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Genetic analyses of sensory characteristics and relationships with fatty acid composition in the meat from Scottish Blackface lambs

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Genetic parameters for eating quality assessed by trained taste panellists were estimated on longissimus thoracis et lumborum (LTL) muscle in Scottish Blackface lambs, comprising lines previously divergently selected for carcass lean content (FAT and LEAN lines) as well as crosses between these lines. Also, relationships between eating quality assessments and fatty acid composition were investigated. Eating quality and fatty acid phenotypic measurements were made on 350 male lambs, at ca. 8 months of age. Eating quality measurements included 18 descriptive terms and fatty acid composition measurements included in total 17 fatty acids of three types: saturated, monounsaturated and polyunsaturated. The FAT line had juicier meat and more vegetable flavour than the LEAN line. Most of the eating quality traits were moderately to highly heritable, with heritabilities ranging from 0.21 (lamb flavour) to 0.92 (sweet flavour). Lamb flavour, juiciness and overall liking were strongly negatively correlated with individual polyunsaturated fatty acids, with the correlations being significantly different from zero. Overall liking was strongly positively correlated with the proportion of total monounsaturated fatty acids. This study provides new information on genetic parameters for eating quality traits in sheep, which may lead to novel opportunities for genetically improving these traits.

Keywords: eating quality, fatty acids, genetic parameters, meat, sheep

Introduction

The most important aspect of meat quality is eating quality, usually defined as scores given by taste panellists for tenderness/toughness, juiciness and flavour. These characteristics are affected by several factors in production, such as breed and diet (Wood *et al.*, 2004a). It is known that muscles differ in the amount and fatty acid composition of the main lipid fractions, neutral and phospholipids, the former constituting marbling fat (depot lipid) and the latter constituting membrane lipids. Variations in these fatty acids explain some of the quality differences between muscles, for example in shelf life and flavour. It is also known that variation in the amount and fatty acid composition of the lipid classes explain meat quality differences brought about by breed and diet, although this is more controversial (Wood *et al.*, 2004b). Fat and fatty acids are important in their own right because of their effects on human health, and it is important to select production options that

maximise both meat quality and healthiness in meat production (Kouba *et al.*, 2003).

Lipid oxidation in muscle systems is initiated at the membrane level in the phospholipid fractions as a free-radical autocatalytic chain mechanism (Labuza, 1971) in which pro-oxidants interact with unsaturated fatty acids resulting in the generation of free radicals and propagation of the oxidative chain (Ashgar *et al.*, 1988). Also, lipid oxidation is a major cause of deterioration in meat quality (Gray and Pearson, 1987; Gray *et al.*, 1996). It limits the storage or shelf life of meat exposed to oxygen under conditions where microbial spoilage is prevented or reduced, such as during refrigeration or freezing. The products of fatty acid oxidation produce off-flavours and odours usually described as rancid (Gray and Pearson, 1994).

Meat has often been identified wrongly as having a high fat and saturated fatty acid content. In fact, lean meat is very low in fat (2 to 3%). Fat, especially animal fat, has been the subject of much interest and debate because of risks of some diseases when consumed in excess. Fat however not only is a concentrated source of energy for the

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body but also provides flavour, aroma and texture. When eaten, fat is also a carrier of the fat-soluble vitamins A, D, E and K and the essential fatty acids, and is important in growth and in the maintenance of many body functions (Nürnberg *et al.*, 2005). As far as most consumers are concerned, meat should contain only a small quantity of fat. However, some fat is always present in meat and indeed is required to impart flavour and juiciness (Melton, 1990). Many reports also show positive effects of fat level on tenderness (Wood, 1990).

This study aims to examine, first, the inheritance of eating quality characteristics in the muscle *longissimus thoracis et lumborum* (LTL) from grass-fed lambs; and second, to investigate relationships between eating quality assessments and fatty acid composition of meat. These results will jointly determine options for genetically improving the eating quality of sheep meat.

Material and methods

Animals

Lambs derived from LEAN and FAT lines of Scottish Blackface sheep, which had been divergently selected for carcass lean content, were used as the experimental resource. Detailed descriptions of the establishment of the selection lines, selection procedure and responses to selection are given by Bishop (1993). Divergent selection ceased in 1996, after which the lines were maintained as closed populations with no further selection. The flock consisted of 200 ewes, split almost equally between LEAN and FAT lines. A small proportion of reciprocal LEAN \times FAT line crosses were made at the 1999 matings, so that a cohort of F₁ lambs were born in April 2000 along with a majority of purebred LEAN and FAT line lambs. The male F₁ lambs were then backcrossed to the purebred LEAN and FAT line ewes to create a population of F₁ \times LEAN and F₁ \times FAT lambs from 2001 to 2003, for the purpose of QTL detection (Karamichou *et al.*, 2006b and 2006c). A small number of F₁ \times (F₁ \times LEAN) and F₁ \times (F₁ \times FAT) were born in 2003 when female backcross lambs from 2001 themselves became dams. Additionally, F₁ females born in 2000 gave rise to a small number of F₂ progeny.

Standard husbandry procedures were applied in this flock; all lambs were tagged at birth, with parentage, day of birth, sex and mortalities recorded. Each year the lambs were kept in two different groups (i.e. on two separate fields), for ease of management. Parentage information was maintained for all animals born after 1986, giving a total of 4847 known animals in the flock pedigree.

Phenotypic measurements of eating quality traits and fatty acids were made on 350 8-month-old male grass-fed lambs, comprising 300 male lambs produced for QTL detection in 2001 to 2003, as described above, plus 25 LEAN and 25 FAT line male lambs born in 2000. Measurements were performed at the University of Bristol, on cohorts of 20 animals treated identically during their growth, transportation and pre-slaughter periods.

The lambs were electrically stunned across the head and killed by exsanguination. In order to prevent cold-shortening of the muscles, the carcasses were hung at the ambient temperature for about 5 h prior to chilling at 1°C overnight before sampling.

Sensory (taste panel) analysis

Descriptive sensory analyses were performed using a trained taste panel. A section of muscle LTL was removed 24 h after slaughter from the left side of the carcass, was packaged under vacuum and conditioned at 1°C for a further 10 days when it was frozen at -20°C prior to assessment of eating quality under standardised conditions. Samples were thawed at 4°C overnight and cut into 2.5 cm chops, which were grilled to an internal temperature of 78°C, as measured by a thermocouple inserted into the centre of the muscle. Sensory descriptors were defined (Table 1) and 10 experienced panellists rated the intensities of lamb flavour, abnormal, acidic, ammonia, bitter, fatty/greasy, fishy, grassy, livery, metallic, rancid, soapy, stale, sweet, vegetable, juiciness and toughness as well as the hedonic overall liking on every animal. Scoring was performed on a 100-mm unstructured line scale with anchor points at each end, where 0 meant no flavour or dislike extremely, and 100 meant very intense flavour or extreme liking. The hedonic scale served as an indication of preference by the panel, but it cannot be used to infer consumer acceptance since the results are based on 10 assessors who can no longer be considered as typical consumers because of the training they have received in meat assessment.

Table 1 Definition of eating quality descriptors

| Attributes | Definition |
|----------------|---|
| Lamb | Flavour associated with cooked lamb: no lamb flavour to full lamb flavour |
| Abnormal | Abnormal flavour not found in cooked lamb: none to strong off-flavour |
| Acidic | Sour taste |
| Ammonia | Pungent, stale urine odour |
| Bitter | Taste on the tongue associated with caffeine/quinine |
| Fatty/greasy | The taste associated with oil and fat |
| Fishy | Flavour associated with fish |
| Grassy | Flavour associated with fresh grass |
| Livery | Flavour associated with liver |
| Metallic | Flavour associated with metallic taste |
| Rancid | The taste associated with rank stale fat |
| Soapy | The taste associated with soap |
| Stale | Old, not fresh taste |
| Sweet | The taste on the tongue associated with sugars |
| Vegetable | The taste on the tongue associated with overcooked vegetables |
| Juiciness | Amount of moisture released: not juicy to extremely juicy |
| Toughness | Very tough to very tender |
| Overall liking | Hedonic liking from the panellists |

Lipid extraction and fatty acid composition

Lipids were extracted from 10 g duplicate samples of *longissimus* (loin) muscle essentially as per Folch *et al.* (1957), separated into neutral and phospholipid, saponified, methylated and individual fatty acids separated by column chromatography and quantified as described by Demirel *et al.* (2004). Total fatty acids were the sum of all the phospholipid and neutral lipid fatty acids that were quantified. Total fatty acids included some unassigned fatty acids. Detailed descriptions of fatty acid extraction and analysis are given by Karamichou *et al.* (2006c).

Fatty acid data are presented as mg/100 g total fatty acids. Two ratios of fatty acids types were calculated as indices of nutritional value. The polyunsaturated:saturated fatty acid ratio (PUFA:SFA) was defined as the ratio of the sum of polyunsaturated to saturated fatty acids. The ratio of the n-6:n-3 fatty acids was also calculated.

Data analysis

Residual maximum likelihood (REML) methods were used to estimate variance components using an animal model, fitting the complete pedigree structure (4847 animals), using ASReml (Gilmour *et al.*, 2004). The fixed effects included in the analysis of sensory traits were year of lamb birth (four classes: 2000, 2001, 2002 and 2003), management group (1 or 2), litter size (two classes: 1 or 2), slaughter day within year (15 classes) and panel number (26 classes). The model for fatty acids included the same fixed effects used for the sensory traits, apart from the panel number. Triplets comprised proportionately less than 0.02 of the data and were combined with the twin lambs in the classification of litter size. The only interaction found to be significant was between fixed effects year and group. Heritability estimates were then calculated for each eating quality trait, using an animal model, fitting the complete pedigree structure (4847 animals), using ASReml (Gilmour *et al.*, 2004). Heritabilities for fatty acids have been previously reported (Karamichou *et al.*, 2006c).

A principal component analysis (PCA) (Statistical Analysis Systems Institute, 2003) was performed on the primary data of eating quality traits. The PCA was used to reduce the primary data into a smaller number of independent traits, and also to investigate any patterns of relationship between the eating quality traits. Before PCA was carried out, the data were standardised by applying regression analysis on each trait, fitting fixed effects and keeping the standardised residuals. The PCA was performed on these standardised residuals.

The dataset was not large enough to carry out bivariate genetic analyses with acceptable precision. Therefore, residual correlations between the individual eating quality traits and the fatty acids were estimated using REML, as an approximation to phenotypic correlations. The model included the fixed effects of year of lamb birth, management group, litter size, year by slaughter day and panel number. Sire was included as a random effect.

Line effects. In order to estimate genetic differences between the LEAN and FAT lines for each trait, using all the data rather than just the 50 pure line lambs, true line effects were estimated as the generalised least-squares solutions to equations describing the genetic composition of each line or cross. Details of the methodology for predicting means and variances for line categories have been provided elsewhere (Karamichou *et al.*, 2006a), using information from all the lines and crosses and assuming that there was no heterosis between the LEAN and FAT lines.

Results

Summary statistics

Summary statistics for eating quality traits are shown in Table 2, with significant ($P < 0.05$) line differences shown in bold. The FAT line meat was perceived to be juicier than the LEAN line meat. A significant trend was also seen for vegetable flavour, with the FAT line meat being more associated with vegetable flavour than the LEAN line meat. Non-significant trends, in the same direction, were also seen for abnormal flavour, bitter and metallic flavour. The LEAN line meat, although not significant, was perceived to have more normal 'lamb' flavour than the FAT line. The significance levels were not adjusted for multiple comparisons; therefore, with 18 traits being compared, at least one false positive significant result might be expected.

Principal component analysis

The results of the PCA for the 18 eating quality traits are presented in Table 3. The five first principal components explain 80.8% of the total variation. The first component (PC₁) explained 40.1% of the standardised variance and can be interpreted as a descriptor of abnormal meat flavours (Table 3). Within PC₁ two groups were clearly distinguished. The first group included abnormal meat flavours (abnormal flavour, bitter, fatty/greasy, rancid and stale), and these variables were negatively correlated with the second group, which described normal meat flavours (lamb flavour and overall liking). The second PC₂ grouped juiciness, grassy and sweet flavour as an independent cause of variation. The third PC₃ explained 10.9% of the total variance and essentially represents toughness of meat. Toughness is negatively correlated with overall liking and juiciness (Table 3). The fourth PC₄ had high positive loadings for metallic and acidic flavours and explained 6.10% of the variance. Finally, the fifth PC₅ was represented mostly by fishy flavour, but explained only 5.10% of the standardised variance.

Genetic parameters

Univariate heritability estimates for eating quality traits are shown in Table 4. The heritabilities were variable but generally moderate, with 12 of the 18 traits having values greater than 0.20.

The estimated residual correlations among eating quality traits are presented in Table 5. The correlation for lamb

Table 2 Predicted line means (0–100 scales), trait phenotypic standard deviations and line differences (with standard error) for sensory panel traits

| Trait | FAT line | LEAN line | s.d. | Line difference (FAT-LEAN) | s.e. (Diff.) |
|------------------|----------|-----------|------|----------------------------|--------------|
| Abnormal flavour | 21.10 | 18.78 | 8.03 | 2.32 | 1.22 |
| Acidic | 4.826 | 3.791 | 3.19 | 1.03 | 0.79 |
| Ammonia | 1.166 | 1.106 | 1.91 | 0.06 | 0.65 |
| Bitter | 5.820 | 4.421 | 3.96 | 1.40 | 0.85 |
| Fatty/greasy | 16.52 | 16.99 | 5.48 | −0.47 | 0.96 |
| Fishy | 1.283 | 1.107 | 1.49 | 0.17 | 0.57 |
| Grassy | 1.600 | 1.597 | 4.88 | 0.003 | 0.24 |
| Juiciness | 43.38 | 40.65 | 2.08 | 2.73 | 1.14 |
| Lamb flavour | 25.20 | 26.86 | 5.93 | −1.66 | 1.04 |
| Livery | 12.58 | 12.15 | 7.19 | 0.43 | 1.17 |
| Metallic | 6.002 | 4.641 | 6.19 | 1.36 | 0.85 |
| Overall liking | 22.02 | 21.96 | 3.28 | 0.06 | 1.22 |
| Rancid | 3.528 | 3.225 | 3.04 | 0.30 | 0.79 |
| Soapy | 4.906 | 4.698 | 4.86 | 0.21 | 1.02 |
| Stale | 4.932 | 4.637 | 3.66 | 0.29 | 0.82 |
| Sweet | 6.300 | 7.192 | 3.68 | −0.89 | 0.77 |
| Toughness | 36.32 | 36.37 | 9.98 | −0.05 | 1.16 |
| Vegetable | 6.555 | 3.208 | 3.68 | 3.35 | 1.14 |

Significant ($P < 0.05$) line differences are shown in bold.

Table 3 Coefficients in the eigenvectors (loadings) for the first five principal components (PC) and their respective variances

| Trait | PC ₁ | PC ₂ | PC ₃ | PC ₄ | PC ₅ |
|-----------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| % of variance accounted for | 40.1 | 18.6 | 10.9 | 6.10 | 5.10 |
| Loadings | | | | | |
| Abnormal flavour | 0.39 | 0.00 | −0.04 | −0.05 | −0.08 |
| Acidic | 0.24 | 0.03 | −0.06 | 0.46 | 0.17 |
| Ammonia | 0.20 | −0.25 | −0.27 | −0.15 | −0.04 |
| Bitter | 0.27 | 0.08 | 0.16 | 0.09 | −0.19 |
| Fatty/greasy | 0.30 | 0.18 | −0.14 | −0.02 | 0.24 |
| Fishy | 0.20 | 0.06 | −0.10 | −0.19 | 0.59 |
| Grassy | 0.16 | 0.44 | −0.16 | −0.11 | −0.14 |
| Juiciness | 0.04 | 0.37 | −0.34 | 0.36 | −0.24 |
| Lamb flavour | −0.33 | 0.07 | −0.10 | 0.10 | 0.05 |
| Livery | 0.17 | −0.28 | −0.39 | −0.11 | −0.23 |
| Metallic | 0.16 | −0.14 | −0.06 | 0.68 | 0.21 |
| Overall liking | −0.28 | 0.17 | −0.31 | 0.00 | 0.26 |
| Rancid | 0.30 | −0.14 | −0.05 | −0.09 | 0.05 |
| Soapy | 0.24 | −0.26 | −0.06 | −0.03 | −0.28 |
| Stale | 0.29 | 0.04 | 0.23 | −0.07 | 0.02 |
| Sweet | 0.11 | 0.54 | −0.09 | −0.11 | −0.26 |
| Toughness | 0.07 | 0.13 | 0.63 | 0.15 | −0.09 |
| Vegetable | 0.19 | 0.22 | 0.11 | −0.22 | 0.34 |

flavour with almost all the adverse eating traits (abnormal flavour, acidic, ammonia and bitter flavour) was significantly negative; however, it was positively correlated with juiciness. Also, juiciness was significantly positively correlated with fatty/greasy flavour and negatively correlated with bitter flavour. Overall liking was significantly positively correlated with fatty/greasy, juiciness and lamb flavour (0.34, 0.25 and 0.62, respectively), and also was negatively correlated with abnormal flavour, ammonia,

Table 4 Univariate heritabilities (h^2), with standard errors (s.e.) for sensory panel traits (0–100 scales)

| Trait | h^2 | s.e. |
|------------------|-------|------|
| Abnormal flavour | 0.27 | 0.14 |
| Acidic | 0.68 | 0.14 |
| Ammonia | 0.25 | 0.13 |
| Bitter | 0.68 | 0.15 |
| Fatty/greasy | 0.57 | 0.19 |
| Fishy | 0.09 | 0.11 |
| Grassy | 0.12 | 0.11 |
| Juiciness | 0.31 | 0.17 |
| Lamb flavour | 0.21 | 0.13 |
| Livery | 0.22 | 0.13 |
| Metallic | 0.09 | 0.10 |
| Overall liking | 0.05 | 0.09 |
| Rancid | 0.30 | 0.16 |
| Soapy | 0.04 | 0.08 |
| Stale | 0.63 | 0.14 |
| Sweet | 0.92 | 0.14 |
| Toughness | 0.15 | 0.13 |
| Vegetable | 0.60 | 0.20 |

bitter and metallic flavour (−0.41, −0.27, −0.31 and −0.20, respectively). Finally, correlations of toughness with juiciness and lamb flavour were negative (−0.43 and −0.11). Thus, high correlations suggest that fatty/greasy flavour, juiciness, lamb flavour and toughness of meat affect overall liking.

Residual correlations between eating quality traits and fatty acid composition (mg/100 g muscle) are given in Table 6. The correlations were significantly negative for all the PUFAs with lamb flavour, and arachidonic acid and eicosapentanoic acid showed the highest correlation

Table 5 Residual correlations for eating quality traits

| Trait | Abnormal flavour | Acidic | Ammonia | Bitter | Fatty/greasy | Fishy | Grassy | Juiciness | Lamb flavour | Livery | Metallic | Overall liking | Rancid | Soapy | Stale | Sweet | Toughness | Vegetable | |
|------------------|------------------|--------------|--------------|--------------|--------------|-------------|--------------|--------------|--------------|--------------|--------------|----------------|--------------|-------|--------------|-------|-------------|-----------|--|
| Abnormal flavour | 1.00 | | | | | | | | | | | | | | | | | | |
| Acidic | 0.36 | 1.00 | | | | | | | | | | | | | | | | | |
| Ammonia | 0.30 | 0.08 | 1.00 | | | | | | | | | | | | | | | | |
| Bitter | 0.39 | -0.01 | 0.20 | 1.00 | | | | | | | | | | | | | | | |
| Fatty/greasy | 0.00 | 0.00 | -0.19 | 0.07 | 1.00 | | | | | | | | | | | | | | |
| Fishy | 0.40 | 0.38 | 0.09 | 0.02 | -0.20 | 1.00 | | | | | | | | | | | | | |
| Grassy | -0.30 | -0.18 | -0.37 | -0.47 | 0.01 | -0.02 | 1.00 | | | | | | | | | | | | |
| Juiciness | 0.01 | 0.03 | -0.08 | -0.25 | 0.22 | 0.17 | 0.11 | 1.00 | | | | | | | | | | | |
| Lamb flavour | -0.58 | -0.20 | -0.29 | -0.33 | 0.05 | -0.04 | 0.18 | 0.22 | 1.00 | | | | | | | | | | |
| Livery | 0.24 | 0.24 | 0.16 | 0.25 | 0.17 | -0.09 | -0.21 | 0.03 | -0.06 | 1.00 | | | | | | | | | |
| Metallic | 0.23 | 0.29 | 0.11 | 0.21 | 0.06 | 0.09 | -0.19 | 0.10 | 0.02 | 0.09 | 1.00 | | | | | | | | |
| Overall liking | -0.41 | -0.18 | -0.27 | -0.31 | 0.34 | -0.02 | 0.09 | 0.25 | 0.62 | -0.17 | -0.20 | 1.00 | | | | | | | |
| Rancid | 0.18 | 0.19 | 0.17 | 0.23 | 0.03 | -0.06 | 0.05 | -0.01 | -0.22 | 0.47 | 0.06 | -0.21 | 1.00 | | | | | | |
| Soapy | 0.22 | 0.31 | 0.15 | 0.12 | 0.18 | 0.20 | -0.17 | 0.29 | 0.07 | 0.25 | 0.40 | -0.02 | 0.08 | 1.00 | | | | | |
| Stale | 0.21 | 0.03 | 0.13 | 0.47 | -0.01 | 0.04 | -0.25 | -0.28 | -0.17 | -0.06 | 0.35 | -0.29 | 0.24 | 0.13 | 1.00 | | | | |
| Sweet | -0.32 | -0.01 | -0.28 | -0.66 | 0.05 | -0.09 | 0.18 | 0.33 | 0.29 | -0.19 | -0.29 | 0.38 | -0.25 | 0.04 | -0.34 | 1.00 | | | |
| Toughness | -0.07 | -0.10 | -0.30 | 0.05 | 0.01 | 0.06 | -0.03 | -0.43 | -0.11 | -0.44 | 0.07 | -0.06 | -0.30 | -0.13 | 0.23 | -0.08 | 1.00 | | |
| Vegetable | -0.16 | -0.09 | 0.09 | 0.02 | 0.11 | -0.08 | -0.19 | -0.09 | 0.06 | -0.33 | -0.32 | 0.06 | -0.28 | -0.19 | 0.11 | 0.15 | 0.34 | 1.00 | |

Residual correlations (except diagonal) significantly ($P < 0.05$) greater than zero are shown in bold.

Table 6 Residual correlations between eating quality traits and fatty acid^a composition of intramuscular fat

| Traits | Lamb flavour | Juiciness | Toughness | Overall liking |
|---|--------------|--------------|-------------|----------------|
| Myristic acid – 14:0 | –0.07 | –0.13 | 0.02 | –0.10 |
| Palmitic acid – 16:0 | 0.02 | –0.08 | –0.12 | 0.07 |
| Stearic acid – 18:0 | –0.03 | –0.20 | –0.09 | 0.07 |
| Palmitoleic acid – <i>cis</i> 16:1 (n-7, n-9) | –0.02 | –0.11 | –0.06 | –0.06 |
| Oleic acid – <i>cis</i> 18:1 n-9 | 0.00 | –0.10 | –0.13 | 0.10 |
| <i>cis</i> -Vaccenic acid – <i>cis</i> 18:1 n-7 | –0.18 | –0.19 | 0.05 | –0.39 |
| Vaccenic acid – <i>trans</i> 18:1 n-7 | 0.10 | –0.19 | –0.04 | 0.05 |
| Gadoleic acid – 20:1 | 0.04 | –0.04 | –0.13 | –0.01 |
| Linoleic acid – <i>cis</i> 18:2 n-6 | –0.25 | –0.12 | –0.05 | –0.31 |
| Linolenic acid – <i>cis</i> 18:3 n-3 | –0.19 | –0.37 | 0.01 | –0.23 |
| Dihomo- γ -linolenic acid – 20:3 n-6 | –0.42 | 0.01 | 0.04 | –0.43 |
| Arachidonic acid – 20:4 n-6 | –0.54 | –0.18 | 0.12 | –0.60 |
| EPA (Eicosapentanoic acid) – 20:5 n-3 | –0.46 | –0.11 | 0.15 | –0.50 |
| Adrenic acid – 22:4 n-6 | –0.21 | –0.27 | 0.02 | –0.34 |
| DPA (Docosapentaenoic acid) – 22:5 n-3 | –0.33 | –0.32 | 0.08 | –0.50 |
| DHA (Docosahexaenoic acid) – 22:6 n-3 | –0.29 | –0.09 | 0.25 | –0.24 |
| Conjugated linoleic acid (CLA) | 0.03 | –0.13 | –0.03 | –0.01 |
| % SFA | 0.07 | –0.09 | –0.07 | 0.16 |
| % MUFA | 0.14 | 0.04 | –0.11 | 0.29 |
| % PUFA | –0.14 | 0.05 | 0.11 | –0.28 |

^aWe use fatty acid nomenclature whereby X:Y (n–z) indicates a carbon chain of length X with Y double bonds, the first double bond located z carbons from the methyl terminal end.

Residual correlations significantly ($P < 0.05$) greater than zero are shown in bold.

coefficients (–0.54 and –0.46, respectively). Correlations for most fatty acids were negative with meat juiciness. However, correlations for fatty acids with toughness of meat were generally low and did not show a particular pattern. Finally, correlations for overall liking followed a similar pattern with lamb flavour. In particular, overall liking was negatively correlated with *cis*-vaccenic and all the individual PUFAs. Interesting were the positive and negative correlations of overall liking with the proportion of total mono-unsaturated fatty acids (MUFA) and PUFA, respectively, meaning that meat with high MUFA and low PUFA proportions will be perceived to taste better. The high correlations suggest that fatty acid composition affects flavour and juiciness to an important extent.

Discussion

The present study has produced novel information on the genetic control of eating quality traits, assessed by a trained taste panel, in Scottish Blackface sheep, and relationships between these traits and fatty acid composition. The heritabilities observed for the eating quality traits indicate opportunities for altering these traits, provided that animal genetic effects can be estimated. Together, these results, along with the strong correlations between eating quality traits and fatty acid composition, provide potential opportunities for genetically improving components of meat quality.

Selection for increased leanness changed some aspects of eating quality, as the FAT line had significantly higher vegetable flavour than the LEAN line. Also, meat from the FAT line was perceived to be juicier than meat from the

LEAN line. The heritability estimates for most of the eating quality traits were moderate to high, with the exception of fishy, grassy, metallic, overall liking, soapy and toughness, which had estimates that were small and not significantly different from zero. Moderate to high estimated heritabilities indicate that indirect selection would be effective provided *in vivo*-measured traits could be identified with which they are correlated.

Due to a lack of information on heritabilities in eating quality traits in sheep, we will compare our results with published studies in other species. However, it should be emphasised that most published estimates are imprecise due to small sample sizes. The estimate of heritability for toughness (0.15) is similar to low values previously for temperate cattle breeds, which are generally close to 0.10 (e.g. Van Vleck *et al.*, 1992; Barkhouse *et al.*, 1996; Splan *et al.*, 1998; Johnston *et al.*, 2003), suggesting that selection for decreased toughness would result in little genetic progress. Only the studies of Wilson *et al.* (1976) and Nephawe *et al.* (2004) report higher heritabilities for toughness, being 0.23 and 0.26, respectively. However, Johnston *et al.* (2003) reported heritabilities for toughness-related traits in tropical cattle breeds that were two to three times higher than those generally found in temperate breeds, begging the question of why the tropical and temperate cattle differ in this trait.

Our heritability estimate for juiciness was moderate (0.31), and in close agreement with Wilson *et al.* (1976), who estimated a heritability of 0.26. In contrast, other studies in beef cattle reported estimates of 0.14, 0.0 and 0.05 (Van Vleck *et al.*, 1992; Splan *et al.*, 1998; Nephawe *et al.*, 2004, respectively).

Flavour is assumed to have a low heritability, based on estimates from the literature. Lamb flavour, in our study, was moderately heritable (0.21), which differs from available estimates in studies in beef cattle. Specifically, published heritabilities of beef flavour are 0.03 (Van Vleck *et al.*, 1992), 0.04 (Splan *et al.*, 1998) and 0.05 (Nephawe *et al.*, 2004).

In pigs, Cameron (1990) reported heritability estimates for toughness, pork flavour, juiciness and overall liking of 0.23, 0.16, 0.18 and 0.16, respectively, from data on 40 full-sib litter groups of Duroc and halothane-negative British Landrace pigs, in agreement with estimates of 0.15 for toughness and 0.21 for lamb flavour, in the present study. In contrast, Lo *et al.* (1992) reported heritability estimates of 0.45, 0.13, 0.12 and 0.34 for toughness, pork flavour, juiciness and overall liking, respectively, from data on Duroc and Landrace pigs. Based on results of a small number of studies, the same eating quality traits, in general, seemed to be low to moderately heritable of the order of 0.10 to 0.20 (Lo, 1990), in agreement with the present study. However, these estimates tend to be quite variable, as would be expected given the relatively small sample sizes generally used in these studies. Overall, these results indicate that sensory meat quality traits, assessed by taste panels, are determined to some extent by additive genetic effects and as such there is some scope for genetic improvement by means of selection.

Relationships between sensory scores and fatty acid concentrations

The residual correlations were used as an approximation to phenotypic correlations, as in a sire model the residual term contains the environmental component plus three-quarters of the genetic component. The correlations were strong for most of the PUFAs with lamb flavour, overall liking and juiciness. The high correlations suggest that fatty acid composition most probably has an important influence on flavour development and juiciness of lamb meat.

Correlations between lamb flavour and PUFAs were strongly negative. Other reports in the literature (Kemp *et al.*, 1981; Larick and Turner, 1990; Melton, 1990; Sanudo *et al.*, 2000) have shown that the n-6 and n-3 PUFAs are important contributors to the flavour of ruminant meats fed grain or grass-fed. The development of rancid flavours in lamb meat comes from the degradation of PUFAs in the tissue membranes. This might explain the negative correlations of flavour and overall liking with PUFAs. In the work on grass-fed and concentrate-fed lambs by Sanudo *et al.* (2000), correlations between n-3 PUFAs and lamb flavour were positive since grass-fed lamb produced higher scores for lamb flavour. The same wide range of n-6 and n-3 fatty acids was not present in the current work. Equally, the antioxidant content of the meat is important, though not measured in this study. Well-growing grass contains a high level of α -tocopherol and is deposited in muscle cell membranes where it protects the PUFA. Warren *et al.* (2007) have shown for beef that in grass-fed animals there

is sufficient α -tocopherol in the muscle and fat oxidation is not related to PUFA content. Conversely, grain-fed animals had inadequate α -tocopherol and fat oxidation was exponentially related to PUFA content.

The strong positive correlation between overall liking and proportion of total MUFA is of particular interest, considering the benefits of MUFA in human diet. The study by Kris-Etherton *et al.* (1999) reported that high-MUFA diets lowered total cholesterol in humans by 10% and low-density lipoprotein (LDL) ('bad') cholesterol by 14%. Also, in the same study triacylglycerol concentrations were 13% lower in subjects consuming the high-MUFA diets. Although the cholesterol-lowering response to PUFA is greater than to MUFA, there has been caution in recommending high PUFA diets because of potentially adverse health effects of their lipoperoxidation products (Williams, 2000). Recent studies show that low-fat diets can raise triglycerides and reduce the levels of protective high-density lipoprotein (HDL) cholesterol (e.g. Sandstrom *et al.*, 1992) have renewed interest in the possibility of altering fat quality, by altering fatty acid composition of animal products, as a cholesterol-lowering strategy within the population.

Conclusions

In summary, this study has shown that altering carcass fatness has simultaneously changed aspects of eating quality, with selection for leanness making meat less juicy and with slightly lower vegetable flavour. Heritabilities for most of the eating quality traits were moderate to high, suggesting that lamb meat sensory quality can be changed genetically, jointly with the fatty acid composition of meat. Under the assumption that the genetic correlations are similar to the residual correlations, the results imply that selection for increased PUFA would lead to a less-acceptable meat flavour, because of the oxidation of PUFA, unless adequate antioxidant is present. Conversely, selection for increased MUFA would lead to a more-acceptable meat flavour. This result, together with the results from other studies where MUFA lowered blood plasma triacylglycerol and LDL cholesterol in humans, suggests that it might be feasible to reduce population cholesterol levels through strategies involving alteration of fatty acid composition, as well as the fat content, of meat.

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