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Meat eating and nutritional quality of lambs sired by high and low muscle density rams

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ABSTRACT

Intramuscular fat (IMF) content affects eating and nutritional quality of lamb meat. Muscle density measured by computer tomography is an *in vivo* proxy measure of IMF content that affects eating and nutritional quality of lamb meat. Lambs sired by high muscle density (HMD) or low muscle density (LMD) rams, selected for slaughter on commercial criteria were measured for meat quality and nutritional traits. A restricted maximum likelihood model was used to compare lamb traits. Additionally, regression analysis of sire estimated breeding value (EBV) for muscle density was performed for each meat quality trait. Muscle density EBV had a negative regression with IMF content ($P < 0.001$). For each unit increase in muscle density EBV, there was a significant decrease in loin (-1.69 mg/100 g fresh weight) and topside IMF (-0.03 mg/100 g fresh weight). Muscle density EBV had a negative regression with grouped saturated and monounsaturated fatty acids concentration (and monounsaturated proportion $P < 0.001$). Muscle density EBV had a negative regression with loin sensory traits tenderness, juiciness and overall liking and many novel tenderness sensory traits measured ($P < 0.05$). Selecting for LMD EBV increased IMF content and favourable meat eating quality traits. In contrast, sire muscle density EBV had a positive regression with loin polyunsaturated:saturated fat ratio and grouped polyunsaturated proportion traits (including total polyunsaturated proportion, total omega-6 ($n-6$) and total omega-3 ($n-3$) fatty acids ($P < 0.001$). This is explained by the fact that as sire muscle density EBV increases, polyunsaturated fatty acid proportion increases and the proportion of saturated and monounsaturated fatty acid content decreases. Muscle density EBV had a positive regression with shear force and the novel toughness sensory traits ($P < 0.05$). Selection for HMD EBV's increased shear force and toughness traits, which is unfavourable for the consumer. Low muscle density sired meat had higher meat colour traits chroma/saturation ($+0.64$, SD 2.30, $P = 0.012$), redness ($+0.52$, SD 1.91, $P = 0.012$) and yellowness ($+0.31$, SD 1.49, $P = 0.08$) compared to HMD sired meat. Selection for LMD could be used within a breeding programme to increase IMF content and enhance both meat colour and improve eating quality parameters.

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Implications

Selection for increased lean and decreased fat has led to lower fat content in lamb meat. Intramuscular fat (marbling) is beneficial for meat eating quality. Muscle density is a novel *in vivo* proxy computer

tomography trait for intramuscular fat. Selecting for rams with low muscle density estimated breeding values enhances lamb meat eating quality by increasing intramuscular fat, decreasing shear force, improving sensory traits relating to tenderness and increases colour traits (saturation, redness and yellowness). Muscle density could be used within a terminal sire breeding programme to improve lamb meat eating quality.

Introduction

Within the sheep sector, there has been genetic selection for increased lean and decreased fat content of the carcass (Simm et al., 2001; Pethick et al., 2006). However, this can reduce intramuscular fat

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(IMF) content (Pannier et al., 2014b) and eating quality (Pannier et al., 2014a). Fat is distributed in internal, subcutaneous, intermuscular and IMF depots. It is difficult to select for changes in an individual fat depot as they have high positive phenotypic and genetic correlations with other depots and overall lamb fatness (Pannier et al., 2014b; Anderson et al., 2015). Lamb, although considered a high-fat meat it has a low marbling/IMF content (ranges of IMF of 1.3–5.7% (Navajas et al., 2008; Mortimer et al., 2010; Lambe et al., 2011)).

Total IMF consists of saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and polyunsaturated fatty acids (PUFA). Polyunsaturated fatty acids include the omega-6 ($n-6$) and the omega-3 ($n-3$) fatty acids. Omega-3's are found specifically in the muscle phospholipid membranes of ruminant meat (Enser et al., 1996). Health beneficial omega-3 PUFA's include alpha-linolenic acid (C18:3 $n-3$) and its long chain derivatives eicosapentaenoic acid (C20:5 $n-3$) and docosahexaenoic acid (C22:6 $n-3$; Simopoulos, 2008).

It is difficult to measure IMF in a live animal. However, muscle density as measured by computer tomography (CT) has been identified as an *in vivo* measure of IMF (Karamichou et al., 2006; Navajas et al., 2006; Clelland et al., 2014). Low CT muscle density could be used as a proxy for increased IMF and improved meat quality. This study was designed to test the hypothesis that selecting rams for CT scanned low muscle density (LMD) will increase progeny IMF content and improve meat eating quality traits without changing the nutritional quality.

Material and methods

Ram selection and mating

A group of Abermax™ ram lambs ($n = 122$) was CT scanned. Five rams with high muscle density (HMD) and five rams with LMD values were selected. Mean muscle density recorded at the fifth lumbar vertebrae (LV) of HMD and LMD ram groups differed by 3 SD (means of 45.06 Hounsfield Units and 38.28 Hounsfield Units, respectively, as described in detail in Thomas et al., 2020). High muscle density ($n = 5$) and LMD ($n = 5$) selected rams were used in a commercial laparoscopic artificial insemination procedure (Innovis Ltd. AI services), with 230 North Country Mule ewes (23 ewes per ram). All lambs ($n = 395$) had growth and carcass traits measured as described by Thomas et al. (2020). MyoMax® is a gene mutation that increases meat yield, therefore status (carrier/noncarrier) was determined for all progeny lambs (Zoetis, Auckland, New Zealand).

Slaughter protocol

Lambs were selected for slaughter on commercial criteria (target carcass weight: 18–21 kg and EUROP fat class of 2/3 1). Mean slaughter age was 146.7 and 146.2 days for HMD and LMD lambs, respectively. Slaughter's live weight was 43.08 and 42.78 kg for HMD and LMD lambs, respectively. Progeny lambs were slaughtered in four batches (Batch 1 $n = 49$, Batch 2 $n = 111$, Batch 3 $n = 66$ and Batch 4 $n = 43$). Lambs were stunned, exsanguinated and individually recorded throughout the study. Carcasses were subjected to low voltage electrical stimulation (<50 V for 60 s at 15 min *post mortem*). Attempts were made to ensure equal numbers of ewe and castrate lambs were in each sire group, resulting in 202 progeny carcasses being used for the study.

Cutting and maturation of the *M. longissimus lumborum* (loin) and *M. semimembranosus* (topside)

For each slaughter group, lamb carcasses were further processed into cuts on day 3 post slaughter; primals and cuts destined for further analysis (Table 1) were weighed (Thomas et al., 2020). The left loin was deboned (Rib 1-LV7), aged for 7 days and then frozen (-20°C) prior to sensory analysis at the University of Bristol. The right

Table 1

Weights of lamb *M. longissimus lumborum* (loin) and *M. semimembranosus* (topside) samples and associated meat quality tests.

Muscle weights	n	Mean	SD
Non matured muscle weights (g)			
Cranial right loin (third section – caudal) for fatty acid analysis	202	78.5	17.20
Cranial left topside for fatty acid analysis	201	157.2	22.86
Matured muscle weight (g)			
Whole left loin for sensory	202	484.9	51.33
Short right loin for CT and shear force	202	246.5	33.30
Cranial left topside shear force	201	159.5	25.70
Caudal left topside sensory	201	156.7	28.70

n – number; g – gram; CT – computer tomography.

loin primals were split into half at the anterior cranial edge of the first LV. The cranial part of the right loins was not aged and was frozen for fatty acid analysis. The caudal right loins (1st to 7th LV, short loin) were aged for 7 days before CT scanning (Clelland et al., 2013) and shear force analysis at the Scotland's Rural College (SRUC). The left topside was revealed after the *M. gracilis* (cap) of the leg primal was removed. The topside was cut into three sections, one third (cranial) for fatty acid analysis (frozen pre-maturation) and two thirds (caudal) were aged for 7 days and frozen for subsequent shear force and sensory analysis.

M. longissimus lumborum fatty acid meat sample preparation and bimethylation

Loin samples ($n = 195$) were defrosted for > 16 h and the thoracic vertebrae, subcutaneous fat, epimysium, connective tissue and intermuscular fat were removed (some loins were damaged during freezing and were removed from the trial). Samples were freeze-dried with analysis of fatty acid composition undertaken using a direct bimethylation procedure following the method outlined by Lee et al. (2012). Optimisation by identifying the correct fatty acid peaks of samples was carried out using Varian (Agilent) Star GC Workstation software. Total fatty acids were taken as the sum of all the fatty acids quantified. The concentrations of individual fatty acids were then grouped into sub-classes (Supplementary Table S1).

M. longissimus lumborum mineral composition methodology

Zinc and iron content was determined on freeze-dried lamb subsamples. These were prepared using the wet digestion method described by Osorio et al. (2007). Zinc and iron concentration was determined by inductively coupled plasma atomic emission spectroscopy (Varian Liberty, Agilent Technologies UK Ltd., Wokingham, UK). Mineral analyses were carried out in duplicate (paired values were averaged for each lamb).

M. longissimus lumborum and *M. semimembranosus* shear force

Right rear loin samples ($n = 202$) and topside shear force analysis ($n = 201$) involved defrosting the samples for 16 h then placing the samples in a labelled unsealed polythene bag submerged in a water bath (loin 80°C and topside 100°C). When the internal temperature of the sample reached $72-75^{\circ}\text{C}$, samples were removed from the heat and placed in an ice bath until the sample internal temperature reached below 3°C . Samples were cut into 10, $10 \times 10 \times 20$ mm blocks, ensuring the long axis was parallel to fibre orientation (at 45° gradient orientation). Shear force was measured as the force needed (Newtons) to cut the muscle fibres at a right angle using a MIRINZ Tenderscot tenderometer for the loin (Tenderscot, Pentland Precision Engineering Limited, Midlothian, UK) and a MIRINZ tenderometer for the topside (Smith-Biolab, Ltd., Auckland, NZ).

M. longissimus lumborum colour

Whole left loins were assessed for colour traits. Samples were thawed for approximately 16 h and cut into nine steak pieces (2 cm depth) and were bloomed underneath oxygen-permeable clingfilm for an hour. Colour coordinates were determined (L^* represents lightness, a^* red–green range redness and b^* the blue–yellow range, yellowness) using an average of three measurements with a Minolta Chroma Meter CR-400 (Minolta Camera Co, Osaka, Japan). Colour chroma (saturation) of each sample was calculated as $\sqrt{a^{*2} + b^{*2}}$. Colour hue was calculated by the formula: Hue = $[\tan^{-1}(b^*/a^*)]$ and tan alpha b^*/a^* (angle whose tangent is (b^*/a^*) when $a^* > 0$ and $b^* > 0$).

M. longissimus lumborum and *M. semimembranosus* sensory evaluation

Following colour measurement, loin samples were cooked by grilling similar to the method described by Nute et al. (2007). Samples were trimmed to 50 × 20 × 10 mm, (with minimal visible gristle, fat or external sides), wrapped in pre-coded foil wrappers and served warm, in a room with booths illuminated by red light and were assessed by 10 trained assessors. Assessors were previously screened according to the British Standards Institute methods for taste sensitivity (British Standards Institution BSI, 1993). The assessors entered scores directly into a computerised sensory assessment programme (Fizz, Version 2.10c, Biosystemes, Couternon, France).

The panelists were asked to rate the meat on a fixed point scale (1–8) for six characteristics: tenderness, juiciness, lamb flavour intensity, abnormal flavour intensity, hedonic flavour liking and hedonic overall liking (as described in Supplementary Table S2). Lamb samples were also rated on a novel sensory tenderness profile using a 0–100 mm unstructured line scale with anchor points at each end (details are in Supplementary Table S3): On cutting: ease of cutting, cleanness of cut. Initial chewing: tough, crunchy, juiciness and sponginess. On eating: tough, moisture, chewiness, greasy, fibres, gristle, pulpy and dissolubility. Residue: greasy mouthfeel, ease of swallow, pulpy, particles and mouthfeel at end. Topside steaks were assessed for the initial six sensory characteristics and prepared similarly as the loin. There were 39 topside steaks deemed too small for analysis and these were removed from the study ($n = 162$). Tenderness assessment was not undertaken due to the small sample size.

Statistical analysis

Data were checked for normal distribution; traits, where residuals were skewed were transformed. Meat quality traits requiring \log_{10} transformation were loin colour traits hue, lightness and redness and the sensory trait loin gristle. Many fatty acid traits required \log_{10} or square root transformation to normalise prior to analysis. A nested ANOVA was used to identify significant fixed effects for each trait (using the programme Genstat 15 (Payne et al., 2011)). A model was fitted with sire nested within muscle density group (high or low). Fixed effects included lamb sex (ewe/wether), dam age (2 year/older), rearing status (single/twin), MyoMAX® status (MyoMAX® carrier and non-carrier) and slaughter batch. Pre-slaughter live weight was used as a covariate for meat and nutritional quality traits (as in practice lambs are slaughtered to achieve a target deadweight). Panel number was used as a covariate for sensory traits.

Restricted maximum likelihood (REML) was used to compare mean performance of lambs sired by HMD and LMD rams. An alternative approach to investigating the association of sire muscle density to lamb performance is the regression coefficient of sire estimated breeding value (EBV) for muscle density on each trait. Muscle density EBVs of the 10 sires used were calculated retrospectively in 2013 using a univariate animal model in ASReml that fitted live weight at CT scanning as a covariate

once sufficient familial data records were available. The progeny lambs included in the trial reported here were not used in this genetic evaluation. The pedigree file included 20 433 animals, of which 869 individuals had CT records for muscle density, including many half-sibs of the sires used (no progeny lambs from this trial were included). A heritability value of 0.40 was used in the genetic evaluation based upon heritability estimates produced by Karamichou et al. (2006). The regression coefficients of the traits on sire muscle density EBV were estimated in a REML model in ASREML by fitting the significant fixed effects that had been previously identified using the unbalanced ANOVA model (described above). Appropriate covariates were also fitted (pre-slaughter live weight for meat and nutritional quality traits).

Table 2

Effect of sire muscle density on lamb individual fatty acid (mg/100 g fresh weight) and mineral composition.

Nutritional composition	HMD	LMD	± SED	P-value
	Geometric mean (mg/100 g FW)			
<i>M. longissimus lumborum</i> fatty acid concentration (mg/100 g FW)				
C12:0 ¹	9	9	0.053	0.655
C14:0 ¹	100	106	0.041	0.526
C16:0 ¹	550	587	0.033	0.412
C16:1cis 9 ¹	32	34	0.032	0.576
C18:0 ¹	344	383	0.030	0.163
C18:1cis 9 ¹	748	830	0.034	0.227
C18:1trans11 ¹	73	86	0.037	0.096
C18:2n-6 ¹ (LA)	73	73	0.011	0.941
C18:3n-3 ¹ (ALA)	48	48	0.014	0.682
C18:3n-6 ¹	1	1	0.019	0.125
CLA cis9 trans11 ¹	36	41	0.041	0.178
CLA trans10 cis12 ¹	0	0	0.010	0.521
C20:3n-6 ¹	3	3	0.013	0.479
C20:4n-6 ¹	29	29	0.011	0.478
C20:3n-3 ¹	0	0	0.026	0.285
C20:5n-3 ¹ (EPA)	29	29	0.011	0.882
C22:4n-6 ¹	1.467	1.469	0.008	0.017
C22:5n-3 ¹ (DPA)	27	27	0.011	0.577
C22:6n-3 ¹ (DHA)	9	9	0.022	0.720
Total intramuscular fat ²	2338	2551	1.512	0.193
Total saturated ²	1000	1100	1.076	0.192
Total C18:1 trans ²	95	110	0.374	0.088
Total monounsaturated ²	957	1069	1.173	0.176
Total polyunsaturated ²	220	220	0.136	0.926
Total n-6 ²	105	105	0.134	0.880
Total n-3 ²	113	114	0.135	0.822
Polynunsaturated: saturated ratio	0.22	0.20	0.014	0.161
n-6:n-3 ratio	0.94	0.93	0.027	0.957
C18:2n-6:C18:3n-3 ratio	1.53	1.53	0.053	0.922
<i>M. semimembranosus</i> total intramuscular fat ¹	2183	2371	0.024	0.177
<i>M. longissimus lumborum</i> fatty acid proportion (% of total IMF × 100)				
Total saturated	42.85	42.85	0.006	0.959
Total C18:1 trans	3.99	4.25	0.018	0.181
Total monounsaturated	40.83	41.69	0.007	0.226
Total polyunsaturated	9.41	8.59	0.024	0.147
Total n-6	4.57	4.18	0.028	0.198
Total n-3	4.85	4.45	0.022	0.140
<i>M. longissimus lumborum</i> mineral traits				
Iron freeze dried (mg/kg)	53.21	53.01	1.469	0.897
Iron FW (mg/100 g)	1.36	1.36	0.038	0.983
Zinc freeze dried ¹ (mg/kg)	69.66	70.96	0.020	0.696
Zinc FW ¹ (mg/100 g)	1.79	1.83	0.018	0.612

HMD – high muscle density sired lamb; LMD – low muscle density sired lamb; FW – fresh weight; IMF – intramuscular fat; LA – linoleic acid; ALA – alpha linolenic acid; EPA – eicosapentaenoic acid; DPA – docosapentaenoic acid; DHA – docosahexaenoic acid.

¹ Log₋₁₀ transformed.

² Square root transformed.

Results

Muscle density effects on fatty acid and minerals traits

Average loin total IMF content was 2.55% for LMD and 2.34% for HMD progeny and these were not significantly different. Sire muscle density groups were not significantly different for the majority of the loin fatty acid concentrations (Supplementary Table S4 and Table 2). Low muscle density relative to HMD sired lamb meat had significantly higher C22:4 n-6 (Table 2). High muscle density and LMD groups were not significantly different for any of the grouped fatty acid concentrations or proportion traits (Table 2). Sire muscle density groups were not significantly different for mineral concentration traits (Table 2).

Muscle density effects on meat quality traits

The majority (n = 187/202) of loin shear force values were considered tender, with the remaining 15 within the acceptable range as defined by Jopson et al. (2001). The topside was tougher than the loin, with the majority of samples (n = 182/201) classed acceptably tender, one sample was classified as tender and 18 samples were within the tough range. Loin and topside shear force traits did not differ between lamb meat sired by HMD or LMD rams (Supplementary Table S5). Low muscle density sired lamb loins had increased chroma, redness and yellowness compared to HMD sired lamb (Table 3). The sire muscle density groups were not significantly different for sensory traits.

(Supplementary Table S6 and Table 4).

Regression of fatty acid and mineral traits with sire muscle density estimated breeding value

Many of the individual loin fatty acid concentrations traits had negative regressions with sire muscle density EBV; C12:0, C14:0, C16:0, C16:1cis9, C18:0, C18:1cis9, C18:1trans11, C18:3n-6, CLAcis9trans11, C20:3n-3 and C22:4n-6 (Table 5). Grouped fatty acid concentration traits; total IMF, C18:1 trans fatty acids, saturated monounsaturated and proportion traits; total monounsaturated fatty acids and C18:1trans fatty acids had negative regressions with sire muscle density EBV (Table 5). Loin fatty acid proportion traits; total polyunsaturated fatty acids, total n-6 and total n-3 and loin polyunsaturated:saturated ratio had positive regressions with sire muscle density EBV (Table 5). Loin mineral traits had no significant regression with sire muscle density EBV.

Table 3

Effect of sire muscle density on shear force and colour traits of lamb meat (at a uniform pre-slaughter live-weight).

Meat quality traits	Mean		± SED	P-value
	HMD	LMD		
<i>M. longissimus lumborum</i> shear force traits (Newtons)				
<i>M. longissimus lumborum</i> shear force	31.97	29.64	1.1	0.067
<i>M. longissimus lumborum</i> shear force SD	6.1	5.3	0.41	0.092
<i>M. semimembranosus</i> shear force	66.9	64.5	1.13	0.075
<i>M. semimembranosus</i> shear force SD	13.4	13.6	0.80	0.806
Colour traits <i>M. longissimus lumborum</i> ¹				
Chroma	17.1	17.8	0.20	0.012
Hue ²	22.03 (1.34)	22.03 (1.34)	0.005	0.885
Lightness (L*) ²	43.20 (1.64)	43.45 (1.64)	0.003	0.290
Redness (a*) ²	15.70 (1.20)	16.22 (1.21)	0.005	0.012
Yellowness (b*)	6.49	6.80	0.122	0.033

HMD – high muscle density sired lambs; LMD – low muscle density sired lambs.

¹ Aged and bloomed for 1 h.

² Log₋₁₀ transformation. Parentheses indicate log mean.

Table 4

Effect of sire muscle density on sensory traits of lamb meat (at a uniform pre-slaughter live-weight and taste panel).

	Higher value denotes	Progeny mean		± SED	P-value
		HMD	LMD		
<i>M. longissimus lumborum</i> Sensory traits (1–8)					
Tenderness	Extremely tender	5.6	5.8	0.11	0.218
Juiciness	Extremely juicy	5.0	5.1	0.08	0.230
Abnormal flavour intensity	Extremely strong	2.1	2.1	0.03	0.562
Lamb flavour intensity	Extremely strong	4.8	4.8	0.04	0.317
Hedonic flavour liking	Like extremely	5.6	5.6	0.05	0.714
Flavour overall liking	Like extremely	5.2	5.2	0.09	0.570
Sensory tenderness traits (0–100)					
Ease of cutting	Easy to cut	69.9	70.8	1.21	0.448
On cut clean	Very clean	69.2	69.8	0.71	0.471
Initial bite toughness	Very tough	29.1	27.0	1.62	0.233
Initial bite crunchiness	Extreme perceived crispiness	23.0	23.3	1.04	0.779
Initial bite juiciness	Juicy	45.5	46.2	1.32	0.640
Initial bite sponge	Extreme bounce back to bite	25.1	25.9	0.44	0.125
Eat toughness	Very tough	29.2	27.7	1.37	0.286
Eat moisture	Very wet	47.1	47.4	1.28	0.793
Eat chewiness	Extreme effort to swallow	28.5	26.4	1.34	0.159
Eat greasiness	Very greasy	20.2	20.2	0.86	0.969
Eat fibres	Extreme perceived fibres	35.4	34.1	1.10	0.243
Eat gristle ¹	Extreme gristle	3.5 (0.5)	3.2 (0.5)	0.05	0.553
Eat pulpy	Very soft/soggy	52.2	53.3	1.38	0.455
Eat dissoluble	Disintegrates in mouth	59.9	61.4	1.50	0.353
Residue greasy mouthfeel	Extreme greasy coating	19.5	19.9	0.43	0.377
Residual ease of swallow	Easy to swallow	65.9	67.4	1.34	0.286
Residual pulpy	Very soft/soggy	50.8	51.5	1.06	0.565
Residual particles	Many fine particles	53.8	53.2	0.66	0.389
Residual mouthfeel at end	Wet sensation in mouth	54.3	55.9	0.77	0.069
<i>M. semimembranosus</i> Sensory (1–8)					
Tenderness	Extremely tender	4.67	4.70	0.11	0.800
Juiciness	Extremely juicy	5.04	5.06	0.05	0.644
Abnormal flavour intensity ¹	Extremely strong	2.23 (0.35)	2.14 (0.33)	0.01	0.124
Lamb flavour intensity	Extremely strong	4.74	4.73	0.04	0.789
Hedonic flavour liking	Like extremely	5.44	5.55	0.05	0.071
Hedonic overall liking	Like extremely	5.00	5.11	0.07	0.170

HMD – high muscle density; LMD – low muscle density.

¹ Log₋₁₀ transformation. Parentheses indicate log geometric mean.

Regression of meat quality traits with sire muscle density estimated breeding value

Loin shear force, topside shear force and loin shear force SD had positive regressions with sire muscle density EBV (Table 6). Chroma and redness in aged and bloomed loin samples had a negative regression coefficient with sire muscle density EBV. Loin sensory traits tenderness, juiciness and hedonic overall liking had negative regressions with sire muscle density EBV (Table 7). Sensory tenderness traits of 'ease of cutting', 'initial bite juiciness', 'eat pulpy', 'eat dissoluble', 'residual ease of swallow' and 'residual mouthfeel' had negative regressions with sire muscle density EBV. Sensory tenderness traits of 'initial bite toughness', 'eat chewiness' and 'eat fibres' had positive regressions with sire muscle

Table 5

Regression of lamb individual fatty acid concentration and mineral traits with sire muscle density estimated breeding value.

Nutritional composition	Sire muscle density EBV		
	Regression coefficient	±SE	P-value
<i>M. longissimus lumborum</i> fatty acid concentration (mg/100 g FW)			
C12:0 ¹	-0.03	0.010	0.003
C14:0 ¹	-0.03	0.009	<0.001
C16:0 ¹	-0.03	0.008	<0.001
C16:1 cis 9 ¹	-0.02	0.009	0.002
C18:0 ¹	-0.03	0.007	<0.001
C18:1 cis 9 ¹	-0.04	0.008	<0.001
C18:1 trans 11 ¹	-0.05	0.010	<0.001
C18:2n-6 ¹ (LA)	-0.004	0.0037	0.385
C18:3n-3 ¹ (ALA)	-0.004	0.0044	0.208
C18:3n-6 ¹	-0.02	0.006	<0.001
CLA cis 9 trans 11 ¹	-0.04	0.011	<0.001
CLA trans 10 cis 12 ¹	0.003	0.0088	0.838
C20:3n-6 ¹	-0.01	0.004	0.086
C20:4n-6 ¹	-0.03	0.007	0.284
C20:3n-3 ¹	-0.02	0.009	0.006
C20:5n-3 ¹ (EPA)	-0.0004	0.0035	0.483
C22:4n-6 ¹	-0.01	0.004	0.008
C22:5n-3 ¹ (DPA)	-0.004	0.0030	0.051
C22:6n-3 ¹ (DHA)	-0.005	0.0056	0.115
Total intramuscular fat ²	-1.69	0.360	<0.001
Total saturated ²	-1.19	0.261	<0.001
Total C18:1 trans ²	-0.49	0.099	<0.001
Total monounsaturated ²	-1.32	0.267	<0.001
Total polyunsaturated ²	-0.05	0.050	0.180
Total n-6 ²	-0.03	0.039	0.445
Total n-3 ²	-0.06	0.040	0.094
Polyunsaturated: saturated ratio ²	0.02	0.004	<0.001
n-6:n-3 ratio	0.003	0.0051	0.141
C18:2n-6:C18:3n-3 ratio	0.001	0.0102	0.450
<i>M. semimembranosus</i> total intramuscular fat ¹	-0.03	0.006	<0.001
<i>M. longissimus lumborum</i> fatty acid proportion (% of total IMF × 100)			
Total saturated	-0.001	0.001	0.362
Total C18:1 trans	-0.01	0.006	0.027
Total monounsaturated	-0.01	0.001	<0.001
Total polyunsaturated	0.03	0.006	<0.001
Total n-6	0.03	0.006	<0.001
Total n-3	0.03	0.006	<0.001
<i>M. longissimus lumborum</i> mineral traits			
Iron freeze dried weight (mg/kg)	-0.005	0.383	0.529
Iron (mg/100 g)	-0.000005	±0.00019	0.558
Zinc freeze dried weight ¹ (mg/kg)	0.002	0.0037	0.446
Zinc fresh weight ¹ (mg/100 g)	0.002	0.0037	0.447

EBV – estimated breeding value; FW – fresh weight; LA – linoleic acid; ALA – alpha linolenic acid; EPA – eicosapentaenoic acid; DPA – docosapentaenoic acid; DHA – docosahexaenoic acid.

¹ Log₋₁₀ transformed.

² Square root transformed.

density EBV (Table 7). Topside hedonic flavour liking had a negative regression with sire muscle density EBV (Table 7).

Discussion

Genetic selection in sheep has focused on growth and carcass-related traits with less attention on meat quality traits. Consumers require lamb that is lean, low in saturated fats, high in polyunsaturated fats and with a high iron and zinc content (Pethick et al., 2006). However, continued selection for increased lean may have adverse effects on eating quality (Pannier et al., 2014a).

Muscle density effect on total intramuscular fat and nutritional traits

The average loin total IMF content was 2.55% for LMD sired and 2.34% for HMD progeny and these are low compared to the optimum lamb IMF content outlined by Australian consumers of 4–5% (Hopkins et al., 2006). This is significant for the sheep industry as many

Table 6

Regression of lamb shear force and colour traits with sire muscle density estimated breeding value.

Meat quality trait	Sire muscle density EBV		
	Regression coefficient	±SE	P-value
Shear force trait (Newtons)			
<i>M. longissimus lumborum</i> shear force	1.09	0.458	0.002
<i>M. longissimus lumborum</i> shear force SD	0.36	0.213	0.017
<i>M. semimembranosus</i> shear force	1.34	0.565	0.009
<i>M. semimembranosus</i> shear force SD	0.01	0.345	0.877
Colour traits <i>M. longissimus lumborum</i> ¹			
Hue ²	0.0001	0.003	0.578
Chroma	-0.28	0.161	0.025
Lightness ² (L*)	-0.001	0.002	0.450
Redness ² (a*)	-0.01	0.003	0.024
Yellowness (b*)	-0.13	0.103	0.067

EBV – estimated breeding value; N – Newtons.

¹ Aged and bloomed for 1 h.

² Log₋₁₀ transformed.

consumers presume that lamb is a fatty/unhealthy product but these values are low signifying a genetic success within the sheep sector. High muscle density and LMD sired progeny did not differ significantly in fatty acid traits. Loin and topside total IMF had a negative regression with sire muscle density EBV. This apparent contradiction may be explained by the comparison of HMD/LMD progeny being based on phenotype and the regression analysis is based on sire muscle density EBV. For every unit increase in sire muscle density EBV, there was a significant decrease in loin (-1.69 mg/100 g fresh weight) and topside IMF (-0.03 mg/100 g fresh weight). Similar to Karamichou et al. (2006) who found that muscle density was strongly negatively genetically correlated with IMF. The number/volume of intramuscular adipocytes (found between fibre bundles) influences IMF content (Hocquette et al., 2010) and therefore LMD sired animals may have a greater number or volume or fuller adipocytes. In another study using these same lambs; carcass weight, meat yield, conformation and loin width muscle traits had positive regressions with sire muscle density EBV (Thomas et al., 2020).

The majority of loin individual (or grouped) SFA and MUFA concentrations had a positive regression; although loin polyunsaturated:saturated ratio and PUFA proportion traits (including total PUFA proportion, total n-6 and total n-3 fatty acids) had a negative regression with sire muscle density EBV. Lean livestock has higher proportion of PUFA mainly because as animals get fatter SFA and MUFA increase, as PUFA are located in the phospholipid membrane of muscle fibres (Enser et al., 1996). Selection for higher muscle density either increases muscle fibre number or size. Further studies are required to fully investigate such factors.

Muscle density effect on mineral traits

There were no significant differences in mineral content of lamb meat sired by HMD or LMD rams. The mean fresh weight iron content of the lamb at 1.36 mg/100 g was similar to literature values (Osorio et al., 2007; Pannier et al., 2014b; Mortimer et al., 2010). Fresh weight zinc content was 1.79 mg/100 g for HMD and 1.83 mg/100 g for LMD sired lambs and were below those reported in the literature, reasons for low zinc levels are not obvious (Osorio et al., 2007; Mortimer et al., 2010; Pannier et al., 2014b). All lamb samples exceeded the thresholds to be considered a 'source of iron and zinc 0.8 mg and 0.95 mg/100 g for iron and zinc, respectively, National Health and Medical Research Council (NHMRC), 2006.

Table 7

Sire muscle density estimated breeding value regression coefficients with lamb *M. longissimus lumborum* and *M. semimembranosus* sensory traits.

Sensory traits	Sire muscle density EBV		
	Regression coefficient	±SE	P-value
<i>M. longissimus lumborum</i> sensory traits (0–8)			
Tenderness	−0.09	0.036	<0.001
Juiciness	−0.08	0.026	0.002
Abnormal flavour intensity	0.01	0.021	0.675
Lamb flavour intensity	0.00	0.017	0.685
Hedonic flavour liking	−0.02	0.022	0.206
Hedonic overall liking	−0.05	0.024	0.014
<i>M. longissimus lumborum</i> sensory traits (0–100)			
On cutting			
Ease of cutting	−0.90	0.370	0.011
On cut clean	−0.34	0.339	0.150
Initial chewing			
In bite toughness	1.33	0.512	<0.001
In bite crunchy	−0.05	0.281	0.795
In bite juiciness	−0.70	0.361	0.031
In bite sponge	−0.31	0.279	0.337
On eating			
Eat toughness	1.01	0.499	0.004
Eat moisture	−0.63	0.369	0.096
Eat chewiness	1.19	0.398	<0.001
Eat greasiness	−0.23	0.238	0.389
Eat fibres	0.86	0.389	0.006
Eat gristle ¹	0.03	0.020	0.194
Eat pulpy	−0.92	0.382	0.007
Eat dissoluble	−0.95	0.443	0.006
Residue			
Residual greasy mouthfeel	−0.34	0.206	0.095
Residual ease of swallow	−1.03	0.327	<0.001
Residual pulpy	−0.66	0.365	0.064
Residual particles	0.34	0.212	0.087
Residual mouthfeel	−0.86	0.279	0.001
<i>M. semimembranosus</i> sensory traits (0–8)			
Tenderness	−0.04	0.045	0.196
Juiciness	−0.03	0.032	0.253
Abnormal flavour intensity	0.01	0.027	0.878
Lamb flavour intensity	0.01	0.005	0.367
Hedonic flavour liking	−0.06	0.032	0.029
Hedonic overall liking	−0.05	0.032	0.060

EBV – estimated breeding value.

¹ Log₁₀ transformed.

Muscle density effect on meat quality traits

Lamb meat sired by HMD or LMD rams did not differ in loin or top-side shear force traits, with means of 32 Newtons and 30 Newtons for HMD for LMD sired lamb, respectively. The majority of loin shear force traits were tender and the majority of topsides had acceptable tenderness as defined by Jopson et al. (2001). Topsides had higher shear force values than loins; this finding is similar to other studies and has been attributed to differences in muscle collagen content (Tschirhart-Hoelscher et al., 2006). It is reported that Australian consumers require shear force values lower than 27 Newtons (Hopkins et al., 2006), which is more tender than most of the measurements from this study.

Shear force had a positive regression with sire muscle density EBV and a negative regression with IMF, this supports the hypothesis that selecting for LMD will improve eating quality. Additionally, fatter animals have a reduced ability to cold shorten as the fat acts as an insulator for the meat, thus producing better meat quality and lower shear force values. Similarly, in the Texel breed, positive correlations have been found between LV5 muscle density and loin shear force (Lambe et al., 2008), which influences tenderness (Karamichou et al., 2006). Thus, selection for reduced muscle density is likely to have a beneficial influence on tenderness.

The lowest consumer acceptance threshold for Australian lamb meat redness was 9.5 (after 30–40 min bloomed Khlij et al., 2010). Lambs

from this study were much redder (HMD 15.70, LMD 16.22) and these high chroma values (intensity of colour) would be more appealing for consumers. However, lambs sired by HMD rams had lower colour traits chroma/saturation (−0.64) redness (−0.52) and yellowness (−0.31) compared to LMD sired lamb (also observed with sire muscle density EBV being negatively regressed with these traits).

Lambs selected for increased muscularity may have lower meat redness values due to increased glycolytic fibre type, often with paler or less red meat (Dransfield and Sosnicki, 1999). Increased glycolytic fibre proportion may have adverse effects on meat quality (Greenwood et al., 2006). Meat redness is associated with a higher concentration of oxidative muscle fibres, greater myoglobin and mitochondria and IMF levels (Oddy et al., 2001). Karamichou et al. (2006) found increased meat yellowness in sheep selected for fatness. Muscle fibre type was not measured in this study and further investigation of muscle enzymatic activity and fibre typing analysis would determine whether the LMD sired lambs had an increased proportion of oxidative muscle fibres which have a higher propensity towards IMF content and colour traits chroma/saturation, redness and yellowness. High muscle density sired lambs may have an increased proportion of white glycolytic muscle fibres.

Loin scored more favourably than topside samples for sensory traits. As hypothesised muscle density EBV had a negative regression with loin tenderness, juiciness and hedonic overall liking. Similarly, Navajas et al. (2008) noted no differences in sensory traits between high and low muscularity sired groups (within breed), but regression analysis indicated juiciness was negatively related with muscularity.

Novel tenderness descriptors derived by the trained taste panel were used in this study. Muscle density EBV was negatively related to many loin sensory tenderness or juiciness traits (including the novel tenderness sensory traits; 'ease of cut', 'initial bite juiciness', 'eat pulpy', 'eat dissoluble', 'residue swallow' and 'residue mouthfeel'). It is proposed that lambs sired by LMD EBV rams have higher IMF content which affects eating quality traits. This is in agreement with Navajas et al. (2008) and Karamichou et al. (2006).

Undesirable loin sensory traits of 'initial toughness', 'eat toughness', 'eat chewiness' and 'eat fibres' had a positive regression with muscle density EBV. Muscle density affects IMF content but it could also reflect a difference in muscle fibre composition characteristics such as number, type, length, area or protein turnover (Bünger et al., 2009) which affect meat quality traits (Greenwood et al., 2006). Further research is needed to assess the intrinsic physiological differences in meat from lambs sired by HMD and LMD rams. This would aid further molecular genetic analysis of gene expression and genetic markers relating to IMF and muscular properties.

Muscle density EBV had a negative regression with topside hedonic flavour liking, although this was not significant for the loin. Lambe et al. (2011) found that lamb loins with LMD were associated with increased hedonic flavour liking. It was found that selection for low loin average muscle density EBVs had a beneficial impact on the meat eating quality in other muscles within the carcass. Previous studies have shown that selecting for increased eye muscle depth can also cause correlated changes in topside muscle fibre type (Greenwood et al., 2006) which may result in the topside being tougher (Hopkins et al., 2007).

Conclusion

Selection for LMD EBV's increases IMF content and consistently improves meat eating quality traits associated with tenderness and juiciness. In contrast, selection for HMD EBV's decreases IMF content, increases shear force and toughness traits, which is unfavourable for customer eating experience. Low muscle density sired lamb meat had improved meat appearance with increased colour traits (chroma, redness and yellowness). Using the *in vivo* CT measure of muscle density as a proxy trait for IMF within terminal sire breeding

programmes could be advantageous for a breeding programme aiming for progeny lambs with improved meat eating quality. However, an antagonistic relationship between increasing carcass muscularity (Thomas et al., 2020) and meat quality attributes (this study) emphasises the need to balance selection criteria appropriately within a lamb selection index.

Supplementary materials

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.animal.2020.100136>.

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository.

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Declaration of interest

None.

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