

Genetic parameters for various growth, carcass and meat quality traits in a New Zealand sheep population

Luiz F Brito^{1,2}, John C McEwan², Stephen P Miller², Wendy E Bain², Michael A Lee³, Ken G Dodds², Sheryl-Anne N Newman², Natalie K Pickering⁴, Flávio S Schenkel¹, Shannon M Clarke^{2,*}

¹Centre for Genetic Improvement of Livestock, University of Guelph, Guelph, N1G 2W1, Canada

²AgResearch, Invermay Agricultural Centre, Private Bag 50-034, Mosgiel, 9053, New Zealand

³Department of Mathematics and Statistics, University of Otago, Dunedin, 9058, New Zealand

⁴Focus Genetics, Napier, 4110, New Zealand

*Corresponding author

Email addresses:

Luiz F Brito: lbrito@uoguelph.ca

John C McEwan: john.mcewan@agresearch.co.nz

Stephen P. Miller: steve.miller@agresearch.co.nz

Wendy E Bain: wendy.bain@agresearch.co.nz

Michael A Lee: mlee@maths.otago.ac.nz

Ken G Dodds: ken.dodds@agresearch.co.nz

Sheryl-Anne N Newman: s.newman@agresearch.co.nz

Natalie K Pickering: natalie@focusgenetics.com

Flávio S Schenkel: schenkel@uoguelph.ca

Shannon M Clarke: shannon.clarke@agresearch.co.nz

Abstract

Background

Genetic and phenotypic parameters were estimated for 33 growth, carcass and meat quality traits using a large and unique dataset from a variety of terminal sire sheep breeds and composites. This is the most comprehensive study to date of genetic parameter estimates for carcass and eating quality traits in New Zealand sheep and includes many traits that are difficult or expensive to measure and novel traits such as number of rib pairs.

Results

Heritability estimates ranged from 0.01 for meat redness at 168 hours after display to 0.44 for ultrasonic eye muscle depth. Most of the genetic correlations among growth and carcass traits were favourable and moderate to high. However, some genetic antagonisms such as those between carcass fatness and carcass weight, were observed indicating that selection to produce heavier carcasses would also result fatter carcasses. The genetic correlations among eating quality traits ranged from -0.91 to 1.00, indicating the need to consider those relationships when defining selection goals. Marbling and tenderness were favourable but weakly genetically correlated, indicating that indirect selection gains would be small and it is recommended that both be included in a breeding program. The genetic correlations among growth/carcass and eating quality traits were moderate to low; however, some genetic antagonisms were observed, such as carcass fatness with marbling and meat redness, indicating that selection for leanness could affect meat quality traits and consequently consumer eating satisfaction.

Conclusions

The heritability estimates and phenotypic variances for the traits analysed suggest that most of them have sufficient phenotypic variation and are under moderate genetic control implying that substantial genetic gains could be achieved through direct and indirect selection. The genetic parameters presented in this study provide an insight into the biological basis of these traits but are also a valuable reference to design and/or update a terminal sire breeding program emphasizing eating quality traits. It is important to note that unfavourable genetic correlations identified in this study were low to moderate, making it practical to select for favourable genetic progress in all traits, if they are measured and balanced in a selection index.

Key words: carcass traits, genetic evaluation, genetic correlations, heritability, meat quality, lamb

Background

To be competitive with other livestock industries, sheep farmers require rapidly growing animals producing tasty meat, which are grazed under exemplary welfare conditions, all at a viable final cost to consumers. Genetic selection has played a very important role in improving productivity gains in sheep farming in New Zealand with an 83% increase in kg of lamb produced per ewe and up to 28% (+4.1 kg) overall increase in carcass weight from 1990 to 2012 [1]. Meat sheep breeding programmes around the world have focused on selection for fast growth and high lean yield; however, there is evidence that continued selection for higher lean meat yield may adversely affect aspects of meat eating quality in sheep and other species [2-6]. For the lamb industry to remain competitive in the long-term, lamb carcass and meat quality traits need to be continually improved along with other productivity traits. Therefore, it is important to ensure that selection for growth and leanness is also accompanied by an improvement in meat eating quality traits, which are typically difficult and expensive to

measure. Physical meat quality estimates are made up of traits such as meat-colour, tenderness, marbling, and pH. These traits influence the eating experience and consequently the failure to meet consumer expectations will result in rejection of product and loss of market access. In endeavours to make genetic progress in carcass and lamb meat quality traits, knowledge of their genetic architecture is crucial to define the selection criteria and the likely outcomes. In this context, the objectives of this study were to: 1) estimate heritabilities for various growth, carcass and eating quality traits and 2) estimate phenotypic and genetic correlations between these traits using a large and unique dataset from a variety of New Zealand sheep breeds and composites.

Methods

The work reported here was undertaken using records sourced from New Zealand sheep breeders and stored in the Sheep Improvement Limited database (SIL, www.sil.co.nz, the genetic evaluation service for the New Zealand sheep industry). The animals were managed in accordance with the provisions of the Animal Welfare Act 1999, and the Codes of Welfare developed under sections 68-79 of the Act. The study was approved by the AgResearch's Invermay Animal Ethics committee. It involved a mixture of commercial and research animals covered by the following permit numbers: 13427, 13419, 13121, 13081, 12846, 12816, 12531 and 12233.

Data

Pedigree and performance records were obtained from the SIL database. Performance records were obtained from 19,466 animals born between 2010 and 2013 in the FarmIQ, Ram Breeding and Progeny Test flocks (www.farmiq.co.nz). Farms were located in the North and South Islands of New Zealand. These animals were primarily progeny from terminal sire

composites and Texels mated to a variety of maternal breeds. The main contributing breeds were: Primera, Texel, Lamb Supreme, Coopworth, Romney and East Friesian. The total pedigree data-set consisted of a maximum number of 20 generations – 3,047 sires, 43,012 dams, 733 sires of sires, 2,235 dams of sires, 1,424 sires of dams and 20,006 dams of dams.

The sires used for mating with the base ewes were selected based on their index value (described below). Different indexes have been used over the flocks and years. Some of them are: 1) Index (\$/ha): $WWT + LW8 + LY + SHLY + HQLY + LNLY - FATY$; 2) Index (\$/lamb): $HCW - CGRM + EMA + PW - CDLEGLT$; and 3) Index (\$/lamb born): $WWT + HCW + SUR + SHLY + HQLY + LNLY - FATY$, where WWT: weaning weight, LW8: Autumn live weight recorded in animals aged between 6 to 8 months, LY: lean yield, SHLY: shoulder lean yield, HQLY: hindquarter lean yield, LNLY: lean loin yield, FATY: fat yield, HCW: hot carcass weight, CGRM: depth of tissue at the GR site over the 12th rib at a distance of 110 mm from mid-line, EMA: eye muscle area, PW: primal weight (tenderloin + boneless loin weight), CDLEGLT: carcass dissected leg length and SUR: survival to weaning. In some flocks new ram hoggets were selected each year, while other flocks also included rams used in either the progeny testing or stud flocks in the previous years.

The majority of ewes were mated naturally. The average number of progeny with performance recorded per sire was 23. Some animals were single sire mated and pedigree and birth date recorded at lambing. However, for the majority of the records ewes were mob mated in groups of up to 100 sires and dams, then pregnancy scanned with number of lambs born and conception (and then have their predicted lambing date) recorded, sires and progeny (at docking) were DNA sampled and pedigree determined by DNA. Most animals were born in August and September and they were raised extensively on pastures of predominantly ryegrass and white clover (*Lolium perenne* and *Trifolium repens*, respectively). The ewes/lambs were grouped in mobs based on week of conception and single/twin/triplet bearing. Males were kept

entire and lambs were weaned at 12 – 14 weeks of age. There were one to three slaughters within flocks across years and processing procedures and times were kept identical for each slaughter. Animals were randomly allocated to each slaughter based on sex, birth rank (when known) and weaning weight. The average age at slaughter was 167 ± 31.4 days.

Traits

The traits included in this study were: live weight at 6 months (LW6, kg), pre-slaughter weight (PRESLT, kg), hot carcass weight (HCW, kg), dressing out percentage (DO%, %), ultrasonic measurements of eye muscle depth (EMD, mm), eye muscle width (EMW, mm) and fat depth (FDM, mm), X-ray carcass weight (XWT, kg), X-ray leg weight (XLEG, kg), X-ray middle or loin weight (XMID, kg), X-ray forequarter weight (XFORE, kg), X-ray number of rib pairs (XNRIB), leg length (LEGLGTH, cm), leg weight (LEGWT, kg), boneless loin weight (LNBNWT, kg), carcass measurement of buttocks circumference (CBUTT, cm), depth of tissue at the GR site over the 12th rib at a distance of 110 mm from mid-line (CGRM, mm) [7], loin meat pH (LPH), marbling score in a scale from 1 to 5 (MARB), shear force in kg as an indicator of tenderness (SHF, kg), loin redness (CIE a*) measured at 24, 48, 96 and 168 hours after blooming (A24, A48, A96 and A168, respectively) and rate of redness decline (ADEC), yellowness (CIE b*) measured at 24, 48, 96 and 168 hours after blooming (B24, B48, B96 and B168, respectively) and lightness (CIE L*) measured at 24, 48, 96 and 168 hours after blooming (L24, L48, L96 and L168, respectively).

Slaughter procedure and traits description

Live weight at 6 months is a trait measured in most flocks in New Zealand and it is also known as autumn weight. EMD, EMW and FDM were measured by ultrasound during the autumn when lambs were also aged around 6 months old. Ultrasound measurements were taken

at the position of 12th rib. EMW is the maximum distance across the muscle (*Longissimus dorsi*), from the spinal process outwards along the 12th rib, while EMD is the greatest distance at right angles to the EMW. Finally, FDM is the thickness of the backfat above the EMD measurement.

Pre-slaughter weight was measured around 24 hours prior to slaughter. Lambs were slaughtered in commercial plants with the carcasses electrically stimulated. After slaughter, carcasses were weighed. HCW is the weight of the hot carcass immediately after the skin, head, feet and internal organs have been removed. Dressing out percentage was estimated as: $\frac{HCW}{PRESLT} * 100$. The carcasses were also graded with X-ray grading system which estimates and records carcass weight (XWT), and the following primal cuts: XLEG, XMID, XFORE and XNRIB. The description of the primal cuts is that the forequarter is separated at the 4th and 5th rib and the hindleg is chump on cut between the 6th lumbar and aitch bone. Before going to the X-ray machine the carcasses were re-weighted. The carcass separation points were determined based on the X-ray skeletal structure and weights of the primal cuts were then determined by various algorithms from carcass weight and pixel density. Estimated primal cuts weights were then scaled to ensure that they add to the pre X-ray weight.

On the day of slaughter, CGRM and CBUTT measurements were also collected. CBUTT was measured using a flexible tape measure on the dressed carcasses hanging from the Achilles tendons and represented the circumference when taken in a parallel plane immediately above the anal opening. The following day at 24 hours post slaughter the carcasses were processed into primal cuts and the measures of LNBNWT, LEGLGTH and LEGWT were taken. LEGWT is a measure of one leg done using a scale while XLEG is related to the weight of both legs predicted by X-ray. LEGLGTH is measured from the crotch to the end of the hind leg, which was cut through the tarsal joint. The boneless loins were vacuum packed and stored at -1°C for 8 weeks (to simulate the period taken for chilled lamb to reach the off-shore retail

market). At 8 weeks post-processing, LPH was measured on the Longissimus dorsi muscle using a temperature-compensated pH meter, as the average of three replicate measurements. Three 2-cm thick slices of the loin were placed on small plastic trays and wrapped using semi permeable cling film and stored at 4°C (to simulate retail display) for colour measurements at 24, 48, 96 and 168 hours (one, two, four and seven days, respectively). Colour measurements were taken using a Minolta Chromometer (Konica Minolta Sensing, Inc., Osaka Japan). Three replicates were collected and the average values for each were analysed. The chromometer measures colour using the standard colour measurements adopted by the Commission Internationale d'Eclairage (CIE) in 1976: CIE L*, a* and b* (CIE L* = lightness/darkness; CIE a* = redness/brownness; CIE b* = yellowness). For convenience, CIE L*, CIE a* and CIE b* will be presented in this paper as L_n , A_n and B_n , respectively, with n being 24, 48, 96 and 168 hours after retail display. ADEC is the slope of the regression based on the four measurements of CIE a* over time. Marbling was visually scored on a five point scale, where 1 corresponds to little or no marbling and 5 corresponds to high marbling equating to approximately 30% visual intramuscular fat on slices of loin taken from the lumbar region (M. longissimus). Scoring was undertaken by two independent assessors with the values averaged. SHF measurements were taken on chilled and frozen loins using the MIRINZ protocol [8]. Higher values of shear force indicate tougher meat.

Data edits

Only records that met the following criteria were used: 1) year of birth and birth flock known; 2) sex identified as male or female, 3) weaning management grouping defined by the breeder, 4) trait management group known, 5) breed composition recorded in SIL and 6) contemporary group for the trait having more than 3 observations. To remove possible outliers, observations with more than three standard deviations outside the global mean were removed.

Statistical analysis

The data analysed in this study was collected in farms located in different regions of New Zealand with variation in environmental conditions. A relationship between contemporary group mean and variance was observed for some traits (data not shown). According to Huisman and Brown [9] this heterogeneity in variances across contemporary groups results in EBVs that do not reliably predict progeny performance across the whole range of production environments, and this in turn leads to lower confidence in the use of breeding values across flocks where environments and management practices may differ. One alternative is to express traits as a proportion of their contemporary group mean to avoid these problems [10]. The transformation applied was: $TR = \frac{RR}{CGM} * GMTR$, where TR is the transformed record used in the analysis, RR is the raw record, CGM is the mean of contemporary group and GMTR is the global mean of the trait. The traits transformed in this way were: LW6, PRESLT, HCW, CGRM, FDM, XWT, XFORE, XLEG, XMID, LEGWT and LPH. Contemporary group (CG) is trait specific and was defined by flock, birth year, sex, weaning mob and trait measurement/slaughter mob.

Data were analysed using linear mixed models. Fixed effects models were selected for each trait separately via backwards elimination using the GLM procedure (SAS Inst. Inc., Cary, NC) and based on data availability, literature evidence and knowledge of the traits. Model selection was carried out on the pre-processed dataset (see “Data edits” section). Linear animal models were used for all traits, although XNRIB and MARB are categorical variables.

To offset the differences in age of measurement, estimated birthday deviation from the mean of the contemporary group was used as a covariate in the analysis. Up to five different contributing breeds are recorded on SIL for each animal. These are determined by (preferentially) averaging the recorded breeds of the parents, direct recording by owner or by

substituting the ‘flock breed’ for the breed of any unknown parent. The averaging process rounds values up to the nearest 0.5% [11]. The decision to adjust for breed effects in New Zealand sheep datasets is somewhat moot, in the sense that breed as recorded in SIL has become a very fluid concept. There are many crossbred animals and some breeds are actually composites. However, not accounting for potential effects of breed admixture in the genetic evaluation model may have an impact on the final estimates. Consequently the analyses were run both with and without breed effects and breed proportion was discarded for traits that presented little variation in genetic additive variance. Breed effects consisted of five covariates (Coop, Peren, Rom, Texel and Other), each calculating the proportion of a breed (Coopworth, Perendale, Romney, Texel or other breeds, respectively) in the animal. The fixed effects and covariate terms fitted for each trait are listed in Table 1 (significance level: $p < 0.01$).

Variance and covariance components were estimated using Restricted Maximum Likelihood (REML) procedures fitting an animal model in ASReml 3.0 [12]. Heritabilities were obtained by running univariate analyses for each trait, whereas bivariate analyses were used to estimate the phenotypic and genetic correlations between the various traits. The genetic correlation matrix for each bivariate analysis was subsequently bent to ensure it was positive definite. Due to the presence of a large number of animals with unknown ancestry (mainly dams), we also fitted a genetic group effect (phantom parents [13]) to take into account possible genetic differences in founders contributing to animals born in different years. For this study, the groups were created based on the progeny birth year and sex of the unknown parent.

In some breeding programs the main goal is to select for traits which are indicators of leanness, fatness and/or meat quality independently of other correlated variables such as carcass weight, live weight or pH. To examine this, genetic parameters were estimated for some traits adjusted by LW6, HCW and/or LPH (linear and/or quadratic effect) by fitting the adjusting trait as a covariate. The abbreviations for traits adjusted for correlated variables are

followed by “ad” (full models described on Table 1). The resultant heritability estimates were then compared to those obtained without adjustment for correlated variables. An advantage of the current dataset was that the animals of an allocated slaughter group with flock were slaughtered on a fixed date (regardless of carcass weight), which allowed comparison of results between adjusted and non-adjusted heritability estimates.

Comparing the genetic parameters and EBVs from traits transformed (as a proportion of contemporary group means) and non-transformed

We estimated genetic parameters for the transformed (as a proportion of contemporary group means) and non-transformed data. The correlations between the breeding values produced from both analyses were compared using Pearson’s correlation coefficient. Breeding values were only retained for comparison if the reliability of the breeding value prediction was $\geq 0.8 \times \text{heritability}$ (approximation for individuals with measurements). Reliability of EBVs was calculated as: $r_{ij}^2 = 1 - \frac{SEP_{ij}^2}{\sigma_{aj}^2}$ [14, 15], where SEP is the standard error of prediction produced by ASReml for the EBV of animal i for the trait j and σ_{aj}^2 is the additive genetic variance of trait j .

Results

Descriptive analysis

Means, standard deviations, number of measurements per trait, minimum and maximum and coefficient of variation (CV) are given in Table 2. Considerable variability (range of CV) was observed for most traits, with FDM and CGRM presenting the greatest levels (41.69 and 65.85%, respectively). The least variable traits were XNRIB and LPH with a coefficient of variation of 2.51 and 2.82 %, respectively. There were 589, 11,207 and 756 animals out of 12,552 (4.7, 89.3 and 6.0 %) with 12, 13 and 14 rib pairs, respectively. Mean

(\pm SD) CIE a* measurements from 24 to 168 hours decreased indicating a gradual darkening of the meat-colour. The means of CIE b* and CIE L* were more stable over time compared to CIE a*.

Transforming traits to a proportion of contemporary group

Table 3 presents the heritabilities of traits and phenotypic variances (corrected for fixed effects) for the traits where there was a relationship between contemporary group mean and variance. The genetic parameter estimates were very similar for all traits, except fatness measurement traits (FDM, FDMad, CGRM and CGRMad). FDM and FDMad presented higher estimates for the transformed data and CGRM and CGRM_{HCW} presented higher estimates for untransformed data estimates. For most traits a slight increase in the phenotypic variance for the transformed data was observed.

Table 3 also presents the Pearson's correlations between EBVs generated when the phenotypes were transformed or not as a proportion of their contemporary group. For all the traits, except fatness measurement traits, the correlations between the EBVs generated from univariate analysis were greater than 0.990. CGRMad presented the lowest correlation (0.908) between EBVs generated using raw and transformed phenotypes.

Statistical models

Table 1 presents the final mixed models and fixed effects used for individual trait analysis.

Fixed effects. The fixed effects tested were: birth year, flock, sex, weaning mob and trait measurement mobs. Breed proportion and birthday deviation as covariates were also analysed. Birth-rearing rank (number of lambs born and raised per litter, respectively) and age of dam could also influence some of the traits. Not including those effects in the models could

suppress the heritability estimates (increase the residual variance). However, for some of the flocks/years included in this study, this information was not available as dams were not recorded (DNA information was used to assign paternity). The decision to adjust some of the traits for correlated variables was based on the significance of the effects using GLM procedure (SAS package) and our knowledge of the traits. EMD, EMW and FDM were adjusted for LW6 as those measurements were taken when the animals were around six months old. For tenderness, significant linear and quadratic effects of pH were observed (Fig. 2) indicating that intermediate pH increases meat toughness, while high pH meat can be “mushy”. For colour traits only a linear effect of pH was statistically significant.

Fitting breed percentage as covariates. Breed proportion was fitted as a covariate for all traits to account for potential effects of breed admixture in addition to the fixed effects fitted. Heritability estimates from univariate analyses, fitting or omitting breed proportion, differed by 0 to 7.41% and additive genetic variances differed by 0 to 7.97%. In the final analyses, breed proportion remained in the models for the traits that presented a greater variation in additive genetic variance and heritability estimates when fitting or omitting breed proportion. In general, the traits that presented greater variations were those related to muscularity (e.g. EMD and EMW), weight (e.g. LW6) and carcass conformation (e.g. CBUTT and XNRIB). The changes in estimates for meat quality traits were very small and thus breed proportion was not fitted in their final models. Additional file 1 presents the heritability estimates and phenotypic variance (corrected for fixed effects) for all traits.

Heritability estimates (h^2)

Table 4 presents the heritability estimates and phenotypic variances (corrected for fixed effects) for various growth, carcass and meat quality traits. Heritability estimates for growth and carcass traits ranged from 0.10 ± 0.02 for XNRIB to 0.44 ± 0.04 for EMDad, while

estimates for meat quality traits ranged from 0.01 ± 0.01 for A168ad to 0.31 ± 0.03 for MARBad. There was significant genetic variation for most of the traits assessed. The trait with the smallest phenotypic variance was ADEC (0.0002).

Growth and carcass traits. LW6 and PRESLT were found to be traits under moderate genetic control, with heritability estimates of 0.32 ± 0.03 and 0.22 ± 0.02 , respectively. Carcass weight is one of the main traits in meat breeding programs. HCW and XWT presented moderate heritability estimates (0.19 ± 0.02 and 0.17 ± 0.02 , respectively). As well as having similar heritability estimates, they also had a high genetic correlation (0.99 ± 0.00), which can be justified as both traits are basically the same, except that XWT went through a process of trimming and water loss. Dressing out percentage presented a moderate heritability estimate (0.25 ± 0.03). The primal cuts XFORE, XMID and XLEG presented moderate heritability estimates, indicating that selection could lead to substantial genetic gains. LEGLGTH also presented a moderate heritability (0.27 ± 0.05).

The ultrasonic measurements when adjusted or not for LW6 (EMD, EMDad, EMW, EMWad, FDM and FDMad) were moderately to highly heritable, with the estimates adjusted for body weight presenting higher values when compared to traits not adjusted for body weight. The heritability estimates for those traits were approximately 18% greater than estimates from models where the LW6 covariate was not included. XNRIB had a low heritability and phenotypic standard deviation.

Meat quality traits. Marbling score and MARBad presented moderate heritability estimates (0.30 ± 0.03 and 0.31 ± 0.03 , respectively) and significant genetic variation, making them suitable targets for selection. Our results indicate that SHF and SHFad are under moderate genetic control, with heritability estimates of 0.24 ± 0.03 and 0.29 ± 0.03 , respectively. Meat redness presented moderate heritability estimates for measurements at 24, 48 and 96 hours post presentation, suggesting that genetic variation does exist and selection could be used to

improve the colour stability of New Zealand chilled lamb. However, the heritability estimate for A168 was close to zero, indicating the high environmental effect at this stage (168 hours).

Correlations among traits

The phenotypic and genetic correlations and their standard errors are reported in Tables 5 to 7 and Additional files 2 and 3. Saying that two traits are genetically correlated implies that selection applied to one of them will cause a change in the other, which enables indirect selection. Although presented for completeness, phenotypic correlations will not be discussed as they are of little interpretative value in relation to the objectives of this study. Phenotypic and genetic correlations (followed by their standard errors) for the traits that were also adjusted for correlated variables were also presented (Additional file 3).

Correlations among growth and carcass traits. The phenotypic and genetic correlations among growth and carcass traits are presented in Table 5. They were generally positive and high among the weight traits (e.g. 0.97 ± 0.01 between LW6 and PRESLT), including live and carcass traits (e.g. 0.92 ± 0.02 between LW6 and PRESLT). DO% presented a positive and moderate genetic correlation with all carcass traits, except XNRIB and LEGLGTH.

Hot carcass weight presented a positive and unfavourable genetic correlation with FDM and CGRM (0.43 ± 0.09 and 0.47 ± 0.07 , respectively). Number of rib pairs had a weak and positive genetic correlation with most traits, with the highest correlation estimates with LNBNWT (0.36 ± 0.17) and EMW (0.29 ± 0.14).

Ultrasonic eye muscle depth and EMW were moderate to highly correlated with most growth and carcass traits. A favourable correlation was found only with LEGLGTH (-0.21 ± 0.16), indicating that taller animals would be leaner. However, the standard error was high. The same trend was supported by the genetic relationship estimates between CGRM and

LEGLGTH (-0.19 ± 0.12). FDM presented a non-significant genetic correlation with CBUTT based on the standard error estimates. As discussed before the heritability for CGRM were smaller than FDM estimates and the genetic correlation among them was very high (0.94 ± 0.05).

Genetic correlations among meat quality traits

Colour stability of lamb meat entering the fresh retail market is a primary factor in determining retail shelf life. Strong and positive genetic correlations (greater than 0.90) were observed among all the measures at 24, 48, 96 and 168 hours for each colour indicator trait (CIE L*, a* and b*), except for A24 with A96 and A168 (0.68 ± 0.07 and 0.67 ± 0.10 , respectively). Genetic correlations between ADEC and other traits were not shown as it had very low genetic variation and most of the genetic co-variances with other traits were not estimable. The correlations between redness and yellowness measurements were variable ranging from -0.28 ± 0.15 between A96 and B168 and 0.89 ± 0.24 between A168 and B96. A24, A48 and A96 had a low negative genetic relationship with CIE L* measurements, while A168 had positive correlations, however, the standard errors were high. CIE b* and CIE L* measurements had high positive genetic correlations.

Meat-colour is also greatly affected by muscle pH. At a high pH, muscle appears dark and at intermediate pH the meat tends to be tough (Figure 2). In this study, pH was negatively and moderate to highly correlated with CIE b*, CIE L* and A24 measurements, whereas A48, A96 and A168 had low to non-significant genetic correlation with pH.

Loin pH presented a positive correlation with MARB and SHF (0.28 ± 0.11 and 0.34 ± 0.11 , respectively). MARB and SHF were favourably but weakly genetic correlated (-0.17 ± 0.08). In general, SHF was favourably genetically correlated with all meat quality traits.

Selection to reduce pH could reduce marbling score, increase meat redness and result in more tender meat.

Genetic correlations between growth and carcass traits and meat quality traits

The genetic correlations among growth and meat quality traits were moderate to low or non-significant based on their standard errors. There was a positive genetic relationship between meat redness and weight traits such as PRESLT (0.22 ± 0.09) and HCW (0.28 ± 0.09). An unfavourable but low genetic relationship between meat lightness and weight traits (e. g. -0.15 ± 0.11 , between HCW and L24) suggests that selection to increase HCW would result in a favourable response in meat redness and possibly an unfavourable response in lightness. However, the correlations were low and had large standard errors. The correlations among weight traits and yellowness were mostly non-significant. HCW, PRESLT, XWT, XFORE, XLEG and XMID had a low, but favourable genetic correlation with SHF (-0.18 ± 0.08 , -0.17 ± 0.09 , -0.16 ± 0.09 , -0.21 ± 0.09 , -0.13 ± 0.10 , -0.15 ± 0.09 , respectively), a favourable and low to moderate genetic correlation with MARB (0.28 ± 0.08 , 0.32 ± 0.07 , 0.30 ± 0.08 , 0.23 ± 0.09 , 0.15 ± 0.09 , 0.38 ± 0.08 , respectively) and non-significant correlations with LPH.

Discussion

Statistical models

Transforming traits to a proportion of contemporary group. The genetic parameter estimates were very similar for all traits, except fatness measurement traits (FDM, FDMad, CGRM and CGRMad). Brown et al. [10] observed that transformed data have a slightly higher heritability and the resultant EBVs better reflect phenotypic differences in production environments. It suggests that for the traits with high EBV correlations, significant differences would not be expected from using one or the other phenotypes in the genetic evaluations based

on the current dataset. However, the current dataset contained phenotypes recorded from 2010 to 2013 and from a small number of farms which could limit the variation seen. Even for the fatness measurement traits, the correlations were still high; however, there was a small number of animals that were not as well correlated as the majority of the data records as is shown in Fig. 1. Therefore, the transformed data (for traits presented in Table 3) was used for further analysis. For traits presenting a relationship between contemporary group mean and variance, data transformation is recommended for estimation of genetic parameters, especially for datasets which include measurements from a wide variety of environments.

Fitting breed percentage as covariates. The small breed effects observed for the traits included in this study suggests that the breeds were sufficiently linked through the industry, possibly by the wide uptake of composite breeds. In New Zealand, many sheep producers are indifferent to breed. Furthermore, the true composition of crossbreds and composite breeds is often unknown. The best way to include breed would be to predict breed and heterosis from genotypes where pure individuals were genotyped, which could be done in future genomic analyses. Even though breed percentage was fitted for some traits in the current analysis, not performing this adjustment would not cause commercially significant differences in the animals' EBV rankings.

Phantom parents groups. In sheep, Jordaan et al. [16] investigated the effect of including phantom parent groups for animals entering the National Dohne Merino breeding flock from the commercial industry. The authors observed that when including phantom parents, progeny of ewes originating from a commercial base were more likely to be selected in the recorded population and they recommended including it in future genetic evaluations. In dairy cattle, phantom parents groups are also used in the genetic evaluations. Currently, the Holstein Association USA Inc. (Brattleboro, VT) defines phantom parent groups based on the year of birth of animals and the sex of unknown parents in the genetic evaluations for type

traits in US Holsteins [17]. In our study, as dams and some sires were not recorded, phantom parents were also fitted.

Heritability estimates (h^2)

Heritability estimates allow us to discriminate traits that can be manipulated genetically from those for which non-genetic management strategies will provide better improvement in the trait expression. The response of a trait to selection is also dependent on having a good range of genetic variation within that trait. There was significant genetic variation for most of the traits assessed. The trait with the smallest phenotypic variance was ADEC (0.0002) indicating that selection for this trait would produce very little genetic change and consequently ADEC is not recommended as a selection target trait.

Growth and carcass traits. High growth rate lambs are preferred to increase the proportion of lambs sent for slaughter at an earlier age in order to capture seasonal prices, reduce feed costs especially during the summer dry season and to use the fields for other livestock or crops. The higher estimates obtained for LW6 (autumn weight) compared to PRESLT could be partially due to not fitting maternal effects for LW6, maternal effects could not be fitted in the current study as dam information was unavailable in some flocks/years. Maternal effects could have a greater influence in LW6 compared to PRESLT. However, Pickering et al. [18] also presented an estimate for live weight at 8 months (autumn weight) of 0.35 ± 0.00 and found no significant maternal effects for this trait. Higher heritability estimates of PRESLT are presented in the literature, i.e. 0.41 ± 0.05 [19] and 0.51 ± 0.10 [20] for Australian Merino sheep. Safari et al. [21] in a review observed heritability estimates for post weaning weight (up to 12 months) of 0.33 ± 0.02 , 0.29 ± 0.03 and 0.21 ± 0.01 for wool, dual-purpose and meat breeds respectively, which is in agreement with our results. Farmers are typically paid on the weight of carcass at slaughter after removal of the head, feet, skin and

digestive tract. Consequently, DO% is a good indicator of profitability. Similar estimates were observed by Greeff et al. [19] (0.25 ± 0.04), Mortimer et al. [22] (0.24 ± 0.05) and Johnson et al. [23] (0.28 ± 0.08). Cloete et al. [24] found a lower estimate (0.20 ± 0.09) for South African terminal crossbred lambs, a higher estimate (0.39 ± 0.10) was presented by Fogarty et al. [20].

Meat companies' profitability is not related only to carcass weight but also to yield of lean tissue within carcass regions as different carcass cuts have different prices in the market. The primal cuts XFORE, XMID, XLEG, LEGWT and LNBNWT presented moderate heritability estimates, indicating that selection could lead to substantial genetic gains.

In general, the estimates adjusted for body weight presented higher values when compared to traits not adjusted for body weight. Mortimer et al. [25] found a heritability estimate for EMD and FDM of 0.19 ± 0.03 and 0.17 ± 0.03 , respectively, when the data was not adjusted for body weight at scanning and 0.25 ± 0.03 and 0.22 ± 0.03 , respectively, when body weight at scanning was included as a covariate. The body weight adjustment represents an increase of approximately 30% in the univariate estimates. The same authors [25] also observed that adjustment for body weight removed the influence of maternal effects on these traits as observed in univariate analysis. According to the authors, it would be more appropriate to derive genetic parameters from models that accounted directly for maternal effects, rather than using a covariate to do so, and then calculate adjusted parameter estimates post analysis. Our estimates for EMD and FDM were also greater than those presented by Greeff et al. [19] whom reported heritability estimates for EMD and FDM adjusted for weight at scanning of 0.22 ± 0.04 and 0.25 ± 0.04 , respectively and Mortimer et al. (2010) who found an estimate of EMD and FDM adjusted for weight at scanning of 0.23 ± 0.03 and 0.15 ± 0.03 , respectively. Safari et al. [21] in a review paper observed average estimates of 0.26 ± 0.02 and 0.25 ± 0.02 for FDM and FDM adjusted for live weight, respectively. CGRM and CGRM_{ad} were also moderately heritable. The heritability estimates for CGRM were smaller than the estimates for

ultrasonic measures of fat depth (FDM). Higher estimates for CGRMad have been reported (0.28 ± 0.04, 0.33 ± 0.09 and 0.50 ± 0.05) [19, 20, 22].

It has been demonstrated in pigs that incorporating information on vertebra characteristics such as number of ribs in the selection process, can benefit production traits. Hence, since rib number varies in sheep as well, it may be possible that a similar application of spine trait records in the selection of sheep will improve carcass quality, in terms of size and meat yields [26]. However, it was observed that XNRIB had a low heritability and phenotypic standard deviation, indicating that low genetic progress would be achieved by selection for this trait. XNRIB could be influenced by a maternal effect during gestation. However, dams were not recorded in this dataset to evaluate the influence of this effect. This low heritability is surprising because we might expect the expression of this trait to be largely due to genetic background. Therefore, this warrants further investigation. In pigs, Borchers et al. [27] estimated heritabilities for rib and vertebrae number of 0.51 ± 0.08 and 0.62 ± 0.06, respectively. High heritability values in pigs were also observed by Fredeen and Newman [28] of 0.73 and 0.59 for rib number by offspring on mid-parent regression and full-sib correlation.

Meat quality traits. Marbling is defined as the intramuscular fat (IMF) or adipose tissue, deposited between perimysium surrounding muscle bundles, and is visible to the human eye as ‘flecks’ or spots of fat. Marbling is a visual score given to a piece of meat, whereas IMF is the chemically measured fat content (includes membrane lipids), although the terms are often used interchangeably [29]. Marbling score and MARBad presented moderate heritability estimates (0.30 ± 0.03 and 0.31 ± 0.03, respectively) and significant genetic variation, making them suitable targets for selection. Johnson et al. [30] reported a similar estimate (0.32 ± 0.10) for a New Zealand Perendale population and Johnson et al. [23] reported an estimate of 0.40 ± 0.06. A similar estimate (0.32 ± 0.09) for IMF was presented by Karamichou et al. [2]. Higher estimates have also been presented for IMF, such as 0.48 ± 0.05 [31] for Merino and crossbred

progeny of Merino, terminal and maternal meat-breed sires and 0.48 ± 0.16 for Nor-X terminal sire breeds [32]. Even though the heritability estimates were lower than literature estimates for IMF, it is important to note that marbling as scored in the current study is much cheaper to measure compared to IMF, which requires destruction of a meat sample.

Meat tenderness is essentially determined by the amount and solubility of connective tissue, sarcomere shortening during rigor development, and post-mortem proteolysis of myofibrillar and myofibrillar-associated proteins [33]. Our results indicate that SHF and SHFad are under moderate genetic control. A similar estimate (0.27 ± 0.04) was obtained by Mortimer et al. [31]. Higher estimates (0.39 ± 0.16 and 0.44 ± 0.08) were obtained by Karamichou et al. [16] and Cloete et al. [3], confirming our findings in New Zealand sheep that this trait is under moderate genetic control.

New Zealand produces 485,800 tonnes of sheep meat annually with 98% available for export [34]. Stability of meat-colour is an important trait as lamb meat is transported worldwide and is required to reach the final destination presenting a desirable colour for the consumer. Consumers judge the freshness of meat by how bright and red it is on display. Our findings suggest that genetic variation does exist and selection could be used to improve the colour stability of New Zealand chilled lamb. However, the heritability estimate for A168 was close to zero, indicating the high environmental effect at this stage (168 hours). Rate of decline also had a very low heritability and very low phenotypic variance, indicating that gains through selection would be very limited. Yellowness measurements CIE b* (B24, B48, B96 and B168) had low estimates, but did exhibit a high co-efficient of variation indicating that this trait is influenced largely by environmental factors as well, hence genetic improvement in this trait may be slow if direct genetic selection is applied. In order to improve colour stability of lamb in the meat case strategies should, target both genetic and environmental influences (pre and post slaughter). Payne et al. [35] reported higher h^2 for CIE L* (0.29 and standard error ranging

between 0.034 and 0.049) and similar h^2 for CIE a^* (0.19 and standard error ranging between 0.034 and 0.049) in New Zealand sheep. Heritability estimates of CIE L^* , CIE a^* , CIE b^* in Merino have been reported as 0.18 ± 0.03 , 0.10 ± 0.03 and 0.10 ± 0.03 , respectively [19]. McLean et al. [36] reported higher heritability estimates for CIE L^* , CIE a^* , CIE b^* measured 8 weeks after chilled storage and 168 hours after cutting (adjusted for HCW) in New Zealand sheep of 0.23 ± 0.04 , 0.26 ± 0.04 and 0.20 ± 0.03 , respectively. Mortimer et al. [31] found h^2 estimates for CIE L^* , CIE a^* and CIE b^* of 0.41 ± 0.05 , 0.25 ± 0.04 and 0.10 ± 0.03 , respectively. [20] found h^2 estimates for CIE L^* , CIE a^* and CIE b^* of 0.14 ± 0.04 , 0.02 ± 0.06 and 0.04 ± 0.06 , respectively. These studies also confirm our findings that meat-colour is under genetic control and are selection target traits.

Ultimate pH of meat is related to shelf life, colour, tenderness, flavour and juiciness [37]. pH heritability estimates were low in this study, with a low phenotypic variance, indicating that selection is unlikely to produce a large change in pH. Payne et al. [28] found a LPH heritability estimate of 0.12 (standard error ranging between 0.034 and 0.049) and Mortimer et al. [22] of 0.08 ± 0.02 . The low heritability estimates suggest that gains from selecting for this trait would be small. However, it is important to continue monitoring this trait in industry datasets to improve pre-slaughter handling and to allow pH adjustment for other traits. Despite the small estimates found in this study, higher estimates have been reported in the literature such as 0.22 ± 0.03 , 0.27 ± 0.09 and 0.44 ± 0.09 [19, 20, 32].

The differences found in heritability estimates from different studies were expected as they are specific to populations. Furthermore, they could be influenced by several factors such as the depth of pedigree, number of records, adjustments for correlated variables and other phenotypic adjustments. It is also important to point out that trait measurements vary considerably between studies.

Genetic correlations among growth and carcass traits. The moderate to positive and

high correlations among the weight traits, including live and carcass traits indicate that selection for growth will also impact the carcass traits in a similar direction. The genetic correlation between LW6 and PRESLT was very high suggesting these parameters effectively describe the same genetic trait in lambs. Hot carcass weight and XWT were extremely correlated (0.99 ± 0.00) indicating that X-ray carcass weight measurement (XWT) is a good predictor of carcass weight. Dressing out percentage presented a positive and moderate genetic correlation with all carcass traits, except XNRIB and LEGLGTH. This shows that selecting for improved dressing percentage may be expected to increase carcass yield over time. Greeff et al. [19] also observed a positive genetic correlation between DO% and carcass fat traits ($0.49 - 0.53$) and with muscle traits ranging from 0.26 to 0.36 . The low genetic correlation between DO% and PRESLT (0.14 ± 0.08) was also observed in Merino hogget rams (0.16 ± 0.09) [19]. Ingham et al. [38] observed a genetic correlation between post-weaning weight (measured at 4 to 6 months of age) and DO% of 0.00 ± 0.18 . Fogarty et al. [20] observed a small and negative genetic correlation between live weight and DO% (-0.22 ± 0.13).

The results show that live weight (LW6 and PRESLT) and carcass weight (HCW and XWT) are highly genetically correlated with the primal cuts XFORE, XMID and XLEG, LEGWT and LNBNWT. The current breeding programs have been making progress in the primal cuts by selecting for carcass or live weight and/or ultrasound scanning. However, the genetic correlations among them are not unity, meaning that the selection response could be improved through incorporating measurements on the primal cuts in the overall breeding objectives. If not considered in the breeding programs, selection to produce heavier carcasses would result in a higher fat carcass level. A similar trend was observed by Ingham et al. [38] who presented a genetic correlation of 0.41 ± 0.12 . The positive genetic correlation found between FDM with most of the other carcass traits is undesirable. A favourable correlation was

found only with LEGLGTH (-0.21 ± 0.16), indicating that taller animals would be leaner. However, the standard error was high. Selection for XNRIB would have little impact on meat production traits. Furthermore, XNRIB presented a low heritability and consequently it would not be a key trait to include in a breeding program and continued measurement of this trait appears of questionable value.

Genetic correlations among meat quality traits. Colour stability of lamb meat entering the fresh retail market is a primary factor in determining retail shelf life. Strong and positive genetic correlations (greater than 0.90) were observed among all the measures at 24, 48, 96 and 168 hours for each colour indicator trait (CIE L*, a* and b*), except for A24 with A96 and A168 (0.68 ± 0.07 and 0.67 ± 0.10 , respectively). CIE b* and CIE L* measurements had high positive genetic correlations. The same trend was observed by Lorentzen and Vangen [32]. They also observed a negative genetic correlation (-0.84) between CIE a* and CIE L*, however, it was higher than the estimates found in the current study. McLean et al. [36] observed a genetic correlation between B168ad and L168ad of 0.60 ± 0.01 and between A168ad and L168ad of 0.12 ± 0.01 , which are smaller than the estimates that we observed in this study. The same authors found a non-significant genetic correlation between A168ad and B168ad while we observed a moderate estimate but with high standard error. Mortimer et al. [31] observed a moderate and positive genetic correlation between CIE a* and CIE b* (0.48 ± 0.12), a negative correlation between CIE L* and CIE a* (-0.37 ± 0.09) and a positive correlation between CIE L* and CIE b* (0.36 ± 0.13) for measurements recorded after 48 hours of retail display. The colour measurements at different stages are time consuming and ideally, it would be better to do only one measurement, early in the post mortem period, without a need to expose the meat to a simulated display period. The very high genetic correlations among the four time points for CIE b* and CIE L* indicate that B24 and L24 would be good predictors of yellowness and lightness stability, respectively. However, for meat redness, the correlation

between A24 and the other points were moderate, indicating the need to measure at later stages in order to attain genetic gains in meat redness stability. A suggestion would be to select for A24 and A48 in order to improve meat-colour stability.

Meat-colour is also greatly affected by muscle pH. At a high pH, muscle appears dark and at intermediate pH the meat tends to be tough (Figure 2). In this study, pH was negatively and moderate to highly correlated with CIE b*, CIE L* and A24 measurements, whereas A48, A96 and A168 had low to non-significant genetic correlation with pH. A similar trend was observed by Fogarty et al. [20], who found a moderately negative correlation between pH and L* (-0.56 ± 0.23). Greeff et al. [19] found genetic correlation estimates between pH and CIE L*, CIE a* and CIE b* of -0.57 ± 0.08 , -0.78 ± 0.08 and -0.94 ± 0.07 , respectively. McLean et al. [36] found a correlation between pH and CIE L*, CIE a* and CIE b* (adjusted for HCW) of -0.46 ± 0.09 , -0.16 ± 0.11 and -0.71 ± 0.07 , respectively.

All the colour measurements presented a low to moderate and favourable genetic correlation with MARB and SHF, indicating that selecting to increase marbling and tenderness would result in better colour meat. The favourable, however weak genetic correlation between MARB and SHF indicates that indirect selection gain would be small and it is recommended to include both of them in a breeding program. The same trend was observed by Mortimer et al. [31] who found a genetic correlation of -0.62 ± 0.07 between intramuscular fat and shear force. In general, SHF was favourably genetically correlated with all meat quality traits. Selection to reduce pH could reduce marbling score, increase meat redness and result in more tender meat.

Genetic correlations between growth and carcass traits and meat quality traits. The genetic correlations among growth and meat quality traits were moderate to low or non-significant based on their standard errors, indicating that continued selection for growth may improve or will not have a large adverse effect on meat quality. Results from this study suggest

that selection to reduce FDM and CGRM would have either a negative or little impact in most traits included in this study. FDM and CGRM are moderately and unfavourably correlated to marbling and meat redness, indicating that selection for leanness alone could affect meat quality traits and consequently consumer eating satisfaction. McLean et al. [36] found a genetic correlation of -0.30 ± 0.13 , 0.13 ± 0.13 and -0.25 ± 0.14 between HCW and CIE L*, CIE a* and CIE b* measured at 168 hours, respectively. LPH presented a low or non-significant correlation with most growth and carcass traits indicating that selecting for other production traits would not affect meat pH. Payne et al. [35] have predicted that index selection for growth rate and meat yield would result in little change in meat quality traits, except for small increases in meat lightness and pH and a decrease in fat yellowness.

Genetic parameters for traits adjusted for correlated variables. Most of the discussion in this paper about genetic correlations among traits were based on traits not adjusted for correlated variables. As expected, it was observed (Additional file 2) that some relationships among the traits adjusted for correlated variables differed from those observed when traits were not adjusted. It could be debated whether those adjustments should be performed or not. The reason for that is mainly related to the breeding program selection goal and it will depend if the breeders want to select for some traits independently from others or if they are just interested in the outcome for that specific trait or group of traits. Either way, the information presented in this paper will be useful in order to help the breeders and geneticists design and update breeding programs.

Implications

The profitability from the different meat sheep industry sectors is related to specific traits. The farmers want a more efficient animal that grows fast and has a high dressing out percentage because they will be paid based on carcass weight. The meat companies would like

animals with high lean meat yield and higher proportion of more valuable cuts, while consumers are looking for products with better visual and eating qualities. Considering that, in order to meet all requirements and make a competitive industry, it is important: 1) to make efforts to improve the animals in all these traits genetically; and 2) to provide the environmental conditions for the animals from gestation to slaughter in order to allow them to express their genetic potential. Including animal management, welfare, biosecurity control, and correct pre- and post-slaughter handling to avoid any kind of stress, and 3) processing, storing and transporting of the meat products to maintain quality for the consumer. All those factors are connected and will influence the final product quality and the industry competitiveness.

This paper focused on the genetic control and relationship among traits. The heritability estimates and phenotypic variances for the traits analysed suggest that most of the traits present sufficient phenotypic variation and are under moderate genetic control implying that substantial genetic gains could be achieved through direct and indirect selection. This study also confirms that ultrasound and X-ray measurements have moderate to strong genetic correlations with their corresponding measurements of carcass merit. The genetic parameters presented in this study provide an insight into the biological basis of these traits but are also a valuable reference to update New Zealand terminal sire breeding programs to emphasize eating quality traits. Parameter estimates from this study indicate that there are not many strong genetic antagonisms among growth, carcass and meat quality traits. It is important to point out that the unfavourable genetic correlations identified in this study were low to moderate and therefore it is possible to select for favourable genetic progress in all traits when all traits are measured and balanced in a selection index.

The ease and cost of measurement of many of the meat quality traits would have traditionally limited the ability to incorporate these traits directly into current industry breeding programs. However, an alternative opportunity to improve those traits is now available via the

use of genomic technologies and this work is part of a wider programme implementing this technology into the New Zealand sheep industry.

Conclusions

The heritability estimates and phenotypic variances for the traits analysed suggest that most of them have sufficient phenotypic variation and are under moderate genetic control implying that substantial genetic gains could be achieved through direct and indirect selection. The genetic parameters presented in this study provide an insight into the biological basis of these traits but are also a valuable reference to design and/or update a terminal sire breeding program emphasizing eating quality traits. It is important to note that unfavourable genetic correlations identified in this study were low to moderate, making it practical to select for favourable genetic progress in all traits, if they are measured and balanced in a selection index.

Abbreviations

A24: loin redness measured at 24 hours after blooming, ADEC: rate of redness decline, B24: yellowness at 24 hours after blooming, CBUTT: carcass measurement of buttocks circumference, CDLEGLT: carcass dissected leg length, CGM: mean of contemporary group, CGRM: depth of tissue at the GR site, CG: contemporary group, CIE: Commission Internationale d'Eclairage, CV: coefficient of variation, DNA: Deoxyribonucleic acid, DO%: dressing out percentage, EBV: Estimated Breeding Value, EMA: eye muscle area, EMD: ultrasonic eye muscle depth, EMW: ultrasonic eye muscle width, FATY: fat yield, FDM: ultrasonic fat depth, GLM: generalized Linear Models, GMTR: global mean of the trait, HCW: hot carcass weight, HQLY: hindquarter lean yield, IMF: intramuscular fat, L24: lightness measured at 24 hours after blooming, LEGLGTH: leg length, LEGWT: leg weight, LNBNWT: boneless loin weight, LNLY: lean loin yield, LPH: loin meat pH, LY: lean yield, LW6: live

weight at 6 months, LW8: Autumn live weight recorded in animals aged between 6 to 8 months, MARB: marbling score, PRESLT: pre-slaughter weight, PW: primal weight, REML: Restricted Maximum Likelihood, RR: raw record, SD: standard deviation, SEP: standard error of prediction, SHF: shear force, SHLY: shoulder lean yield, SIL: Sheep Improvement Limited, SUR: survival to weaning, TR: transformed record, WWT: weaning weight, XFORE: X-ray forequarter weight, XLEG: X-ray leg weight, XMID: X-ray middle or loin weight, XNRIB: X-ray number of rib pairs, XWT: X-ray carcass weight.

Competing interests

The authors declare that there are no competing interests.

Funding

This research has been funded by: FarmIQ (Ministry for Primary Industries' Primary Growth Partnership fund) – FIQ Systems – Plate to Pasture (Reference: PGP06-09020) and AgResearch.

Authors' contributions

LFB participated in the design of the study, carried out the analyses and results interpretation, was involved in the discussions, prepared and drafted the manuscript. JCM, SPM, KGD, SMC, NP and ML participated in the design of the study, results interpretation and were involved in the discussions. WB and SAN managed the data collection and organization on SIL and were involved in the discussions. FSS provided training to the first author, participated in discussions and gave editorial assistance. All authors have read and approved the final manuscript.

Acknowledgements

The authors gratefully acknowledge the following organizations: FarmIQ (Ministry for Primary Industries' Primary Growth Partnership fund) for funding the work, Landcorp and Focus Genetics for undertaking the progeny test evaluation, Silver Fern Farms for processing the animals, especially the staff at the Finegand and Takapau plants, and Grant Pearson and his team for undertaking the majority of the meat tenderness measurements. The authors would also like to recognize the significant and on-going contribution of AgResearch farm and technical staff in management and trait recording, AgResearch core funding and the Brazilian Government through the Science without Borders Program that provides a graduate fellowship for the first author.

Availability of data and materials

All relevant information supporting the results not already presented in the article are given in additional files. The raw data cannot be made available, as it is property of the sheep producers in New Zealand and this information is commercially sensitive.

References

1. Beef and Lamb New Zealand. 2012. Domestic Trends and Measuring Progress against the Red Meat Sector Strategy. Presentation to: Red Meat Sector Conference 2012. <http://beeflambnz.com/Documents/Information/Red%20meat%20sector%20conference.pdf>. Accessed 11 January 2015.
2. Karamichou E, Richardson RI, Nute GR, McLean KA, Bishop SC: Genetic analyses of carcass composition, as assessed by X-ray computer tomography, and meat quality traits in Scottish Blackface sheep. *Animal Science* 2006, 82(2):151-62.
3. Hopkins DL, Hegarty RS, Farrell TC: Relationship between sire estimated breeding values and the meat and eating quality of meat from their progeny grown on two planes of nutrition. *Australian Journal of Experimental Agriculture* 2005, 45(5):525-33.
4. Miar Y, Plastow G, Bruce H, Moore S, Manafiazar G, Kemp R, Charagu P, Huisman A, van Haandel B, Zhang C *et al*: Genetic and phenotypic correlations between performance traits with meat quality and carcass characteristics in commercial crossbred pigs. *PloS one* 2014, 9(10):e110105.
5. Oksbjerg N, Petersen J, Sørensen IL, Henckel P, Vestergaard M, Ertbjerg P, Møller A, Bejerholm C, Støier S: Long-term changes in performance and meat quality of Danish

- Landrace pigs: a study on a current compared with an unimproved genotype. *Animal Science* 2000, 71(1):81-92.
6. Pannier L, Pethick DW, Geesink GH, Ball AJ, Jacob RH, Gardner GE: Intramuscular fat in the longissimus muscle is reduced in lambs from sires selected for leanness. *Meat Science* 2014, 96(2):1068-75.
7. Jopson N, McEwan J, Logan C, Muir P: Genetic parameters for primal cut meat yield traits in sheep. *Proceedings of the New Zealand Society of Animal Production* 2009, 69:215-9.
8. AgResearch MIRINZ: <http://www.mirinz.org.nz>. Accessed 20 Feb 2015.
9. Huisman AE, Brown DJ: Predictive ability of sire weaning weight breeding values estimated across environments in terminal sire sheep breeds. In: *8th World Congress on Genetics Applied to Livestock Production: August 13-18, 2006; Belo Horizonte, MG, Brazil*.
10. Brown D, Atkins K, Huisman A: Expression of body weight, fleece weight and fibre diameter in across flock genetic evaluation. In: *Proceedings of the Association for the Advancement of Animal Breeding and Genetics: 2005*. 84-7.
11. Dodds K, Newman S, Auvray B, McEwan J, Villalobos N: Breeds of New Zealand sheep—as recorded or by genomic prediction. In: *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 2013. 274-7.
12. Gilmour AR, Gogel B, Cullis B, Thompson R: ASReml user guide release 3.0. VSN International Ltd, Hemel Hempstead, UK 2009.
13. Westell RA, Quaas RL, Van Vleck LD: Genetic Groups in an Animal Model. *Journal of Dairy Science* 1988, 71(5):1310-18.
14. Mrode RA: Linear models for the prediction of animal breeding values: CABI; 1996.
15. Lutaaya E, Misztal I, Mabry J, Short T, Timm H, Holzbauer R: Joint evaluation of purebreds and crossbreds in swine. *Journal of Animal Science* 2002, 80(9):2263-6.
16. Jordaan W, Cloete S, Olivier J, Dzama K: Using Phantom Groups to Increase the Accuracy of Breeding Values of Dohne Merinos Upgraded From a Commercial Base to the Pedigreed Population. In: *10th World Congress on Genetics Applied to Livestock Production: 2014*.
17. Tsuruta S, Misztal I, Lourenco D, Lawlor T: Assigning unknown parent groups to reduce bias in genomic evaluations of final score in US Holsteins. *Journal of Dairy Science* 2014, 97(9):5814-21.
18. Pickering NK, Dodds KG, Blair HT, Hickson RE, Johnson PL, McEwan JC: Genetic parameters for production traits in New Zealand dual-purpose sheep, with an emphasis on dagginess. *Journal of Animal Science* 2012, 90(5):1411-20.
19. Greeff JC, Safari E, Fogarty NM, Hopkins DL, Brien FD, Atkins KD, Mortimer SI, van der Werf JH: Genetic parameters for carcass and meat quality traits and their relationships to liveweight and wool production in hogget Merino rams. *Journal of Animal Breeding and Genetics* 2008, 125(3):205-15.
20. Fogarty NM, Safari E, Taylor PJ, Murray W: Genetic parameters for meat quality and carcass traits and their correlation with wool traits in Australian Merino sheep. *Australian Journal of Agricultural Research* 2003, 54(7):715-22.
21. Safari E, Fogarty NM, Gilmour AR: A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. *Livestock Production Science* 2005, 92(3):271-89.
22. Mortimer S, Van der Werf J, Jacob R, Pethick D, Pearce K, Warner R, Geesink G, Edwards JH, Gardner G, Ponnampalam E: Preliminary estimates of genetic parameters for carcass and meat quality traits in Australian sheep. *Animal Production Science* 2010, 50(12):1135-44.

23. Johnson P, Younga E, Ruddenklau D, Anderson T, Dodds K: Genetic parameters for meat yield and quality traits derived from the New Zealand Perendale progeny test. In: *Proceedings of the New Zealand Society of Animal Production: 2015*. 106-10.
24. Cloete S, Cloete J, Hoffman L: Heritability estimates for slaughter traits in South African terminal crossbred lambs. In: *Proceedings of the 54th International Congress of Meat Science and Technology, Cape Town, South Africa Session: 2008*. 3.
25. Mortimer S, Swan A, Brown D, van der Werf J: Genetic Parameters Revisited for Ultrasound Scanning Traits in Australian Sheep. In: *10th World Congress on Genetics Applied to Livestock Production: 2014*. Vancouver, Canada.
26. Donaldson C, Lambe N, Maltin C, Knott S, Bunger L: Between-and within-breed variations of spine characteristics in sheep. *Journal of Animal Science* 2013, 91(2):995-1004.
27. Borchers N, Reinsch N, Kalm E: The number of ribs and vertebrae in a Pietrain cross: variation, heritability and effects on performance traits. *Journal of Animal Breeding and Genetics* 2004, 121(6):392-403.
28. Fredeen H, Newman J: Rib and vertebral numbers in swine: II. Genetics aspects. *Canadian Journal of Animal Science* 1962, 42(2):240-51.
29. Warner RD, Greenwood PL, Pethick DW, Ferguson DM: Genetic and environmental effects on meat quality. *Meat science* 2010, 86(1):171-83.
30. Johnson P, Charteris A, Tate M, Dodds K: Brief communication: Genetic parameters for meat traits assessed in the Headwaters New Zealand Progeny Test. In: *Proceedings of the New Zealand Society of Animal Production 2015*.
31. Mortimer SI, van der Werf JH, Jacob RH, Hopkins DL, Pannier L, Pearce KL, Gardner GE, Warner RD, Geesink GH, Edwards JE *et al*: Genetic parameters for meat quality traits of Australian lamb meat. *Meat Science* 2014, 96(2):1016-24.
32. Lorentzen TK, Vangen O: Genetic and phenotypic analysis of meat quality traits in lamb and correlations to carcass composition. *Livestock Science* 2012, 143(2-3):201-209.
33. Koohmaraie M, Geesink G: Contribution of postmortem muscle biochemistry to the delivery of consistent meat quality with particular focus on the calpain system. *Meat Science* 2006, 74(1):34-43.
34. Beef and Lamb New Zealand. 2015. Compendium of New Zealand Farm Facts 2015. <http://www.beeflambnz.com/Documents/Information/Compendium%20of%20New%20Zealand%20farm%20facts.pdf>. Accessed 15 May 2015.
35. Payne G, Campbell A, Jopson N, McEwan J, Logan C, Muir P: Genetic and phenotypic parameter estimates for growth, yield and meat quality traits in lamb. In: *Proceedings of the New Zealand Society of Animal Production 2009*, 69:210-14.
36. McLean N, Johnson P, Bain W, Greer G, Dodds K: Genetic parameters for colour stability of chilled lamb. In: *Proceedings of the New Zealand Society of Animal Production: 2009*. 69:220-222.
37. Hopkins D, Fogarty N: Diverse lamb genotypes—2. Meat pH, colour and tenderness. *Meat Science* 1998, 49(4):477-488.
38. Ingham VM, Fogarty NM, Gilmour AR, Afolayan RA, Cummins LJ, Gaunt GM, Stafford J, Edwards JEH: Genetic evaluation of crossbred lamb production. 4. Genetic parameters for first-cross animal performance. *Australian Journal of Agricultural Research* 2007, 58(8):839-46.

Tables

Table 1. Final mixed models and fixed effects used for individual trait analysis.

Trait ¹	Fixed effects ²	Co-variables ³	Random effects
LW6	Sex, CG	breedp, bdev	Animal
PRESLT, HCW, DO%	Sex, CG	breedp, bdev	Animal
EMD, EMW, FDM	Sex, CG	breedp, bdev	Animal
EMDad, EMWad, FDMad	Sex, CG	breedp, bdev, LW6	Animal
CBUTT, LEGWT, LEGLGTH, LNBNWT, CGRM	Sex, CG	breedp, bdev	Animal
CBUTTad, CGRMad	Sex, CG	breedp, bdev, HCW	Animal
XWT, XLEG, XMID, XFORE	Sex, CG	breedp, bdev	Animal
XNRIB		breedp	Animal
LPH	Sex, CG		Animal
LPHad	Sex, CG	HCW	Animal
MARB	Sex, CG	bdev	Animal
MARBad	Sex, CG	HCW, bdev	Animal
SHF	Sex, CG	bdev	Animal
SHFad	Sex, CG	HCW, pH (linear and quadratic effects)	Animal
ADEC, A24, A48, A96, A168, B24, B48, B96, B168, L24, L48, L96, L168	Sex, CG	bdev	Animal
ADECad, A24ad, A48ad, A96ad, A168ad, B24ad, B48ad, B96ad, B168ad, L24ad, L48ad, L96ad, L168ad	Sex, CG	HCW, bdev, pH	Animal

¹: traits followed by “ad” indicates that they were adjusted for correlated variables; LW6: live weight at six months; PRESLT: pre-slaughter weight; HCW: hot carcass weight; DO%: dressing out percentage; EMD: ultrasonic eye muscle depth; EMW: ultrasonic eye muscle width; FDM: ultrasonic fat depth measurement; CBUTT: butt circumference; LEGWT: carcass leg weight; LEGLGTH: carcass leg length; LNBNWT: carcass boneless loin weight; CGRM: depth of tissue 110 mm off the mid-line in the region of the 12th rib; XWT: X-ray carcass weight; XLEG: X-ray leg weight; XMID: X-ray middle weight; XFORE: X-ray fore weight; XNRIB: X-ray number of rib pairs; LPH: loin pH; MARB: marbling score; SHF: shear force; ADEC: rate of decline of meat redness; *An*, *Bn* and *Ln*: meat redness, meat yellowness and meat lightness at 24, 48, 96 and 168 hours.

²: breedp: breed percentage; CG: contemporary group for each trait was defined by flock, birth year, sex, weaning mob and trait measurement/slaughter mob.

³: bdev: birthday deviation; LW6: adjusted for live weight at six months; HCW: adjusted for carcass weight; pH and pH²: adjusted for pH, linear and quadratic effects.

Table 2. Descriptive unadjusted statistics for growth, carcass and meat quality traits.

Trait, measurement unit	Abbreviation	N	Mean \pm SD	Range	CV (%)
Traits measured in the live animal¹					
Live weight at 6 months, kg	LW6	13,369	37.00 \pm 5.32	20.80 – 53.20	14.38
Pre-slaughter weight, kg	PRESLT	14,564	41.67 \pm 6.14	23.00 – 60.20	14.73
Ultrasonic eye muscle depth, mm	EMD	8,610	24.84 \pm 2.42	18.00 – 32.00	9.76
Ultrasonic eye muscle width, mm	EMW	8,628	64.19 \pm 5.03	49.00 – 79.00	7.84
Ultrasonic fat depth, mm	FDM	8,604	2.61 \pm 1.09	0.00 – 05.00	41.69
Carcass traits					
Hot carcass weight, kg	HCW	13,089	17.93 \pm 3.31	8.40 – 27.90	18.43
Dressing out percentage, %	DO%	13,050	43.03 \pm 3.24	32.82 – 53.27	7.53
Leg length ³ , cm	LEGLGTH	4,347	31.64 \pm 2.18	25.50 – 38.00	6.91
Leg weight ³ , kg	LEGWT	2,918	2.52 \pm 0.43	1.31 – 3.76	17.24
Carcass boneless loin weight ³ , kg	LNBNWT	2,920	0.27 \pm 0.06	0.10 – 0.45	22.82
Butt circumference, cm	CBUTT	14,366	65.04 \pm 3.25	55.20 – 75.00	5.00
GR ² , mm	CGRM	14,234	5.16 \pm 3.39	0.00 – 16.00	65.85
X-ray weight, kg	XWT	12,704	17.37 \pm 3.22	7.73 – 27.16	18.54
X-ray leg weight, kg	XLEG	12,510	6.08 \pm 1.04	3.01 – 9.24	17.04
X-ray middle weight, kg	XMID	12,507	5.32 \pm 1.11	2.03 – 8.73	20.90
X-ray number of rib pairs, n	XNRIB	12,552	13.01 \pm 0.33	12.00 – 14.00	2.51
X-ray fore weight, kg	XFORE	12,513	5.95 \pm 1.15	2.65 – 9.43	19.26
Meat quality traits					
Loin meat pH	LPH	9,338	5.81 \pm 0.16	5.48 – 6.43	2.82
Marbling score	MARB	9,420	3.05 \pm 0.58	1.50 – 4.50	19.09
Tenderness, kgF	SHF	9,372	6.47 \pm 2.23	1.45 – 13.50	34.49
CIE a* rate of decline, per hour	ADEC	8,871	-0.04 \pm 0.01	-0.12 – 0.01	39.62
CIE a* after 24 hours	A24	9,570	16.73 \pm 2.55	9.37 – 24.44	15.22
CIE a* after 48 hours	A48	9,547	14.96 \pm 2.12	9.06 – 21.49	14.13
CIE a* after 96 hours	A96	9,562	12.58 \pm 1.94	6.92 – 18.47	15.41
CIE a* after 168 hours	A168	8,940	10.49 \pm 2.08	3.98 – 17.08	19.86
CIE b* after 24 hours	B24	9,587	12.87 \pm 2.63	5.68 – 20.74	20.47
CIE b* after 48 hours	B48	9,585	12.21 \pm 2.48	4.86 – 19.59	20.33

CIE b* after 96 hours	B96	9,573	11.52 ± 2.24	4.81 – 18.22	19.45
CIE b* after 168 hours	B168	8,988	10.50 ± 2.63	2.48 – 17.85	25.04
CIE L* after 24 hours	L24	9,446	40.63 ± 3.48	29.09 – 51.48	8.56
CIE L* after 48 hours	L48	9,443	40.51 ± 3.46	28.92 – 51.46	8.54
CIE L* after 96 hours	L96	9,496	40.55 ± 3.53	29.31 – 51.49	8.71
CIE L* after 168 hours	L168	8,932	40.27 ± 3.61	28.74 – 51.33	8.97

¹: N: number of observations; SD: standard deviation; CV: coefficient of variation;

²: Depth of tissue 110 mm off the mid-line in the region of the 12th rib;

³: Traits measured only in 2010.

881

882

Table 3. Heritability estimates (\pm SE) and phenotypic variance (corrected for fixed effects) for each trait using transformed or untransformed data and the Pearson correlations among the EBVs generated from each univariate analysis.

Trait ¹	Transformed data		Not transformed data		EBV correlations
	$h^2 \pm SE$	σ^2_P	$h^2 \pm SE$	σ^2_P	
LW6	0.32 ± 0.03	20.265	0.31 ± 0.03	20.173	0.995
PRESLT	0.22 ± 0.02	21.533	0.23 ± 0.03	20.881	0.995
HCW	0.19 ± 0.02	5.960	0.19 ± 0.02	5.847	0.996
XWT	0.17 ± 0.02	5.376	0.17 ± 0.02	5.543	0.996
XFORE	0.16 ± 0.02	0.722	0.15 ± 0.02	0.702	0.994
XLEG	0.15 ± 0.02	0.604	0.15 ± 0.02	0.612	0.996
XMID	0.22 ± 0.03	0.597	0.22 ± 0.03	0.672	0.994
LEGWT	0.11 ± 0.04	0.091	0.11 ± 0.04	0.091	0.994
FDMad	0.33 ± 0.03	0.957	0.28 ± 0.03	0.707	0.972
FDM	0.28 ± 0.03	1.299	0.24 ± 0.03	0.943	0.979
CGRMad	0.20 ± 0.02	5.723	0.23 ± 0.02	4.223	0.908
CGRM	0.21 ± 0.02	7.653	0.23 ± 0.02	6.064	0.958
LPHad	0.09 ± 0.02	0.024	0.09 ± 0.02	0.023	0.999
LPH	0.10 ± 0.02	0.024	0.10 ± 0.02	0.023	0.999

¹: LW6: live weight at six months; PRESLT: pre-slaughter weight; HCW: hot carcass weight; XWT: X-ray carcass weight; XFORE: X-ray fore weight; XLEG: X-ray leg weight; XMID: X-ray middle weight; LEGWT: carcass leg weight; LPH: loin pH; FDM: ultrasonic fat depth measurement; CGRM: depth of tissue 110 mm off the mid-line in the region of the 12th rib; traits followed by “ad” indicate that they were adjusted for correlated variables.

Table 4. Estimates of heritabilities (\pm SE) and phenotypic variance (corrected for fixed effects) for each trait.

Trait ¹	Heritability	σ^2_p	Trait	Heritability	σ^2_p
LW6	0.32 \pm 0.03	20.2650	SHF	0.24 \pm 0.03	3.9902
PRESLT	0.22 \pm 0.02	21.5330	A24ad	0.18 \pm 0.02	2.0642
HCW	0.19 \pm 0.02	5.9600	A24	0.19 \pm 0.03	2.4166
DO%	0.25 \pm 0.03	5.3470	A48ad	0.14 \pm 0.02	1.8919
XWT	0.17 \pm 0.02	5.3760	A48	0.15 \pm 0.02	1.9716
XFORE	0.15 \pm 0.02	0.7220	A96ad	0.16 \pm 0.02	1.9181
XLEG	0.15 \pm 0.02	0.6040	A96	0.17 \pm 0.02	1.9662
XMID	0.22 \pm 0.03	0.5970	A168ad	0.01 \pm 0.01	2.8508
LEGLGTH	0.27 \pm 0.05	1.7760	A168	0.02 \pm 0.01	2.8751
LEGWT	0.11 \pm 0.04	0.0907	ADEC	0.04 \pm 0.01	0.0002
LNBNWT	0.23 \pm 0.05	0.0024	ADECad	0.03 \pm 0.01	0.0002
EMDad	0.44 \pm 0.04	2.8811	B24ad	0.08 \pm 0.02	1.4770
EMD	0.37 \pm 0.04	4.7217	B24	0.13 \pm 0.02	2.2969
EMWad	0.32 \pm 0.03	12.3940	B48ad	0.06 \pm 0.02	1.3287
EMW	0.27 \pm 0.03	22.3400	B48	0.11 \pm 0.02	2.1675
FDMad	0.33 \pm 0.03	0.9571	B96ad	0.04 \pm 0.02	1.9161
FDM	0.28 \pm 0.03	1.2990	B96	0.06 \pm 0.02	3.1098
CBUTTad	0.27 \pm 0.03	1.6519	B168ad	0.02 \pm 0.01	3.0595
CBUTT	0.25 \pm 0.03	6.4687	B168	0.06 \pm 0.02	5.2290
CGRMad	0.20 \pm 0.02	5.7231	L24ad	0.22 \pm 0.03	4.0513
CGRM	0.21 \pm 0.02	7.6534	L24	0.17 \pm 0.02	6.6615
XNRIB	0.10 \pm 0.02	0.1066	L48ad	0.19 \pm 0.03	3.9412
LPHad	0.09 \pm 0.02	0.0240	L48	0.18 \pm 0.02	6.5195
LPH	0.10 \pm 0.02	0.0240	L96ad	0.21 \pm 0.03	3.9964
MARBad	0.31 \pm 0.03	0.2603	L96	0.20 \pm 0.03	6.8595
MARB	0.30 \pm 0.03	0.2821	L168ad	0.19 \pm 0.03	4.3684
SHFad	0.29 \pm 0.03	3.4827	L168	0.17 \pm 0.02	7.3123

¹:traits followed by “ad” indicates that they were adjusted for correlated variables; LW6: live weight at six months; PRESLT: pre-slaughter weight; HCW: hot carcass weight; DO%: dressing out percentage; EMD: ultrasonic eye muscle depth; EMW: ultrasonic eye muscle width; FDM: ultrasonic fat depth measurement; CBUTT: butt circumference; LEGWT: carcass leg weight; LEGLGTH: carcass leg length; LNBNWT: carcass boneless loin weight; CGRM: depth of tissue 110 mm off the mid-line in the region of the 12th rib; XWT: X-ray carcass weight; XLEG: X-ray leg weight; XMID: X-ray middle weight; XFORE: X-ray fore weight; XNRIB: X-ray number of rib pairs; LPH: loin pH; MARB: marbling score; SHF: shear force; ADEC: rate of decline of meat redness; *An*, *Bn* and *Ln*, with *n* being 24, 48, 96 and 168 indicates meat redness, meat yellowness and meat lightness at 24, 48, 96 and 168 hours.

Table 5. Estimates of genetic (below diagonal) and phenotypic (above diagonal) correlations, heritabilities (diagonal), and their standard error of estimates among growth and carcass traits.

Trait ¹	LW6	HCW	DO%	XFORE	XLEG	XMID	XNRIB
LW6	0.32 ± 0.03	0.85 ± 0.00	0.38 ± 0.01	0.78 ± 0.00	0.72 ± 0.01	0.73 ± 0.01	0.02 ± 0.01
HCW	0.92 ± 0.02	0.19 ± 0.02	0.61 ± 0.01	0.93 ± 0.00	0.93 ± 0.00	0.92 ± 0.00	0.03 ± 0.01
DO%	0.09 ± 0.09	0.57 ± 0.05	0.25 ± 0.03	0.56 ± 0.01	0.56 ± 0.01	0.57 ± 0.01	-0.01 ± 0.01
XFORE	0.92 ± 0.02	0.97 ± 0.01	0.55 ± 0.06	0.15 ± 0.02	0.90 ± 0.00	0.87 ± 0.00	-0.02 ± 0.01
XLEG	0.89 ± 0.03	0.97 ± 0.00	0.57 ± 0.06	0.85 ± 0.02	0.15 ± 0.02	0.85 ± 0.00	-0.02 ± 0.01
XMID	0.84 ± 0.03	0.96 ± 0.01	0.53 ± 0.06	0.81 ± 0.03	0.74 ± 0.04	0.22 ± 0.03	0.09 ± 0.01
XNRIB	0.20 ± 0.12	0.11 ± 0.10	-0.01 ± 0.09	0.01 ± 0.11	0.07 ± 0.24	0.21 ± 0.10	0.10 ± 0.02
EMD	0.49 ± 0.06	0.67 ± 0.05	0.49 ± 0.08	0.60 ± 0.07	0.58 ± 0.07	0.73 ± 0.05	0.16 ± 0.13
EMW	0.58 ± 0.05	0.71 ± 0.06	0.41 ± 0.09	0.64 ± 0.01	0.64 ± 0.07	0.76 ± 0.05	0.29 ± 0.14
FDM	0.40 ± 0.07	0.43 ± 0.09	0.26 ± 0.10	0.39 ± 0.09	0.21 ± 0.11	0.55 ± 0.07	0.18 ± 0.13
CBUTT	0.76 ± 0.04	0.81 ± 0.03	0.71 ± 0.06	0.77 ± 0.03	0.56 ± 0.06	0.66 ± 0.04	0.01 ± 0.10
CGRM	0.30 ± 0.09	0.47 ± 0.07	0.39 ± 0.07	0.40 ± 0.08	0.29 ± 0.08	0.63 ± 0.05	0.15 ± 0.10

¹: LW6: live weight at six months; HCW: hot carcass weight; DO%: dressing out percentage; EMD: ultrasonic eye muscle depth; EMW: ultrasonic eye muscle width; FDM: ultrasonic fat depth measurement; CBUTT: butt circumference; CGRM: depth of tissue 110 mm off the mid-line in the region of the 12th rib; XLEG: X-ray leg weight; XMID: X-ray middle weight; XFORE: X-ray fore weight; XNRIB: X-ray number of rib pairs.

897

898

899

900

901

902

Table 5. (cont.)

Trait¹	EMD	EMW	FDM	CBUTT	CGRM
LW6	0.62 ± 0.01	0.67 ± 0.01	0.51 ± 0.01	0.76 ± 0.01	0.39 ± 0.01
HCW	0.65 ± 0.01	0.68 ± 0.01	0.52 ± 0.01	0.86 ± 0.00	0.54 ± 0.01
DO%	0.48 ± 0.01	0.47 ± 0.01	0.38 ± 0.01	0.52 ± 0.01	0.40 ± 0.01
XFORE	0.60 ± 0.01	0.64 ± 0.01	0.49 ± 0.01	0.81 ± 0.00	0.49 ± 0.01
XLEG	0.57 ± 0.01	0.61 ± 0.01	0.43 ± 0.01	0.80 ± 0.00	0.46 ± 0.01
XMID	0.64 ± 0.01	0.65 ± 0.01	0.54 ± 0.01	0.77 ± 0.00	0.56 ± 0.01
XNRIB	-0.00 ± 0.01	-0.01 ± 0.01	-0.02 ± 0.01	0.01 ± 0.01	0.02 ± 0.01
EMD	0.37 ± 0.04	0.76 ± 0.00	0.48 ± 0.01	0.57 ± 0.01	0.39 ± 0.01
EMW	0.87 ± 0.02	0.28 ± 0.03	0.50 ± 0.01	0.60 ± 0.01	0.35 ± 0.01
FDM	0.34 ± 0.07	0.36 ± 0.07	0.28 ± 0.03	0.40 ± 0.01	0.51 ± 0.01
CBUTT	0.55 ± 0.08	0.60 ± 0.08	0.09 ± 0.12	0.25 ± 0.02	0.40 ± 0.01
CGRM	0.51 ± 0.10	0.41 ± 0.11	0.94 ± 0.05	0.22 ± 0.07	0.21 ± 0.02

¹: LW6: live weight at six months; HCW: hot carcass weight; DO%: dressing out percentage; EMD: ultrasonic eye muscle depth; EMW: ultrasonic eye muscle width; FDM: ultrasonic fat depth measurement; CBUTT: butt circumference; CGRM: depth of tissue 110 mm off the mid-line in the region of the 12th rib; XLEG: X-ray leg weight; XMID: X-ray middle weight; XFORE: X-ray fore weight; XNRIB: X-ray number of rib pairs.

903

904

905

906

907

908

909

Table 6. Estimates of genetic (below diagonal) and phenotypic (above diagonal) correlations, heritabilities (diagonal), and their standard error of estimates among meat quality traits.

Trait ¹	LPH	MARB	SHF	A24	A48	A96	A168	B24
LPH	0.10 ± 0.02	0.12 ± 0.01	0.09 ± 0.01	-0.29 ± 0.01	-0.15 ± 0.01	0.06 ± 0.01	0.02 ± 0.01	-0.55 ± 0.01
MARB	0.28 ± 0.11	0.30 ± 0.03	-0.17 ± 0.01	0.05 ± 0.01	0.04 ± 0.01	0.05 ± 0.01	0.05 ± 0.01	-0.10 ± 0.01
SHF	0.34 ± 0.11	-0.17 ± 0.08	0.24 ± 0.03	-0.07 ± 0.01	0.00 ± 0.01	0.03 ± 0.01	0.04 ± 0.01	-0.01 ± 0.01
A24	-0.34 ± 0.11	0.16 ± 0.09	-0.41 ± 0.09	0.19 ± 0.03	0.66 ± 0.01	0.42 ± 0.01	0.24 ± 0.01	0.57 ± 0.01
A48	0.02 ± 0.13	0.28 ± 0.09	-0.23 ± 0.10	0.94 ± 0.03	0.15 ± 0.02	0.58 ± 0.01	0.28 ± 0.01	0.28 ± 0.01
A96	0.22 ± 0.12	0.31 ± 0.09	-0.13 ± 0.10	0.68 ± 0.07	0.91 ± 0.04	0.17 ± 0.03	0.32 ± 0.01	0.09 ± 0.01
A168	-0.13 ± 0.27	0.54 ± 0.26	-0.41 ± 0.21	0.67 ± 0.10	0.99 ± 0.09	0.91 ± 0.15	0.02 ± 0.01	0.02 ± 0.01
B24	-0.79 ± 0.07	0.10 ± 0.10	-0.47 ± 0.09	0.51 ± 0.08	0.26 ± 0.11	0.09 ± 0.12	0.57 ± 0.23	0.13 ± 0.02
B48	-0.81 ± 0.07	0.10 ± 0.11	-0.44 ± 0.10	0.47 ± 0.10	0.14 ± 0.12	0.03 ± 0.12	0.75 ± 0.22	0.99 ± 0.02
B96	-0.83 ± 0.08	0.12 ± 0.13	-0.46 ± 0.13	0.28 ± 0.13	-0.08 ± 0.15	-0.06 ± 0.15	0.89 ± 0.24	0.97 ± 0.05
B168	-0.91 ± 0.06	0.10 ± 0.13	-0.47 ± 0.13	0.18 ± 0.14	-0.24 ± 0.15	-0.28 ± 0.15	0.58 ± 0.28	0.99 ± 0.06
L24	-0.54 ± 0.09	0.18 ± 0.09	-0.26 ± 0.10	-0.13 ± 0.11	-0.26 ± 0.11	-0.21 ± 0.10	0.27 ± 0.24	0.78 ± 0.06
L48	-0.56 ± 0.08	0.20 ± 0.09	-0.35 ± 0.09	-0.21 ± 0.10	-0.30 ± 0.11	-0.29 ± 0.10	0.14 ± 0.23	0.78 ± 0.06
L96	-0.61 ± 0.08	0.21 ± 0.09	-0.17 ± 0.09	-0.17 ± 0.10	-0.30 ± 0.11	-0.22 ± 0.10	0.29 ± 0.23	0.75 ± 0.06
L168	-0.55 ± 0.09	0.18 ± 0.10	-0.24 ± 0.10	-0.19 ± 0.11	-0.33 ± 0.11	-0.32 ± 0.10	0.40 ± 0.24	0.75 ± 0.06

¹: LPH: loin pH; MARB: marbling score; SHF: shear force; An, Bn and Ln: meat redness, meat yellowness and meat lightness at 24, 48, 96 and 168 hours.

Table 6. (cont.)

Trait ¹	B48	B96	B168	L24	L48	L96	L168
LPH	-0.57 ± 0.01	-0.59 ± 0.01	-0.63 ± 0.01	-0.58 ± 0.01	-0.59 ± 0.01	-0.59 ± 0.01	-0.58 ± 0.01
MARB	-0.11 ± 0.01	-0.11 ± 0.01	-0.10 ± 0.01	-0.11 ± 0.01	-0.12 ± 0.01	-0.13 ± 0.01	-0.12 ± 0.01
SHF	0.02 ± 0.01	0.00 ± 0.01	-0.04 ± 0.01	0.01 ± 0.01	0.00 ± 0.01	0.01 ± 0.01	0.00 ± 0.01
A24	0.41 ± 0.01	0.28 ± 0.01	0.26 ± 0.01	0.08 ± 0.01	0.16 ± 0.01	0.16 ± 0.01	0.14 ± 0.01
A48	0.45 ± 0.01	0.25 ± 0.01	0.19 ± 0.01	0.10 ± 0.01	0.03 ± 0.01	0.08 ± 0.01	0.07 ± 0.01
A96	0.12 ± 0.01	0.18 ± 0.01	0.04 ± 0.01	-0.04 ± 0.01	-0.07 ± 0.01	-0.12 ± 0.01	-0.08 ± 0.01
A168	0.00 ± 0.01	-0.10 ± 0.01	-0.10 ± 0.01	-0.03 ± 0.01	-0.04 ± 0.01	-0.06 ± 0.01	-0.20 ± 0.01
B24	0.81 ± 0.00	0.72 ± 0.01	0.65 ± 0.01	0.61 ± 0.01	0.63 ± 0.01	0.63 ± 0.01	0.60 ± 0.01
B48	0.11 ± 0.02	0.78 ± 0.00	0.68 ± 0.01	0.66 ± 0.01	0.63 ± 0.01	0.63 ± 0.01	0.62 ± 0.01
B96	0.97 ± 0.03	0.07 ± 0.02	0.77 ± 0.00	0.65 ± 0.01	0.66 ± 0.01	0.69 ± 0.01	0.65 ± 0.01
B168	0.96 ± 0.05	0.96 ± 0.05	0.06 ± 0.02	0.39 ± 0.01	0.65 ± 0.01	0.43 ± 0.01	0.74 ± 0.00
L24	0.86 ± 0.05	0.94 ± 0.05	0.85 ± 0.04	0.17 ± 0.03	0.63 ± 0.01	0.80 ± 0.00	0.80 ± 0.00
L48	0.84 ± 0.05	0.93 ± 0.05	0.88 ± 0.06	0.99 ± 0.02	0.18 ± 0.03	0.83 ± 0.00	0.67 ± 0.00
L96	0.75 ± 0.06	0.94 ± 0.04	0.93 ± 0.16	0.99 ± 0.01	1.00 ± 0.01	0.20 ± 0.03	0.69 ± 0.01
L168	0.81 ± 0.06	0.87 ± 0.06	0.83 ± 0.06	0.94 ± 0.03	0.98 ± 0.03	0.99 ± 0.02	0.17 ± 0.03

¹: LPH: loin pH; MARB: marbling score; SHF: shear force; *An*, *Bn* and *Ln*: meat redness, meat yellowness and meat lightness at 24, 48, 96 and 168 hours.

Table 7. Estimates of genetic correlations and their standard error of estimates between growth and carcass traits and meat quality traits.

Trait¹	LW6	HCW	DO%	XFORE	XLEG	XMID	XNRIB
LPH	0.18 ± 0.14	0.06 ± 0.13	-0.01 ± 0.12	0.02 ± 0.13	0.10 ± 0.13	0.09 ± 0.12	0.21 ± 0.14
MARB	0.33 ± 0.09	0.28 ± 0.08	0.09 ± 0.08	0.23 ± 0.09	0.15 ± 0.09	0.38 ± 0.08	0.09 ± 0.10
SHF	0.00 ± 0.10	-0.17 ± 0.09	-0.08 ± 0.09	-0.21 ± 0.09	-0.13 ± 0.10	-0.15 ± 0.09	0.05 ± 0.11
A24	0.18 ± 0.11	0.28 ± 0.09	0.17 ± 0.09	0.23 ± 0.10	0.15 ± 0.10	0.25 ± 0.09	-0.09 ± 0.12
A48	0.10 ± 0.13	0.25 ± 0.10	0.24 ± 0.10	0.13 ± 0.11	0.16 ± 0.11	0.22 ± 0.10	-0.18 ± 0.12
A96	0.20 ± 0.12	0.33 ± 0.09	0.28 ± 0.09	0.19 ± 0.10	0.24 ± 0.10	0.29 ± 0.09	-0.04 ± 0.12
A168	0.17 ± 0.13	0.48 ± 0.43	0.06 ± 0.28	0.39 ± 0.37	0.46 ± 0.41	0.35 ± 0.35	0.14 ± 0.25
B24	-0.10 ± 0.12	0.12 ± 0.13	0.01 ± 0.11	-0.02 ± 0.12	-0.09 ± 0.12	-0.09 ± 0.11	-0.16 ± 0.13
B48	-0.10 ± 0.13	-0.02 ± 0.12	0.04 ± 0.11	-0.03 ± 0.13	-0.04 ± 0.13	-0.14 ± 0.12	-0.26 ± 0.13
B96	-0.19 ± 0.17	0.01 ± 0.14	0.09 ± 0.13	-0.02 ± 0.15	-0.05 ± 0.15	-0.14 ± 0.14	-0.26 ± 0.16
B168	-0.14 ± 0.18	-0.04 ± 0.15	0.03 ± 0.14	0.02 ± 0.15	-0.07 ± 0.16	-0.12 ± 0.14	-0.18 ± 0.16
L24	-0.18 ± 0.11	-0.15 ± 0.11	-0.09 ± 0.09	-0.17 ± 0.10	-0.20 ± 0.10	-0.25 ± 0.09	-0.14 ± 0.12
L48	-0.19 ± 0.11	-0.12 ± 0.10	-0.05 ± 0.10	-0.13 ± 0.11	-0.14 ± 0.11	-0.17 ± 0.10	-0.06 ± 0.12
L96	-0.15 ± 0.11	-0.13 ± 0.10	-0.07 ± 0.09	-0.12 ± 0.10	-0.16 ± 0.10	-0.17 ± 0.09	0.00 ± 0.11
L168	-0.19 ± 0.11	-0.17 ± 0.11	-0.11 ± 0.10	-0.19 ± 0.11	-0.22 ± 0.11	-0.26 ± 0.10	-0.04 ± 0.12

¹: LW6: live weight at six months; HCW: hot carcass weight; DO%: dressing out percentage; XLEG: X-ray leg weight; XMID: X-ray middle weight; XFORE: X-ray fore weight; XNRIB: X-ray number of rib pairs; LPH: loin pH; MARB: marbling score; SHF: shear force; *A_n*, *B_n* and *L_n*: meat redness, meat yellowness and meat lightness at 24, 48, 96 and 168 hours.

927

Table 7. (cont.)

Trait¹	EMD	EMW	FDM	CBUTT	CGRM
LPH	-0.08 ± 0.15	0.16 ± 0.17	0.03 ± 0.15	0.17 ± 0.11	-0.13 ± 0.11
MARB	0.23 ± 0.10	0.20 ± 0.11	0.43 ± 0.09	0.19 ± 0.08	0.44 ± 0.07
SHF	-0.06 ± 0.11	0.03 ± 0.12	-0.10 ± 0.11	-0.09 ± 0.08	-0.21 ± 0.08
A24	0.15 ± 0.12	0.24 ± 0.13	0.46 ± 0.10	0.15 ± 0.09	0.41 ± 0.08
A48	0.22 ± 0.13	0.26 ± 0.14	0.41 ± 0.12	0.26 ± 0.09	0.40 ± 0.09
A96	0.04 ± 0.13	0.10 ± 0.14	0.19 ± 0.13	0.34 ± 0.08	0.32 ± 0.09
A168	0.02 ± 0.13	0.21 ± 0.14	0.11 ± 0.25	0.23 ± 0.22	0.46 ± 0.28
B24	-0.24 ± 0.12	-0.20 ± 0.14	0.14 ± 0.13	-0.14 ± 0.10	0.05 ± 0.10
B48	-0.17 ± 0.14	-0.24 ± 0.16	0.05 ± 0.14	-0.09 ± 0.11	0.04 ± 0.11
B96	-0.21 ± 0.20	-0.39 ± 0.21	-0.02 ± 0.20	-0.10 ± 0.13	-0.04 ± 0.13
B168	-0.12 ± 0.19	-0.31 ± 0.21	0.01 ± 0.19	-0.16 ± 0.13	-0.09 ± 0.13
L24	-0.22 ± 0.12	-0.43 ± 0.12	-0.06 ± 0.12	-0.25 ± 0.09	-0.14 ± 0.09
L48	-0.13 ± 0.12	-0.36 ± 0.12	-0.04 ± 0.12	-0.21 ± 0.09	-0.11 ± 0.09
L96	-0.24 ± 0.11	-0.43 ± 0.11	-0.10 ± 0.12	-0.24 ± 0.09	-0.08 ± 0.09
L168	-0.29 ± 0.12	-0.48 ± 0.12	-0.11 ± 0.13	-0.32 ± 0.09	-0.19 ± 0.10

¹: EMD: ultrasonic eye muscle depth; EMW: ultrasonic eye muscle width; FDM: ultrasonic fat depth measurement; CBUTT: butt circumference; CGRM: depth of tissue 110 mm off the mid-line in the region of the 12th rib; LPH: loin pH; MARB: marbling score; SHF: shear force; *An*, *Bn* and *Ln*: meat redness, meat yellowness and meat lightness at 24, 48, 96 and 168 hours.

928

929

930

931 **Figures**

932 **Figure 1.** EBV estimates for CGRM generated when using the raw versus transformed
933 phenotypes.

934 Format file: Word (.docx).

935 **Figure 2.** Phenotypic relationship between tenderness score (shear force in kgf) and loin pH.

936 Format file: Word (.docx).

937

938 **Additional files**

939 **Additional file 1** – (Table S1): Heritability estimates and phenotypic variance when breed
940 percentage was fitted or omitted as a covariable.

941 Format file: Excel (.xls).

942 **Additional file 2** – (Table S2): Estimates of genetic (below diagonal) and phenotypic (above
943 diagonal) correlations, heritabilities (diagonal), and their standard error of estimates.

944 Excel file (.xls) showing estimates for traits not adjusted for correlated variables.

945 **Additional file 3** – (Table S3): Estimates of genetic (below diagonal) and phenotypic (above
946 diagonal) correlations, heritabilities (diagonal) and their standard error of estimates.

947 Excel file (.xls) showing estimates for traits adjusted for correlated variables.