rarely show intra- or interspecies variation, remaining at a fixed total of 7 for the majority of species (Galis, 1999; Hautier et al., 2010). In contrast, variation is common in the

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Table 1. Summary of data by breed or cross[1]

Breed or cross	n	Sex		Rearing rank			Dam age range, yr
		Male	Female	Single	Twin	Hand reared	
TEX	254	110	144	103	137	14	2 to 6
SBF	1100	560	540	485	611	4	2 to 7
TEX × MULE	326	154	172	31	295	–	3 to 6
PD × MULE	178	86	92	–	178	–	4 to 5

[1]TEX = Texel; SBF = Scottish Blackface; TEX × MULE = Texel × Mule; PD × MULE = Poll Dorset × Mule.

vertebral combinations of postcervical regions both between (e.g., Owen, 1853) and within species (e.g., Green, 1939; McLaren and Michie, 1954; Stecher, 1962; Pilbeam, 2004).

The findings regarding vertebral variation in the thoracolumbar (thoracic plus lumbar) region of the bacon pig is of particular interest to livestock breeders. The commercial selection for breeding stock with longer backs means commercial pigs can possess up to 4 more vertebrae than the ancestral 19 (Fredeen and Newman, 1962a; Mikawa et al., 2007; Yang et al., 2009; Mikawa et al., 2011). This manner of selection may have the potential to increase meat yield from the commercially valuable LM which extends over the whole thoracolumbar spinal section. Hence, obtaining similar knowledge regarding vertebrae variation in sheep could prove to be of considerable importance in terms of lamb production.

The objectives of the present study are therefore to i) summarize the extent of variation in spine traits in the thoracolumbar spine region of sheep and assess if significant differences exist between sexes and/or breeds and crosses, and ii) examine, within breed or cross, how spine traits correlate with each other and with selected production traits (total predicted fat and muscle in the carcass and the average LM area).

MATERIALS AND METHODS

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.

Data Set

The present study was conducted using tissue and spine measures from 1858 lambs of Texel (TEX), Scottish Blackface (SBF), Texel cross Mule (TEX × MULE), and Poll Dorset cross Mule (PD × MULE) breeds/crosses; ewes used for breeding were of mixed age (Mule ewes in this study were Bluefaced Leicester cross SBF). Female and entire male lambs had been raised as either singles, twins, or hand-reared on three different research farms (all based in Scotland: 2 in the south-west of Edinburgh and 1 in Perthshire), grazed on pasture, and followed until weaning or slaughter (Table 1).

All lambs had been scanned using x-ray computed tomography (**CT**), a noninvasive technique that allows a wide range of measurements to be collected from the animal in vivo [detailed descriptions of this CT procedure can be found in Jones et al. (2002) and Bunger et al. (2011)]. These scans were taken during the years 2003 to 2008, with the lambs at an average age of 107 d (TEX, range 90 to 119 d), 120 d (SBF, range 95 to 153 d), 132 d (TEX × MULE, range 114 to 152 d), and 113 d (PD × MULE, range 108 to 117 d). Body weight of lambs was recorded pre-CT scan; average BW (kg) for each group was 33.6 (TEX, SE = 0.38), 29.6 (SBF, SE = 0.14), 37.7 (TEX × MULE, SE = 0.26), and 31.1 (PD × MULE, SE = 0.24). All tissue and spine traits (defined in next section) were measured post-CT scan with the use of cross-sectional reference scans and topograms generated from the CT procedure.

Traits Derived from Computed Tomography

Tissue Traits. Pixel analysis of cross-sectional CT reference scans allows the area of each different tissue type (fat, muscle, and bone) to be derived (see Glasbey and Robinson, 2002). Application of the appropriate breed-specific prediction equations to these values, such as those developed and used by Lambe et al. (2003), provides a reliable prediction of whole body tissue volumes and weights. For this study, prediction of total carcass fat (kg) and muscle (kg) were included (**PR_FAT** and **PR_MUSC**, respectively) along with an estimate of the average area (mm^2) of the LM (**LM$_{AREA}$**), measured in the cross-sectional scan taken at the fifth lumbar vertebra. Including traits PR_FAT, PR_MUSC, and LM$_{AREA}$ in the current study was to provide an initial indication of any possible changes in production traits (i.e., muscularity and lean meat yield) that may be associated with variations in spine traits.

Spine Traits. The 2-dimensional (**2D**) topograms of each lamb were analyzed using Sheep Tomogram Analysis Routines software (**STAR**; Mann et al., 2013), developed jointly by Biomathematics and Statistics Scot-

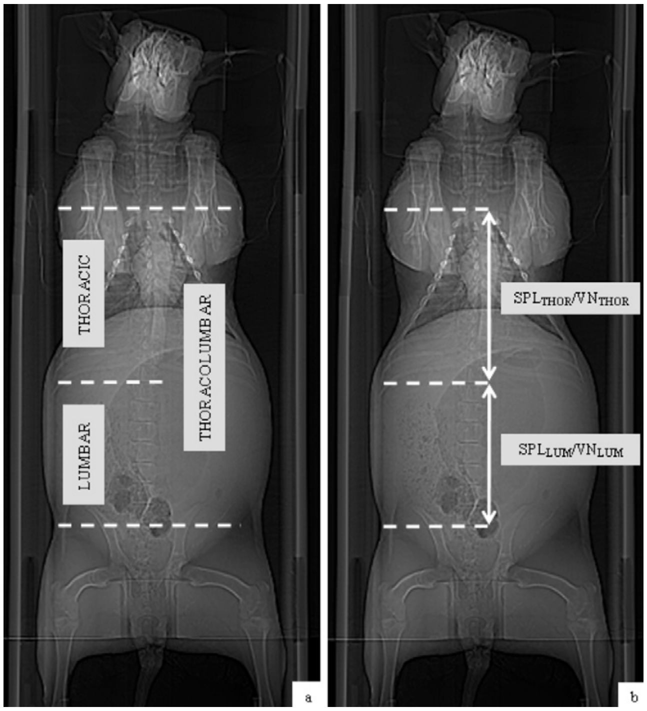

Figure 1. Example 2D-topogram generated from computed tomography. (a) Classification of vertebrae allows the boundary (represented as broken white lines) between the cervical-thoracic (top), thoracic-lumbar (middle), and lumbar-sacral (bottom) spinal regions to be identified and the location of the spine regions of interest to be highlighted. (b) The intervertebral discs positioned at these boundaries can then be used as reference points for taking length measures (SPL) and vertebral counts (VN) directly from the topogram, for the thoracic ($_{THOR}$) and lumbar ($_{LUM}$) spinal regions.

land (**BioSS**, Edinburgh, Scotland) and SRUC, Edinburgh, Scotland. Similar to the cross-sectional reference scans, these longitudinal images of the body of the animal permit excellent discrimination between the tissue types (fat, muscle and bone), allowing vertebrae to be counted and lengths of desired spinal regions to be measured. Figure 1a is an example of a typical topogram and highlights the spine regions of interest: thoracic, lumbar and thoracolumbar (thoracic plus lumbar). Four of the 9 spine traits included in the data set, number of thoracic (**VN_{THOR}**) and lumbar (**VN_{LUM}**) vertebrae and length (mm) of the thoracic (**SPL_{THOR}**) and lumbar (**SPL_{LUM}**) spine region, were measured directly from each topogram by 1 of the 4 protocol-trained operators involved in the analysis of CT images. The protocol defined for measuring spine characteristics from CT scans closely followed that previously described by Jones et al. (2002), which has also been used in Navajas et al. (2007).

First, before the measurement procedure is described, it is important to note that vertebrae were classified as thoracic when bearing symmetric or asymmetric ribs, true (attached to sternum) or rudimentary, whereas vertebrae bearing no ribs and positioned between the cranial side of the pelvis and the most caudal positioned thoracic vertebra were identified as lumbar. The SPL_{THOR} was then measured as the distance from the intervertebral disc immediately caudal to the last thoracic vertebra to the intervertebral disc immediately cranial to the first thoracic vertebra, and SPL_{LUM} measured as the distance from the intervertebral disc positioned to the cranial side of the pelvis to the first intervertebral disc caudal to the last thoracic vertebra. The number of vertebrae belonging to each of these sections (VN_{THOR} and VN_{LUM}) was then counted. Figure 1b provides a diagrammatic representation of these measurements. The spine traits VN_{THOR}, VN_{LUM}, SPL_{THOR}, and SPL_{LUM} were then used to derive the number of thoracolumbar vertebrae (**VN_{T+L}**) and length of the thoracolumbar spine region (mm; **SPL_{T+L}**) as follows:

Number of thoracolumbar vertebrae (VN_{T+L}) = $VN_{THOR} + VN_{LUM}$

Length of thoracolumbar spine region (SPL_{T+L}) = $SPL_{THOR} + SPL_{LUM}$

Finally, with the use of all of the above measurements, an average length for individual vertebrae (mm) in each region could be derived as follows:

Average length of individual thoracic vertebrae (**VL_{THOR}**) = SPL_{THOR}/VN_{THOR}

Average length of individual lumbar vertebrae (**VL_{LUM}**) = SPL_{LUM}/VN_{LUM}

Average length of individual thoracolumbar vertebrae (**VL_{T+L}**) = SPL_{T+L}/VN_{T+L}

Intra- and Interoperator Repeatability of Spine Measurements from Topograms

Classifying vertebrae from topograms requires a subjective decision (i.e., to which region a single vertebra should be allocated). It is therefore important to have a detailed protocol in place, particularly when multiple operators are involved, to reduce as far as possible the influence of the judgement of an individual on results. The repeatability and agreement of measurements within and between operators, after using a fixed protocol, was evaluated to validate CT as a reliable method for quantifying spine characteristics. A total of 100 topograms of TEX (n = 47) and SBF (n = 53) were used for the analysis. Spine traits VN_{THOR}, VN_{LUM}, SPL_{THOR}, and SPL_{LUM} were scored directly from the topograms by 3 observers, coded as A, B, and C, using the fixed protocol (as described in previous section). This was performed twice for each topogram by each observer, the repeat being performed at least 24 h after the first run of measurements. Operators A and B did this for the total 100 scans, and C analyzed 50 of these scans (TEX, n = 25; SBF, n = 25). The spine traits VN_{T+L}, SPL_{T+L}, VL_{THOR}, VL_{LUM}, and VL_{T+L} are not included in this test, as these traits are values derived from VN_{THOR}, VN_{LUM}, SPL_{THOR} and SPL_{LUM}, which were directly measured from topograms.

Statistical Analysis

All data were analyzed using SAS (SAS Inst. Inc., Cary, NC). To investigate the reliability of the method used to quantify the spine characteristics, ANOVA mixed model analyses for repeated measures were performed to calculate the intra class correlation coefficient ($\boldsymbol{r_t}$) to estimate inter- and intraoperator repeatability of spine trait measures taken from CT topograms.

The ANOVA generalized model procedure was used to analyze the effects of breed and sex on spine count (VN_{THOR}, VN_{LUM}, VN_{T+L}) and length (SPL_{THOR}, SPL_{LUM}, SPL_{T+L}, VL_{THOR}, VL_{LUM}, VL_{T+L}) characteristics. Fitted in the model as fixed effects were breed, with 4 levels (TEX, SBF, TEX × MULE, and PD × MULE); sex, with 2 levels (male and female); dam age, with 6 levels (2, 3, 4, 5, 6, and 7 yr); and rearing rank, with 3 levels (single, twin, or hand-reared). The significance of interaction between fixed effects and each trait were tested and final models altered for the count and length traits separately. With dam age nonsignificant for all length traits, the fixed effects in the final length trait model included breed, sex, and rearing rank. Sex and dam age were shown to be nonsignificant for count traits; therefore, fixed effects included in the final count trait model were breed and rearing rank. Each of the fixed effects included in the final models were significant for all or the majority of traits.

All of the above models were run once with no covariate adjustment, and once with the correction made for BW (measured on day of CT scan). Doing so, in terms of the biological nature of vertebrae number, should reveal that this meristic characteristic of the spine, once determined genetically in early development (Burke et al., 1995), will not then be influenced by environmental factors (such as nutrition) later in life; results are hypothesized to remain the same for each instance (BW not corrected and BW corrected). With regards to spine length traits, it was of interest to investigate if any particular breed or cross exhibited significantly longer spine regions and/or vertebrae (BW not corrected) and if these differences were removed when comparing the groups all at the same BW (BW corrected). The least-squares means for each breed and sex and SE of difference between the groups were generated for each trait.

Correlation coefficients (***r***) were also examined between all CT spine and tissue traits (PR_FAT, PR_MUSC, LM_{AREA}) to derive any trait associations. Fitted as a covariate in the model, BW was significant for all spine length traits and tissue traits and nonsignificant for the majority of spine count traits. Correlations of residuals were therefore estimated, by breed, after spine length traits were adjusted for sex, rearing rank and BW, tissue traits adjusted for sex, dam age, rearing rank and BW, and spine count traits adjusted for rearing rank. In this study, the degree of correlation was categorised into 6 levels [as described in Williams and Monge, (2000)]: very high ($r/r_t \geq 0.90$), high ($0.90 > r/r_t \geq 0.70$), moderate ($0.70 > r/r_t \geq 0.50$), low ($0.50 > r/r_t \geq 0.30$), little, if any ($r/r_t < 0.03$), and nonsignificant ($P > 0.05$).

RESULTS

Intra- and Interoperator Repeatability of Spine Measurements from Topograms

The use of CT topograms to quantify spine traits can be confidently accepted as a reliable method, as there is high reproducibility of identical or near-matching measures for spine characteristics when recorded either by the same or different individuals who followed a fixed protocol. Intraoperator intraclass correlation coefficients varied from high to very high for all spine characteristics (observer A, r_t = 0.82 to 0.93; observer B, r_t = 0.80 to 0.88; observer C, r_t = 0.77 to 0.83). Similarly, interoperator results show high agreement with intraclass correlation coefficients ranging from 0.80 to 0.91 between all observer paired comparisons for all spine characteristics.

Intra- and Interbreed Variations in Spine Traits

The degree of thoracolumbar vertebral variation within breeds was investigated (Fig. 2). Frequency distributions reveal that, from this sample, TEX exhibits the widest range of thoracolumbar vertebrae number (17 to 21), TEX × MULE the smallest (18 to 20), whereas SBF and PD × MULE show an intermediate range (18 to 21) between these 2 groups. Despite the larger range of thoracolumbar vertebrae totals in TEX, the percentage of animals that possess the extreme vertebral counts are very low; <1% of the total sample possess 17 or 21 thoracolumbar vertebrae (1 lamb in each case). Also (seen from Table 2), in contrast to SBF and PD × MULE, TEX lambs show a greater incidence (~70% of the sample) of 19 thoracolumbar vertebrae, the majority (~59%) of which have the vertebral combination of 13 thoracic and 6 lumbar, whereas the majority of SBF and

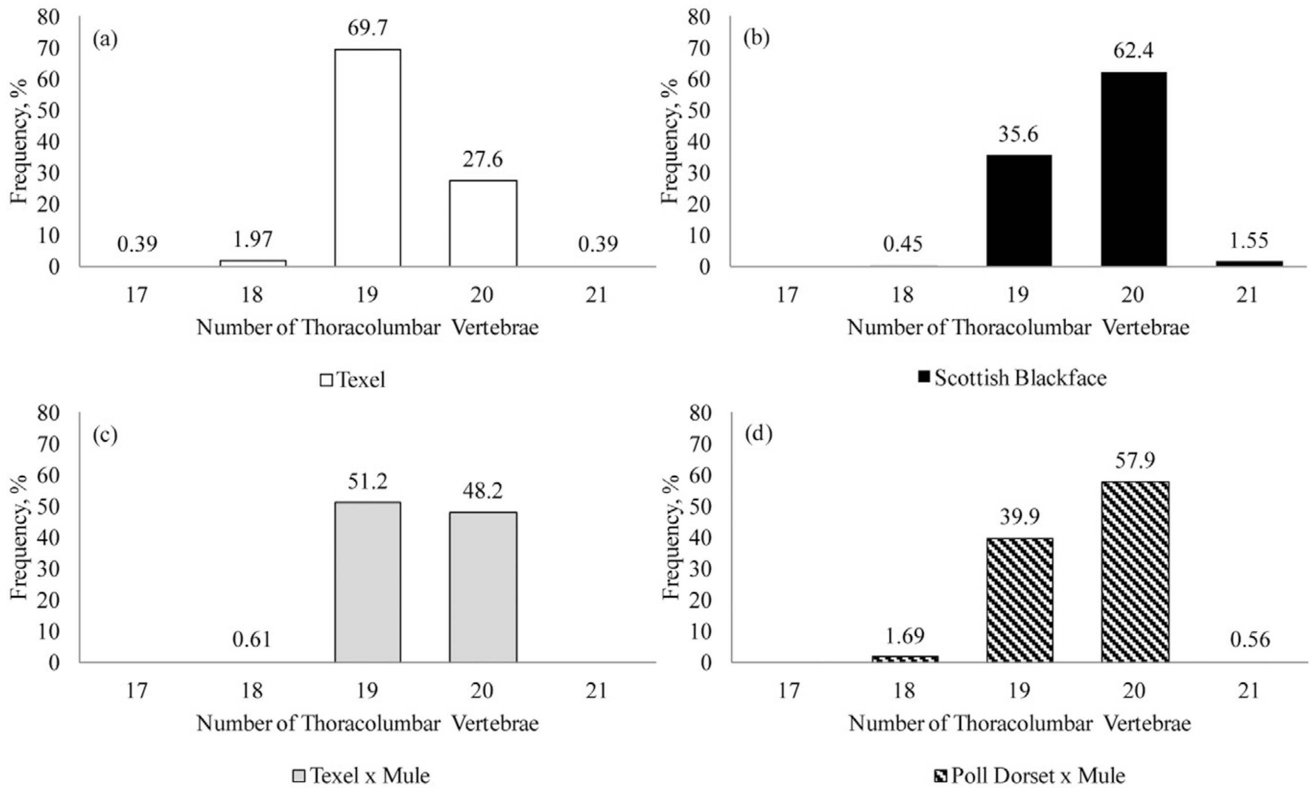

Figure 2. Frequency of lambs (by breed or cross) in each class for total thoracolumbar vertebrae: (a) Texel, (b) Scottish Blackface, (c) Texel cross Mule, (d) Poll Dorset cross Mule.

PD × MULE lambs have 20 thoracolumbar vertebrae (62 and 58%, respectively) with the most common thoracolumbar vertebral combination being 13 and 7 lumbar vertebrae. Almost all lambs (~99%) belonging to the TEX × MULE group either possess 19 or 20 thoracolumbar vertebrae, with a near-equal ratio between the 2 categories, 51 and 48%, respectively. For those TEX × MULE lambs that fall in the thoracolumbar count category of 19, the most common thoracolumbar vertebral combination is 13 thoracic and 6 lumbar; and those with 20 thoracolumbar vertebrae, the majority show a 13 thoracic and 7 lumbar vertebral combination.

Significant differences in VN were also identified between the breeds and crosses (Table 3). The count traits VN_{LUM} and VN_{T+L} were significantly less ($P < 0.05$) in TEX compared with SBF and the crosses, but VN_{THOR} and VN_{T+L} were significantly greater ($P < 0.05$) in SBF than other groups. Spine region and vertebrae length traits (SPL and VL respectively) were also significantly different between the breeds and crosses. For the most part, the spine regions and the average length of individual vertebrae of the crosses were observed to be longer than TEX and SBF. Again the smallest values appear in TEX; however, for some length traits (SPL_{THOR}, VL_{T-}

Table 2. Percentage of lambs within each breed[1] with each thoracic (Thor.) and lumbar (Lum.) vertebrae number combination

No. of vertebrae			TEX	SBF	TEX × MULE	PD × MULE
Thoracolumbar	Thor.	Lum.	(n = 254)	(n = 1100)	(n = 326)	(n = 178)
17	13	4	0.39			
18	12	6	1.97	0.45	0.61	1.69
19	12	7	11.0	1.82	3.37	5.62
	13	6	58.7	33.8	47.9	34.3
20	12	8		0.09		
	13	7	24.4	57.5	44.8	53.4
	14	6	3.15	4.73	3.37	4.49
21	13	8		0.09		
	14	7	0.39	1.45		0.56

[1]TEX = Texel; SBF = Scottish Blackface; TEX × MULE = Texel × Mule; PD × MULE = Poll Dorset × Mule

Table 3. Least-squares means (and SE) for CT measured spine traits[1] in different breeds or crosses[2]

Trait	TEX (n = 254)	SBF (n = 1100)	TEX × MULE (n = 326)	PD × MULE (n = 178)
VN_{THOR}	12.84^{c} (0.028)	12.96^{a} (0.026)	12.92^{b} (0.031)	$12.90^{b,c}$ (0.035)
VN_{THOR}_BW	12.84^{b} (0.028)	12.98^{a} (0.027)	12.89^{b} (0.032)	12.90^{b} (0.035)
VN_{LUM}	6.392^{c} (0.045)	6.662^{a} (0.042)	6.527^{b} (0.049)	6.639^{a} (0.056)
VN_{LUM}_BW	6.394^{c} (0.046)	6.659^{a} (0.043)	6.534^{b} (0.052)	6.639^{a} (0.056)
VN_{T+L}	19.24^{c} (0.048)	19.63^{a} (0.044)	19.44^{b} (0.052)	19.54^{b} (0.058)
VN_{T+L}_BW	19.23^{d} (0.048)	19.64^{a} (0.045)	19.42^{c} (0.054)	19.54^{b} (0.058)
SPL_{THOR}	252.7^{c} (1.719)	254.5^{c} (1.614)	279.0^{a} (1.813)	270.8^{b} (2.043)
SPL_{THOR}_BW	250.5^{d} (1.067)	261.7^{c} (0.999)	265.9^{b} (1.220)	270.5^{a} (1.305)
SPL_{LUM}	181.8^{c} (1.619)	190.9^{b} (1.521)	199.1^{a} (1.708)	198.7^{a} (1.925)
SPL_{LUM}_BW	181.8^{d} (1.226)	196.0^{b} (1.147)	193.4^{c} (1.401)	200.8^{a} (1.499)
SPL_{T+L}	434.4^{d} (2.419)	445.4^{c} (2.272)	478.2^{a} (2.551)	469.5^{b} (2.875)
SPL_{T+L}_BW	432.3^{c} (1.397)	457.7^{b} (1.308)	459.2^{b} (1.597)	471.3^{a} (1.708)
VL_{THOR}	19.67^{c} (0.121)	19.61^{c} (0.114)	21.59^{a} (0.128)	20.98^{b} (0.144)
VL_{THOR}_BW	19.52^{d} (0.073)	20.15^{c} (0.068)	20.63^{b} (0.083)	20.96^{a} (0.089)
VL_{LUM}	28.63^{d} (0.142)	28.84^{c} (0.133)	30.71^{a} (0.149)	30.21^{b} (0.168)
VL_{LUM}_BW	28.50^{d} (0.087)	29.49^{c} (0.081)	29.66^{b} (0.099)	30.28^{a} (0.106)
VL_{T+L}	22.63^{c} (0.114)	22.72^{c} (0.107)	24.63^{a} (0.120)	24.09^{b} (0.135)
VL_{T+L}_BW	22.50^{d} (0.061)	23.31^{c} (0.057)	23.66^{b} (0.070)	24.12^{a} (0.075)

[a–d]Within a row, means without a common superscript differ ($P < 0.05$).

[1]CT = x-ray computed tomography; BW = BW (kg) fitted as a covariate in model; VN_{THOR} = number of thoracic vertebrae; VN_{LUM} = number of lumbar vertebrae; VN_{T+L} = number of thoracolumbar vertebrae; SPL_{THOR} = length of thoracic spine region (mm); SPL_{LUM} = length of lumbar spine region (mm); SPL_{T+L} = length of thoracolumbar spine region (mm); VL_{THOR} = average length of individual thoracic vertebrae (mm); VL_{LUM} = average length of individual lumbar vertebrae; VL_{T+L} = average length of individual thoracolumbar vertebrae (mm).

[2]TEX = Texel; SBF = Scottish Blackface; TEX × MULE = Texel × Mule; PD × MULE = Poll Dorset × Mule.

HOR, VL_{T+L}) there were no significant differences between TEX and SBF. These breed differences remained consistent, for the majority of spine traits, across the 2 models (BW corrected and BW not corrected), giving an indication to a genetic basis for the variation in spine characteristics.

To note, sex effects on spine traits were also tested, but for the majority there were no significant differences between males and females; VL_{LUM} was the single trait where significant differences between sexes appeared (males were slightly shorter than females, results not shown).

Intrabreed Trait Correlations

Further to the investigation of intrabreed vertebral variation, correlation coefficients among all CT spine and tissue traits were examined; these are given in Table 4 for breeds TEX and SBF and Table 5 for crosses TEX × MULE and PD × MULE.

Spine Traits. How variation in spine count traits (VN_{THOR}, VN_{LUM}, VN_{T+L}) was associated with spine length traits (SPL_{THOR}, SPL_{LUM}, SPL_{T+L}, VL_{THOR}, VL_{LUM}, VL_{T+L}) within each breed or cross was assessed. First, correlations between traits concerning the combined thoracic and lumbar (thoracolumbar) spine region show significant ($P < 0.001$) moderate positive linear associations between VN_{T+L} and SPL_{T+L} (TEX, $r = 0.41$; SBF, $r = 0.60$; TEX × MULE, $r = 0.50$; PD × MULE, $r = 0.64$) and between SPL_{T+L} and VL_{T+L} (TEX, $r = 0.62$; SBF, $r = 0.65$; TEX × MULE, $r = 0.64$; PD × MULE, $r = 0.50$), but negative correlations between VN_{T+L} and VL_{T+L} (TEX, $r = -0.46$; SBF, $r = -0.21$; TEX × MULE, $r = -0.34$; PD × MULE, $r = -0.33$). These correlations give an indication that an increased thoracolumbar spine region length may arise from 2 situations: a greater number of shorter vertebrae or a smaller number of vertebrae that are longer.

Assessing the thoracic spine region alone, in TEX, there were significant ($P < 0.001$) positive correlations between VN_{THOR} and SPL_{THOR} ($r = 0.43$) and between SPL_{THOR} and VL_{THOR} ($r = 0.79$), and again a significant ($P < 0.001$) negative correlation between VN_{THOR} and VL_{THOR} ($r = -0.21$). The SBF, TEX × MULE, and PD × MULE exhibited similar positive correlations for the former 2 traits, but unlike TEX there were no significant ($P > 0.05$) associations between VN_{THOR} and VL_{THOR}. The greater correlations occurred between SPL_{THOR} and VL_{THOR} within each group (SBF, $r = 0.85$; TEX, $r = 0.79$; TEX × MULE, $r = 0.88$; PD × MULE, $r = 0.76$) which could suggest that, if a lamb has a long thoracic region,

Table 4. Correlation coefficients[1] (r) between CT measured traits[2] for Texel (above diagonal; n = 254[3]) and Scottish Blackface (below diagonal; n = 1100[4]) lambs

Trait	PR_FAT	PR_MUSC	LM_{AREA}	VN_{THOR}	VN_{LUM}	VN_{T+L}	SPL_{THOR}	SPL_{LUM}	SPL_{T+L}	VL_{THOR}	VL_{LUM}	VL_{T+L}
PR_FAT		–0.31***	–0.03	–0.03	0.02	–0.01	–0.05	–0.01	–0.05	–0.03	–0.06	–0.04
PR_MUSC	0.01		0.66***	0.14*	–0.16*	–0.05	0.15*	–0.20**	–0.06	0.06	–0.06	–0.01
LM_{AREA}	0.27***	0.59***		0.18**	–0.15*	–0.01	0.14*	–0.18**	–0.04	0.03	–0.03	–0.03
VN_{THOR}	0.01	–0.01	–0.03		–0.36***	0.41***	0.43***	–0.40***	0.01	–0.21***	–0.01	–0.35***
VN_{LUM}	–0.05	–0.04	–0.10***	–0.20***		0.70***	–0.52***	0.92***	0.41***	–0.31***	–0.46***	–0.19**
VN_{T+L}	–0.04	–0.05	–0.11***	0.37***	0.84***		–0.18**	0.60***	0.41***	–0.47***	–0.46***	–0.46***
SPL_{THOR}	–0.05	0.02	–0.01	0.48***	–0.32***	–0.03		–0.45***	0.50***	0.79***	0.33***	0.64***
SPL_{LUM}	–0.08**	–0.04	–0.14***	–0.21***	0.90***	0.74***	–0.20***		0.55***	–0.21**	–0.11	0.03
SPL_{T+L}	–0.11***	–0.02	–0.13***	0.17***	0.53***	0.60***	0.56***	0.70***		0.54***	0.20**	0.62***
VL_{THOR}	–0.06	0.03	0.00	–0.04	–0.24***	–0.25***	0.85***	–0.10***	0.54***		0.37***	0.93***
VL_{LUM}	–0.06*	0.02	–0.06	0.04	–0.44***	–0.40***	0.32***	–0.01	0.23***	0.34***		0.59***
VL_{T+L}	–0.09**	0.02	–0.05	–0.13***	–0.15***	–0.21***	0.72***	0.15***	0.65***	0.90***	0.65***	

[1]Significant phenotypic correlations: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[2]CT = x-ray computed tomography; PR_FAT = predicted weight of total carcass fat (kg); PR_MUSC = predicted weight of total carcass muscle (kg); LM_{AREA} = average LM area (mm^2); VN_{THOR} = number of thoracic vertebrae; VN_{LUM} = number of lumbar vertebrae; VN_{T+L} = number of thoracolumbar vertebrae; SPL_{THOR} = length of thoracic spine region (mm); SPL_{LUM} = length of lumbar spine region (mm); SPL_{T+L} = length of thoracolumbar spine region (mm); VL_{THOR} = average length of individual thoracic vertebrae (mm); VL_{LUM} = average length of individual lumbar vertebrae; VL_{T+L} = average length of individual thoracolumbar vertebrae (mm).

[3]n = 246 for those correlations against the trait PR_FAT.

[4]n = 1099 for those correlations against the trait PR_FAT.

a greater proportion of this is due to individual vertebrae being longer, rather than an increased number of bones.

Investigating associations between spine count and length traits concerning only the lumbar region revealed that all breed or cross groups displayed very strong and significant positive correlations between traits VN_{LUM} and SPL_{LUM} (TEX, r = 0.92; SBF, r = 0.90; TEX × MULE, r = 0.89; PD × MULE, r = 0.93) and negative correlations between VN_{LUM} and VL_{LUM} (TEX, r = –0.46; SBF, r = –0.44; TEX × MULE, r = –0.37; PD × MULE, r = –0.44). However, nonsignificant correlations ($P > 0.05$) occurred between SPL_{LUM} and VL_{LUM} for TEX, SBF, and TEX × MULE. This may suggest that, for these breeds or cross groups, if an increase in the lumbar region occurs, a greater proportion of this is due to additional lumbar vertebrae, in contrast to the

Table 5. Correlation coefficients[1] (r) between CT measured traits[2] for Texel cross Mule (above diagonal; n = 326) and Poll Dorset cross Mule (below diagonal; n = 178) lambs

Trait	PR_FAT	PR_MUSC	LM_{AREA}	VN_{THOR}	VN_{LUM}	VN_{T+L}	SPL_{THOR}	SPL_{LUM}	SPL_{T+L}	VL_{THOR}	VL_{LUM}	VL_{T+L}
PR_FAT		–0.27***	0.11	–0.09	0.06	0.01	–0.14*	0.06	–0.05	–0.10	–0.01	–0.07
PR_MUSC	–0.44***		0.53***	0.07	–0.09	–0.05	0.05	–0.09	–0.04	0.01	0.01	–0.01
LM_{AREA}	0.16*	0.33***		0.10	0.03	0.08	–0.01	–0.02	–0.03	–0.07	–0.11*	–0.10
VN_{THOR}	0.06	–0.03	0.06		–0.23***	0.31***	0.43***	–0.31***	0.06	–0.05	–0.13*	–0.21***
VN_{LUM}	0.02	–0.10	0.08	–0.22**		0.85***	–0.42***	0.89***	0.47***	–0.35***	–0.37***	–0.23***
VN_{T+L}	0.06	–0.11	0.11	0.46***	0.77***		–0.19***	0.70***	0.50***	–0.37***	–0.44***	–0.34***
SPL_{THOR}	–0.04	–0.09	–0.01	0.59***	–0.47***	–0.04		–0.33***	0.50***	0.88***	0.30***	0.71***
SPL_{LUM}	0.00	–0.17*	0.01	–0.22**	0.93***	0.70***	–0.37***		0.65***	–0.20***	0.06	0.08
SPL_{T+L}	–0.04	–0.24**	0.00	0.27***	0.51***	0.64***	0.46***	0.65***		0.52***	0.29***	0.64***
VL_{THOR}	–0.10	–0.09	–0.06	–0.07	–0.40***	–0.41***	0.76***	–0.28***	0.35***		0.40***	0.90***
VL_{LUM}	–0.06	–0.16*	–0.21**	0.07	–0.44***	–0.35***	0.40***	–0.11	0.22**	0.43***		0.71***
VL_{T+L}	–0.11	–0.17*	–0.13	–0.18*	–0.23**	–0.33***	0.61***	0.00	0.50***	0.90***	0.68***	

[1]Significant phenotypic correlations: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[2]CT = x-ray computed tomography; PR_FAT = predicted weight of total carcass fat (kg); PR_MUSC = predicted weight of total carcass muscle (kg); LM_{AREA} = average LM area (mm^2); VN_{THOR} = number of thoracic vertebrae; VN_{LUM} = number of lumbar vertebrae; VN_{T+L} = number of thoracolumbar vertebrae; SPL_{THOR} = length of thoracic spine region (mm); SPL_{LUM} = length of lumbar spine region (mm); SPL_{T+L} = length of thoracolumbar spine region (mm); VL_{THOR} = average length of individual thoracic vertebrae (mm); VL_{LUM} = average length of individual lumbar vertebrae; VL_{T+L} = average length of individual thoracolumbar vertebrae (mm).

thoracic, where it is more likely to be due to an increase in the length of the individual bones.

Tissue Traits. Correlations between tissue and spine traits appeared to be more breed or cross specific. The tissue traits PR_MUSC and LM_{AREA} in TEX were only showing low but significant correlations with VN_{THOR}, VN_{LUM}, SPL_{THOR}, and SPL_{LUM}; these were positive with VN_{THOR} and SPL_{THOR}, but negative with VN_{LUM} and SPL_{LUM}. Hence, TEX lambs that have a longer thoracic and shorter lumbar region may be, on average, more likely to have slightly more muscle in their carcass and a larger LM area, at a given BW.

For SBF lambs, there were no significant correlations between PR_MUSC and spine traits. On the other hand, low but significant negative relationships were found between PR_FAT and SPL_{LUM}, SPL_{T+L}, VL_{LUM}, and VL_{T+L} and between LM_{AREA} and VN_{LUM}, VN_{T+L}, SPL_{LUM}, and SPL_{T+L}. This suggests that SBF lambs that were observed to possess a longer lumbar length may also be observed to have a slightly decreased volume of carcass fat and a smaller eye muscle area at a given BW.

Very few correlations between tissue and spine traits showed significance within the TEX × MULE group; PR_FAT showed a negative correlation with SPL_{THOR} (r = –0.14) and LM_{AREA} showed a negative correlation with VL_{LUM} (r = –0.11). Within the PD × MULE lamb group, significant negative correlations occurred between PR_MUSC and SPL_{LUM}, SPL_{T+L}, VL_{LUM}, and VL_{T+L} and between LM_{AREA} and VL_{LUM}.

DISCUSSION

Deriving Spine Traits from Computed Tomography

Early methods used by the livestock sector to measure variation in the thoracolumbar region of commercial pigs included slaughter of the animal and radiography (Martin and Fredeen, 1966). Computed tomography, however, can operate as a more reliable and advanced alternative for measuring spine traits in vivo. A computer-aided 3-dimensional representation of the animal can be produced from the procedure, providing a means to gain a more comprehensive set of measurements describing the whole carcass. Robust predictions of empirical carcass length can be obtained from the topograms rather than relying on subjective visual judgement.

There is a stratified system of sheep breeding in the UK, with the majority of slaughter lambs (~70%) sired by rams of terminal sire breeds (e.g., Texel, Suffolk, Charollais; Pollott and Stone, 2006). The selection goals in these terminal sire breeds are centered on the size of the breed, carcass characteristics, and particularly faster lean growth (Bunger et al., 2011) and used in the final stage of the breeding system to produce the desired lamb for market (Pollott and Stone, 2006). Due to its more advanced capabilities, many more selection candidate rams are routinely placed under the CT scanning procedure to assess their carcass quality (e.g., tissue composition, proportions, and distributions). Topograms are, therefore, readily available to take measures of spine traits simultaneously. The addition of spine trait records in sheep breeding programs and sire referencing schemes could inform breeders about other areas of potential stock improvement [i.e., the prospect of added value from each slaughter lamb if an increase of average carcass length (or length of a high-priced region such as the loin) was achieved].

Learning from Pigs

In fact, with the implementation of spine traits in pig selection, increases of up to 15 mm in thoracolumbar length have been reported with each additional vertebra present in this region (King and Roberts, 1960). It is this variation in vertebrae number, specifically in the thoracolumbar region, that is a major contributor to the diversity observed in body (and carcass) length (Berge, 1948; i.e., animals have shorter backs if there is a reduced number of vertebrae and vice versa). Furthermore, a number of beneficial responses in production traits have been associated with an increased number of presacral vertebrae (combined number of cervical, thoracic, and lumbar vertebrae); for example, a decrease in loin fat depth (Borchers et al., 2004). Such benefits have been achieved, and can be maintained, through the genetic change of spine characteristics. Carcass length has been described as a highly heritable trait in pigs (Berge, 1948; Fredeen and Newman, 1962b; Borchers et al., 2004) with QTL identified on SSC 1 and 7 that are associated with an increase in VN (Mikawa et al., 2005, 2007, 2011).

Spine Traits in Sheep

For the majority of mammals, a departure from a total of 7 cervical vertebrae is uncommon; on the other hand, variation in the number of vertebrae comprising the postcervical regions occurs frequently (Galis et al., 2006). The sheep spine is commonly used as a model for investigating musculoskeletal conditions relating to the human spine. A few of these anatomy texts give reference to the presacral vertebral formulae in sheep (Wilke et al., 1997; Lori et al., 2005), highlighting some degree of variability in vertebrae number, but only to their specific study breeds. Unlike the bacon pig, little has been reported on the extent of vertebral variation in sheep with particular reference as to how its investigation may impact the agricultural industry (i.e., meat yields, change in shape and composition of carcasses).

This study has aimed to help fill this gap in knowledge. It included the assessment of a large sample of topograms of males and females belonging to 4 different breeds or crosses. Although little to no variation was observed in spine traits between the sexes, the study has revealed marked differences in vertebrae number and length between the breeds and crosses, which are also indicative of a genetic basis to the variation.

Similarly to pigs, there was an association between an increased thoracolumbar length and the possession of 1 or more additional vertebrae. Rather than an instance of larger numbers of smaller-sized vertebrae with no subsequent increase in overall carcass length, correlations between the traits VN_{T+L} and SPL_{T+L} for each breed or cross support the fact that additional vertebrae, albeit slightly shorter (as suggested by the correlations between traits SPV_{T+L} and VL_{T+L}), will still contribute to the animal having a longer thoracolumbar region. However, an extra vertebra is not the only source of additional length in the body. Another way by which animals may have a longer thoracolumbar region (revealed by correlations between traits SPL_{T+L} and VL_{T+L}) is through the possession of a smaller number of vertebrae that are individually larger in size. Growth of bones in both instances will, to some degree, be determined by the availability of a favorable environment. Those animals with the propensity to possess extra vertebrae through genetic inheritance, nevertheless, could have the potential to display improved performance in phenotype for body length over those that express the primitive 19 (or fewer) thoracolumbar vertebrae.

How Changes in Spine Traits Associate with Production Traits

In terms of changes in the production traits PR_FAT, PR_MUSC, and LM_{AREA}, there were very few significant directional relationships with the spine traits for each breed or cross, and in those that did occur, the magnitude of the correlations were small (r = 0.06 to 0.24).

Where PR_FAT did show a correlation with spine traits, the quantity of fat in the carcass showed a decrease with a longer thoracolumbar region, a result similarly interpreted from comparisons made in meat to fat ratios between larger- and smaller-bodied pigs by Tohara (1967). This result would be favored in the current market due to the demand from the consumer for leaner sheep meat. However, excluding a couple of incidences in TEX lambs, negative correlations are again observed between the production trait PR_MUSC and spine traits, indicating a decline in the percentage of muscling in the carcass when there is an increase in its length. The results for PR_FAT and PR_MUSC were not consistent over all spine traits, however, and for the majority of trait correlations in each breed or cross, they were shown to be nonsignificant. Furthermore, PR_FAT and PR_MUSC are traits concerning the carcass as a whole; factors other than a change in spine characteristics (e.g., environment or management, may have a significant influence on such aspects).

The LM_{AREA} was the only production trait included in this study that concerned the loin area exclusively. Its correlations with the spine traits are very variable across the breeds and crosses. The only situation where positive associations were observed was in the TEX breed; there was an increased LM_{AREA} with spine traits VN_{THOR} and SPL_{THOR}. However, considering that, also in TEX, the association between LM_{AREA} and traits VN_{LUM} and SPL_{LUM} are negative and nonsignificant with the thoracic plus lumbar spine traits (VN_{T+L} and SPL_{T+L}), an increase in either the thoracic or lumbar region may be counterbalanced with a reduction in the other, resulting in a nonsignificant net effect between LM_{AREA} and vertebral increase.

Future Work

The sheep industry is important in UK exports of lamb meat, but there is still a high requirement for the industry to increase its efficiency further. It has been demonstrated in pigs that, by incorporating information on vertebra characteristics in the selection process, there can be benefits to the production of bacon. Hence, it may be possible that the similar application of spine trait records in the selection of sheep will to improve carcass quality, in terms of size and meat yields. This could be a particularly useful method in breeds where there are no associated negative effects on welfare, the spine traits of the breed appear less than average, or there appears to be a greater tendency to possess the primitive 19 thoracolumbar vertebrae, in TEX for instance.

The present study alone does not give a comprehensive prediction to the potential quantity of saleable lean meat yield of lamb (i.e., number or size of chops from the LM). Future analyses on production traits will benefit by including information on the tissue weights and components (fat and muscle proportions) of prime cuts as individual units of the carcass. Speculation into associated locomotion problems with an increased vertebrae number has been raised in some reports (Duckworth and Holmes, 1968), but such welfare considerations have not been fully examined. Locomotion scores have been recorded for a number of TEX lambs and will be used in future assessment of such queries. Future studies will also include assessment of tissue components of other prime cuts such as the hind leg, which may also have the potential to inform of any negative or positive relationships between muscular structure and shape with variation in skeletal properties of the spine that could subsequently hinder the animals. Furthermore, genetic parameters for these spine traits will be investigated, and genetic correlations with the above and other economically important traits estimated.

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