Australian Government
Department of Agriculture, Fisheries and Forestry

Technical Report

Program and KPI: Sub-program 4.2 KPI 3.30

Report Title: Report on the preliminary analysis of model refinement for the genetic evaluation of shear force in lamb

Prepared by: R. Alexandri[1], S. Walkom[1], P. McGilchrist[2], G. Gardner[3], A. Williams[3] and D. Brown[1]
[1]Animal Genetics & Breeding Unit, UNE
[2]University of New England, Armidale NSW
[3]Murdoch University, WA

Date published: 27 January 2023

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Citation

R. Alexandri, S. Walkom, P. McGilchrist, A. Williams and D. Brown (2023). Report on the preliminary analysis of model refinement for the genetic evaluation of shear force in lamb. An *Advanced measurement technologies for globally competitive Australian meat* Project.

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

1 Contents

Citation 2
2 Introduction 4
3 Materials and methods 4
3.1 Animals and measurements 4
3.2 Capturing cold shortening effects 5
3.3 Filtering out extreme values 6
3.4 Data transformation 6
3.5 Genetic analysis 9
3.6 Model validation 10
4 Results and Discussion 10
4.1 Cold shortening definition 10
4.2 Data filtering and effect on genetic parameters 12
4.3 Genetic parameters for transformed and non-transformed data 13
4.4 Model validation 14
4.5 Correlations with other carcase traits 19
5 Conclusions 22
6 References 22

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

2 Introduction

Improving eating quality of Australian lamb meat will enhance the industry's capacity to meet increasing consumer expectations for lamb products. Meat tenderness is one of the major factors contributing to overall eating quality of lamb meat (Thompson *et al.* 2005). To improve lamb meat tenderness by selection, the trait needs to be accurately defined and consistently measured and have genetic variation. Meat tenderness can be objectively measured using mechanical shear force, which is a measure of myofibrillar toughness (Purchas 2014). Meat tenderness can be influenced by environmental parameters post-slaughtering such as the interaction between pH and temperature decline which can influence the occurrence of cold shortening in the muscles and increase the toughness of meat (Warner 2016). The aim of this study was to review the models used for shear force analysis by Sheep Genetics and determine suitable methods to edit the raw data in order to improve the genetic parameter and breeding value estimation.

3 Materials and methods

3.1 Animals and measurements

Measures of shear force were collected between 2007 and 2020 from 32,913 Merino and Merino crossed animals originating from 46 commercial flocks, the 8 Information Nucleus and MLA Resource Flocks (Van der Werf *et al.* 2010). The animals were the progeny of 2,260 sires. The sire types include Merino sires (Merino, Poll Merino, Dohne Merino), Maternal sires (Border Leicester, Booroola Leicester, Coopworth, Bond, Corriedale, East Friesian, Prime South African Meat Merino) and Terminal sires (Dorper and White Dorper, Hampshire Down, Ile De France, Poll Dorset, Southdown, Suffolk, Texel, White Suffolk). Average number of progeny per sire was 14. The average age at slaughter in days (standard deviation) was 279 (95.4), across 1,772 contemporary groups.

All animals were slaughtered at commercial abattoirs. Carcases were subjected to electrical stimulation and trimmed according to AUS-MEAT specifications (Anonymous 1992). Hot carcase weight (HCWT) was recorded at slaughter. Carcases were chilled overnight (3-4 ºC) and then were cut between the 12th and 13th rib to expose the surface of the *M. longissimus thoracis et lumborum* (LL). Depth of the LL muscle (EMD) and the depth of fat at the c – site (CFAT, depth of fat over the maximum depth of the LL) were measured with callipers. The pH of the LL was measured at different carcase target temperatures (35 ºC, 20 ºC and 12 ºC). The ultimate pH (ph24ll) was determined 19 – 24 hours after slaughter as described by Pearce *et al.* (2010). Carcase temperature when carcase reached pH 6 was also calculated using the method described by Pearce *et al.* (2010). The percentage of lean meat (LMY) in each carcase was predicted through a partial bone-out procedure as described in Gardner *et al.* (2010).

The lumbar portion of the LL was excised from the carcase at 24h post slaughter. A section of the LL (65 g) was aged for 5 days at 3–4 °C, and stored frozen. For shear force testing (SF5), these samples then were cooked from frozen for 35 min in plastic bags at 71 °C in a water bath and tested using a Lloyd texture analyser (Model LRX, Lloyd Instruments, Hampshire, UK) with a Warner– Bratzler type shear blade fitted as described by Hopkins *et al.* (2010). Percentage of intramuscular fat (IMF) was determined using a near infrared procedure (NIR) as described by Perry *et al.* (2001).

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Summaries of shear force and other carcase traits used in the analysis are shown in *Table 1*.

Table 1. Summary statistics for all data used in the analyses: CV: coefficient of variation, SF5: shear force 5 days after slaughter, pH6temp: temperature when pH = 6, pH24ll: pH 24h after slaughter, HCWT: hot carcase weight, CFAT: carcase c-side fat, EMD: carcase eye muscle depth, EMW: carcase eye muscle width, IMF: intramuscular fat, LMY: lean meat yield.

Trait	Breed	Records	Sires	Contemporary groups	Mean (sd)	CV (%)
SF5 (N)	all	29697	2260	1772	32.00 (11.88)	37.12
	merino	7680	609	446	31.87 (12.30)	38.60
	maternal	3507	332	451	31.25 (10.70)	34.24
	terminal	16401	1162	1121	32.26 (12.02)	37.27
ph6temp (ºC)	all	18379	2023	1538	19.68 (8.09)	41.12
	merino	4187	560	338	18.88 (8.39)	44.44
	maternal	2392	289	405	19.45 (8.07)	41.49
	terminal	10619	1026	1003	20.06 (7.93)	39.55
ph24ll	all	27838	2238	1708	5.65 (0.16)	2.78
	merino	6164	601	390	5.68 (0.17)	2.99
	maternal	3441	319	449	5.64 (0.16)	2.84
	terminal	16507	1162	1121	5.63 (0.15)	2.63
HCWT (Kg)	all	33651	2271	1315	23.27 (4.02)	17.30
	merino	7680	609	446	21.29 (3.99)	18.73
	maternal	3507	332	451	23.74 (3.62)	15.26
	terminal	16401	1162	1121	24.48 (3.87)	15.79
CFAT (mm)	all	20814	1824	1042	4.52 (2.50)	55.24
	merino	4104	509	250	3.62 (2.10)	58.18
	maternal	2814	251	331	5.24 (2.67)	50.88
	terminal	12514	917	664	4.71 (2.53)	53.65
EMD (mm)	all	31703	2257	1281	30.77 (4.97)	16.14
	merino	4105	509	251	27.93 (4.05)	14.49
	maternal	2812	251	332	30.19 (4.27)	14.13
	terminal	12615	917	669	32.37 (4.51)	13.92
IMF (%)	all	20922	1811	1057	4.65 (1.20)	25.79
	merino	4103	509	258	5.08 (1.38)	27.09
	maternal	2809	251	338	4.81 (1.13)	23.53
	terminal	12364	917	669	4.42 (1.07)	24.20
LMY (%)	all	9363	498	639	58.11 (3.06)	5.27
	merino	4090	509	100	58.52 (2.76)	4.72
	maternal	2808	251	133	56.92 (2.97)	5.22
	terminal	12450	917	435	58.19 (3.13)	5.37

3.2 Capturing cold shortening effects

Cold shortening occurs when a muscle contracts before entering the rigor mortis (conversion from muscle to meat) stage. It increases cellular calcium and depends on the cooling rate of the muscle and the energy deposits of the muscle cells. It is more common if the temperature

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

falls below 14 ºC (Ertbjerg & Puolanne 2017) when the muscle is still in pre-rigor and its pH is higher than 6 (Thompson *et al.* 2006).

Out of 32,913 carcases with shear force records in the data set, 19,640 had records for temperature at pH 6 (ph6temp) and were used to determine possible temperature thresholds to identify cold shortened carcases. These thresholds were estimated in two steps in order to adjust shear force records for fixed effects. In the first step solutions for the temperature effect were obtained under two different models:

$$SF5 = cg + HCWT + ph6temp + bt + rt + age + damage + e \quad [1]$$

$$SF5 = cg + HCWT + ph6temp + bt + rt + age + damage + CFAT + e \quad [2]$$

For both models, $SF5$ is the shear force observation, cg is the contemporary group (defined by breed, flock, management group, sex, date of measurement and kill group; 686 levels), $HCWT$ is the hot carcase weight, $ph6temp$ is the temperature variable, bt is the birth type (6 levels), rt the rear type (5 levels), age is the age of the animal, $damage$ is the age of the dam and e is the random error. Fixed effects were used for the analysis of carcase traits in previous studies (Mortimer *et al.* 2010; Mortimer *et al.* 2014). For model [2], CFAT is the fat depth in the c-side previously found to have a negative correlation with shear force (Mortimer *et al.* 2010; Brito *et al.* 2017).

In the second step, solutions obtained from each run of models [1] and [2] were used to estimate the temperature threshold using the approach proposed by Muggeo (2003) and implemented in the Segmented R package (Muggeo 2008). One initial threshold was provided as a way to examine the effect of lower temperature on eye muscle tenderness.

3.3 Filtering out extreme values

An initial series of analyses was performed to identify outliers that have extreme shear force values either due to recording errors or potentially due to the impact of cold shortening. Analyses investigated several different procedures for removing data for the entire data set and for animals within contemporary groups. Data was filtered using a three-step approach to exclude extreme individuals:

1. Records with shear force values higher than 4 standard deviations from the mean (*mean(SF5) ± 4*sd(SF5))*.

2. Records with shear force values outside the interval formed by the contemporary group median shear force plus 4 median absolute deviations (*CGmean (SF5) ± 4*sd(CGSF5))*.

3. Records with shear force values outside threshold using methods combined.

The effect of the data filtering procedure was determined by examining the number of records removed and its effects on the trait mean and standard deviation (Table 2) and on variance component estimates.

3.4 Data transformation

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Even after removal of outlier individuals, shear force data was not normally distributed (Figure 1). In addition to the analysis of SF5 records on the observed scale ($SF5^0$), to produce a distribution that is close to normality, two methods were applied to transform the data:

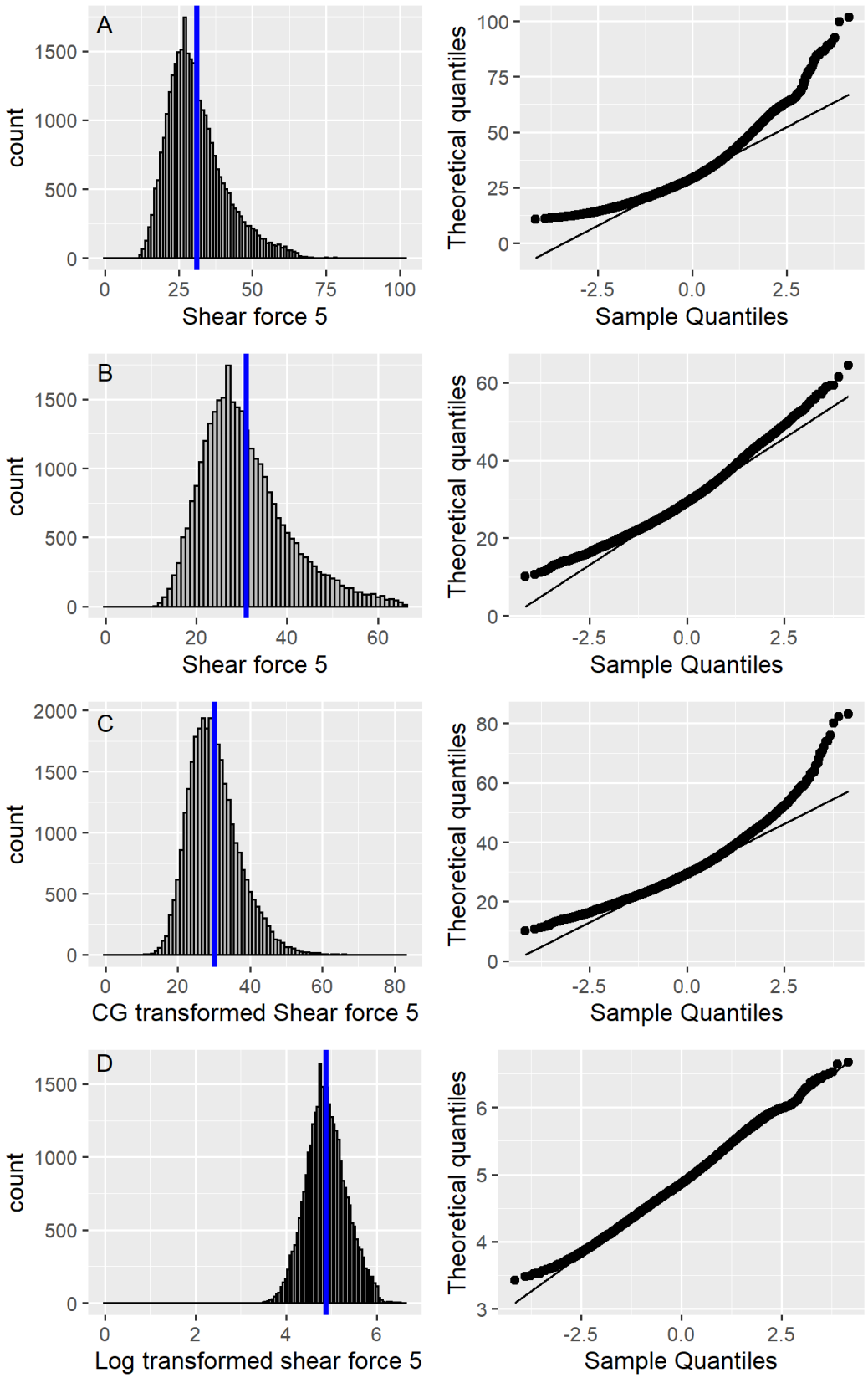
1. Shear force was expressed as a proportion of the contemporary group mean. The transformation applied was $SF5^{GM} = \frac{SF5^0}{\overline{SF5}_{CG}} \times \mu$ where $SF5^{GM}$ is the transformed observation, $SF5^0$ was the raw observation, $\overline{SF5}_{CG}$ the mean of the contemporary group and μ the universal mean.

2. Individual records were log (base 2) transformed after filtering ($SF5^{Log}$).

Log transformation has been previously used for the analysis of lamb shear force data (Hopkins *et al.* 2010), while trait values expressed as a contemporary group mean has been previously described by Huisman *et al.* (2015).

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Figure 1. Distributions and normality plots for raw data (A), filtered data (B), filtered data transformed as a proportion of contemporary group mean (C) and filtered log2 transformed data (D).



This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

3.5 Genetic analysis

Variance components and genetic parameters for shear force were estimated using a series of linear mixed models and REML methods with ASReml software (Gilmour *et al.* 2015). Different analyses were used to account for: i) influence of data filtering, ii) impact of transforming the data ($SF5^0$, $SF5^{Log}$ and SF^{GM}), and iii) impact of including different covariates to account for temperature and pH decline. All analyses started from a basic linear mixed model (Model 1, Table 3). For this basic model, fixed effects included birth type (6 levels), rear type (5 levels), contemporary group (686 levels), sex (male or female), animal age, dam age and the linear covariate of hot carcase weight (HCWT). Contemporary group was as defined by breed, flock, management group, sex, date of measurement and kill group. Different covariates fitted for each of the other models are shown in Table 3. All models included the random effects of animal (pedigree) and genetic group defined by flock of origin or sheep type (Swan *et al.* 2016). Maternal effects were not fitted since preliminary and previous analysis showed they were non-significant (Mortimer *et al.* 2010). For all models the animal effect represented the additive genetic variance. Phenotypic variance was calculated as the sum of the additive genetic and residual variance.

To determine whether the linear or quadratic effect of ph6temp and ph24ll would be used (Models 2 and 3 on Table 2) a separate analysis was carried out fitting the basic linear model (1) and including different effects (Table 3).

Bivariate analyses carried out in ASReml (Gilmour *et al.* 2015) provided estimates of phenotypic and genetic covariances and correlations between SF5 and other carcase traits based on the univariate analysis described above. For a more accurate estimation of genetic parameters bivariate analysis was carried out in two steps: a) using all animals after filtering; b) partitioning the data in different breeds (Table 1).

Table 2. *Mixed models and fixed effects used for the shear force analysis. hot carcase weight (HCWT) was used as a covariate for all models. pH6temp: temperature when pH = 6, ph24ll: eye muscle pH 24h after slaughter, CFAT: carcase c-side fat. pH6temp.cg: interaction between pH6temp and contemporary group, pH24ll: interaction between ph24ll and contemporary group.*

Model	Covariates	Fixed effects	Random Effects	Analysis
1	HCWT	Birth type, rear type, sex, contemporary group, age of dam	Animal, genetic groups	Univariate
2	HCWT, ph24ll			
3	HCWT, ph6temp			
4	HCWT, CFAT			
5	HCWT			Bivariate: SF5 - CFAT

Table 3. Co-variates used when ph24ll and ph6temp were included.

Model		Covariates	Fixed effects	Random Effects	Analysis
1		-	Birth type, rear type, sex, contemporary group, age of dam	Animal, genetic groups	Univariate
2	a	pH24ll.cg			
	b	pH24ll, pH24ll.cg			
	c	$pH24ll^2$			
3	a	pH6temp.cg			
	b	pH6temp, pH6temp.cg			
	c	$pH6temp^2$			

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

3.6 Model validation

Cross validation of the different models investigated in the analysis was performed using forward prediction as described by Huisman *et al.* (2015). For each genetic model data was randomly split into a training data set (containing 75% of records) to estimate genetic parameters and obtain Estimated Breeding Values (EBVs), and one validation data set (remaining 25% of records). These EBVs were used in regression analysis regressing offspring performance on sire EBV. The offspring data used in the regression were adjusted for the appropriate fixed effects of each model (Table 3). The regression carried out in ASReml (Gilmour *et al.* 2015) using the model:

$$y_{ijk} = cg_i + f + bEBV_j + e_{ijk}$$

Where y_{ijk} is the performance value of offspring k of sire j, cg_i is the contemporary group i for offspring k, b is the regression coefficient of y_{ijk} on EBV_j, EBV_j is the estimated breeding value of sire j, f is the vector of fixed effects and e_{ijk} is a random residual term. Since animals get half of their genes from their sire, the expectation of b is 0.5. A b-value below 0.5 indicates that for each unit in EBV the expected progeny difference is less than half of the EBV. A b-value above 0.5 indicates that for each unit in EBV the expected progeny difference is more than half of the EBV (Huisman *et al.* 2015). In total five random replicates of this procedure where carried out. The regression results for each model were averaged across the random groups and the model with the best predictive ability was selected.

4 Results and Discussion

4.1 Cold shortening definition

The first part of this study aimed to define possible temperature thresholds for which the effect of temperatures on *SF5* is more pronounced. For this purpose, the least square means for the temperature variable obtained from mixed models were used in a piecewise-linear regression procedure to characterize the temperature thresholds. For piecewise-linear regression method is that threshold estimation can sometimes be strongly dependent on the starting point (Muggeo 2003). For this study, a starting point at 16 °C for pH6temp was initially used. Independence of temperature thresholds was confirmed by repeating the analysis with different initial values. Temperature thresholds estimated with the two different models (including *CFAT* or not) ranged between 12 and 14 °C (Figure 2).

These thresholds agree with previously recommended temperature windows at pH 6. To avoid cold shortening, the industry recommendation is for carcases to be cooled down at a controlled rate, so that pH is below 6 when the loin is between 18 and 35 °C (Pearce *et al.* 2010; Gutzke *et al.* 2014). Previous studies showed that the lowest shear force occurred when carcases achieved pH=6 when temperature was between 21 and 25 °C (Thomson *et al.* 2005; Hopkins & Toohey 2006). Similarly, higher shear force values were observed when carcases were exposed to temperatures between 2 and 4 °C (Muela *et al.* 2010). Therefore, higher shear force values are expected when carcases achieve pH 6 in lower temperatures. In this report, summarised raw data shows that shear force increases when carcase temperature declines (Figure 3).

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

However when these thresholds were used to distinguish between possible cold shortened and non-cold shortened carcases, it was difficult to discriminate between the two. Similarly, temperature thresholds were not able to distinguish between potentially cold shortened and non-cold shortened carcases when temperature and SF5 values were averaged for each contemporary group and each sire (Figure 4). This is probably because of the fact that the relationship estimated between shear force and temperature looks a bit more linear with no obvious cliff (Figure 2). In addition, there is a lot of variation in shear force between different contemporary groups and different sires (Figure 4) which cannot be explained by variations in temperature (Pearson's correlation coefficient between raw shear force and temperature data was -0.17).

Figure 2.Temperature thresholds based on piecewise linear regression results.

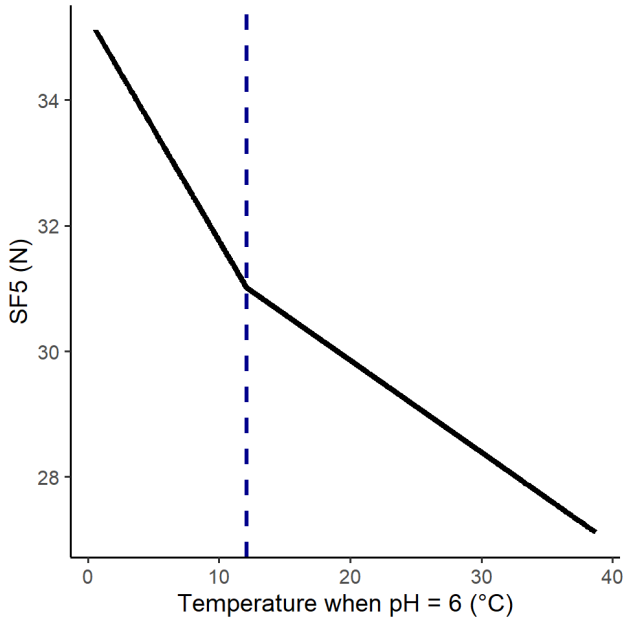
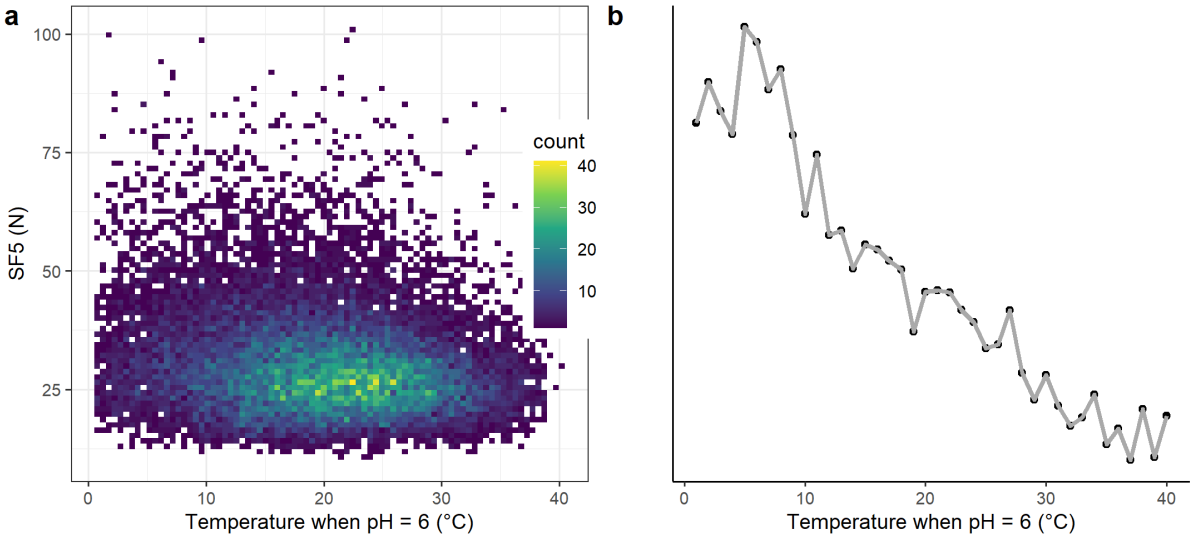
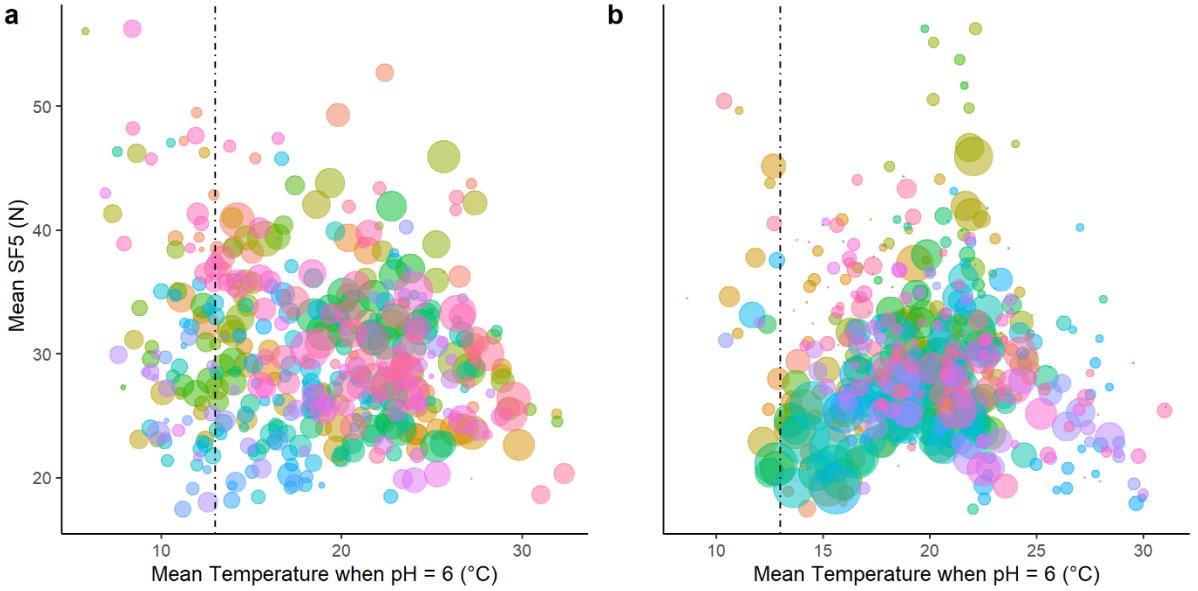


Figure 3. Effect of temperature at pH = 6 on shear force 5 (SF5). a: raw data, b: SF5 records were summarised for each temperature degree for better representation.



This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Figure 3. Average shear force for contemporary groups (a) and sires (b). Different colours represent different contemporary groups and sires respectively. Dot size represents number of records for every contemporary group (a) and number of progeny per sire (b) and dotted black line represents temperature thresholds based on piecewise regression.



Shear force variation in the eye muscle in lamb has been shown to be explained by sex and animal age, but most importantly by factors like sarcomere length (Starkey *et al.* 2016). Sarcomere length could be used to identify cold shortened carcases, but has not been recorded for the carcases used in this report. Identifying the effect of temperature decline on shear force can be complicated. Previous reports about it have been contradictive: some studies found that it had no effect on SF5 (Hopkins *et al.* 2015; Starkey *et al.* 2016), while others argued it was sufficient to explain SF5 variation (Hopkins *et al.* 2011b). Our results suggest that a cold shortening temperature threshold cannot be defined with the current data. Although evidence suggests that colder carcases tend to be tougher, more research is needed to address this issue properly.

4.2 Data filtering and effect on genetic parameters

Different methods were used to remove carcases with extreme values and the effect of removing these records on the genetic variance components was examined. The reduction of residual variance was used as a key parameter to assess different edited strategies. Results from this series of analyses are presented on Table 4. The first method removed extreme records with values higher than 79.52 N (4 standard deviations above the mean). The overall mean and standard deviation reduced slightly. The additive genetic variance were also reduced but little change in heritability was observed. The second method removed carcases with SF5 values with shear force values outside the interval formed by the contemporary group median plus 4 median absolute deviations. There was a further reduction in additive and residual variance but again there was small change in heritability using this method. The

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

lowest residual variance was observed when the two previous editing strategies were combined. In that case the heritability estimate was 0.25, which was in agreement with previously reported estimates (Mortimer *et al.* 2014; Brito *et al.* 2017). As a result, the combination of the above to methods is considered the best approach to remove individuals with extreme shear force values.

Table 4. Number of records, removed records, sires, contemporary groups (CG), mean SF5 (standard deviation) and variance components using the basic model after each filtering step. Heritability (h^2), additive ($\hat{\sigma}_a$), genetic group ($\hat{\sigma}_{gg}$), residual ($\hat{\sigma}_\varepsilon$), and phenotypic ($\hat{\sigma}_p$) variance.

Filter	Records	Removed Records	Sires	CG	Mean SF5 (sd)	h^2	$\hat{\sigma}_a$	$\hat{\sigma}_{gg}$	$\hat{\sigma}_\varepsilon$	$\hat{\sigma}_p$
None	32,913	0	2260	1772	32.00 (11.88)	0.26 (0.02)	21.05 (1.3)	4.36 (1.57)	56.29 (1.17)	81.70 (1.71)
*mean(SF5) + 4*sd(SF5)*	32,216	697	2258	1767	31.07 (10.00)	0.27 (0.02)	16.4 (1.00)	3.55 (1.29)	41.08 (0.89)	61.04 (1.38)
*CGmean (SF5) + 4*sd(CGSF5)*	32042	871	2255	1765	31.5 (11.54)	0.25 (0.02)	17.48 (1.13)	3.04 (1.14)	49.87 (1.03)	70.39 (1.28)
Combined	31,345	1568	2253	1760	30.53 (9.48)	0.25 (0.02)	12.32 (0.8)	2.20 (0.83)	33.86 (0.72)	48.39 (0.92)

4.3 Genetic parameters for transformed and non-transformed data

Different models were used to estimate genetic variance components including a series of different covariates (as shown in Table 2 and Table 3) and data transformation. Variance components for each series of analyses are shown in Table 5 and Table 6. All analyses included data after filtering (using combined 1 and 2 filtering methods). Heritability estimates were similar between different models and data transformations and in agreement with previous studies (Mortimer *et al.* 2014; Brito *et al.* 2017). For analyses using phenotypic data measured on the same scale ($SF5^0$ and $SF5^{GM}$) additive and residual variance estimates were lower for the $SF5^{GM}$ compared to $SF5^0$ but heritability estimates were similar. Because of similar heritability estimates obtained with different models and transformations, the best model/transformation combination was selected after cross validation using forward predictions (Table 7).

Table 5. Estimates of variance components obtained from different co-variate analysis using $SF5^0$. Heritability (h^2), additive ($\hat{\sigma}_a$), genetic group ($\hat{\sigma}_{gg}$), residual ($\hat{\sigma}_\varepsilon$), and phenotypic ($\hat{\sigma}_p$) variance. Covariates for different models can be found in Table 3.

Model		h^2	$\hat{\sigma}_a$	$\hat{\sigma}_{gg}$	$\hat{\sigma}_\varepsilon$	$\hat{\sigma}_p$
1		0.24 (0.02)	18.20 (1.43)	10.86 (3.98)	46.2 (1.3)	75.26 (4.03)
2	a	0.22 (0.02)	18.66 (1.28)	9.66 (3.51)	54.96 (1.17)	83.28 (3.56)
	b	0.24 (0.02)	17.30 (1.42)	10.42 (3.82)	44.06 (1.3)	71.78 (3.87)
	c	0.23 (0.02)	11.28 (4.07)	17.32 (1.37)	45.35 (1.26)	73.95 (4.11)
3	a	0.26 (0.02)	18.38 (1.46)	10.45 (3.82)	43.23 (1.32)	72.06 (3.87)
	b	0.25 (0.02)	18.39 (1.47)	10.47 (3.83)	43.35 (1.33)	72.21 (3.88)
	c	0.24 (0.02)	17.61 (1.39)	10.87 (3.95)	45.55 (1.27)	74.02 (4.00)

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Table 6. Estimates of variance components obtained from different models and phenotype transformations. Heritability (h^2), additive ($\hat{\sigma}_a$), genetic group ($\hat{\sigma}_{gg}$), residual ($\hat{\sigma}_\varepsilon$), and phenotypic ($\hat{\sigma}_p$) variance.

Transformation	Model	h^2	$\hat{\sigma}_a$	$\hat{\sigma}_{gg}$	$\hat{\sigma}_\varepsilon$	$\hat{\sigma}_p$
$SF5^0$		0.25 (0.02)	12.32 (0.80)	2.20 (0.83)	33.86 (0.72)	48.39 (0.92)
$SF5^{Log}$	1	0.26 (0.02)	0.03 (0.002)	0.01 (0.002)	0.07 (0.001)	0.10 (0.002)
$SF5^{GM}$		0.26 (0.02)	11.30 (0.72)	2.14 (0.80)	30.74 (0.65)	44.18 (0.88)
$SF5^0$		0.25 (0.02)	11.71 (0.78)	2.53 (0.92)	32.59 (0.71)	46.83 (1.00)
$SF5^{Log}$	2	0.26 (0.02)	0.03 (0.002)	0.01 (0.002)	0.06 (0.001)	0.09 (0.002)
$SF5^{GM}$		0.25 (0.02)	10.74 (0.7)	2.48 (0.89)	29.53 (0.64)	42.75 (0.96)
$SF5^0$		0.25 (0.02)	10.85 (0.90)	3.41 (1.23)	29.49 (0.82)	43.76 (1.30)
$SF5^{Log}$	3	0.25 (0.02)	0.02 (0.002)	0.01 (0.003)	0.06 (0.002)	0.09 (0.003)
$SF5^{GM}$		0.24 (0.02)	9.06 (0.75)	3.00 (1.08)	25.65 (0.70)	37.71 (1.15)
$SF5^0$		0.25 (0.02)	12.15 (0.80)	2.19 (0.83)	33.52 (0.72)	47.86 (0.93)
$SF5^{Log}$	4	0.26 (0.02)	0.03 (0.002)	0.01 (0.002)	0.07 (0.001)	0.10 (0.002)
$SF5^{GM}$		0.25 (0.02)	11.09 (0.72)	2.14 (0.81)	30.5 (0.65)	43.74 (0.89)
$SF5^0$		0.26 (0.02)	12.37 (0.81)	2.28 (0.86)	33.56 (0.73)	48.22 (0.95)
$SF5^{Log}$	5	0.26 (0.02)	0.03 (0.001)	0.01 (0.002)	0.07 (0.001)	0.10 (0.001)
$SF5^{GM}$		0.26 (0.02)	11.3 (0.73)	2.22 (0.82)	30.56 (0.66)	44.08 (0.90)

4.4 Model validation

Regression results are shown in Table 7 for unfiltered and filtered data and different models. Model 1 without any data filtering or transformation ($SF5^0$) was the reference since it was based on phenotype and pedigree information and only used HCWT as a covariate (which is the current model used by Sheep Genetics). When different sire models are validated using forward predictions, the regression coefficient (b) is expected to be 0.5, since each animal gets half of their genes from their sire. A b-value below 0.5 indicates that the EBV is underestimating the genetic variance, while a b-value above 0.5 indicates that the genetic variance is overestimated. Results showed that the basic model (1) exceeded (0.88) the expectation of 0.5 when predicted progeny performance. Filtering data for extreme values improved the prediction (0.39) even when no transformation was applied. Transformations based on the contemporary group mean ($SF5^{GM}$) reliably predicted progeny performance (regression coefficients between 0.40 and 0.44) across models using different covariates. Similar results were obtained when log2 transformation ($SF5^{Log}$) was used (regression coefficients between 0.41 and 0.44). Comparisons between observed and predicted performances in a cross validation analysis is important because it is a measure of the efficiency of the application of the proposed models to specific data sets (Legarra *et al.* 2008). Model 2, using ph24ll, filtered data and log transformed phenotypes ($SF5^{Log}$), had the best predictive ability (0.44), followed by Model 3 with the same transformation and accounting for ph6temp (0.42), and Model 5 which included $SF5^{Log}$ data and the same fixed effects as the

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

basic model but in a bivariate analysis with CFAT (0.42). However, ph24ll records were not available for all animals and ph6temp was not recorded for almost one third of the animals included in the SF5 data set (Table 1). In order to be able to use the full data set for the genetic evaluation, and since the genetic evaluation currently run in OVIS, the genetic evaluation software used by LAMBPLAN (Brown *et al.* 2000) uses a multi-trait approach, **Model 5 with log2 ($SF5^{Log}$) data transformation was the preferred model because it combined a bigger number of records and it reliably predicted progeny performance**.

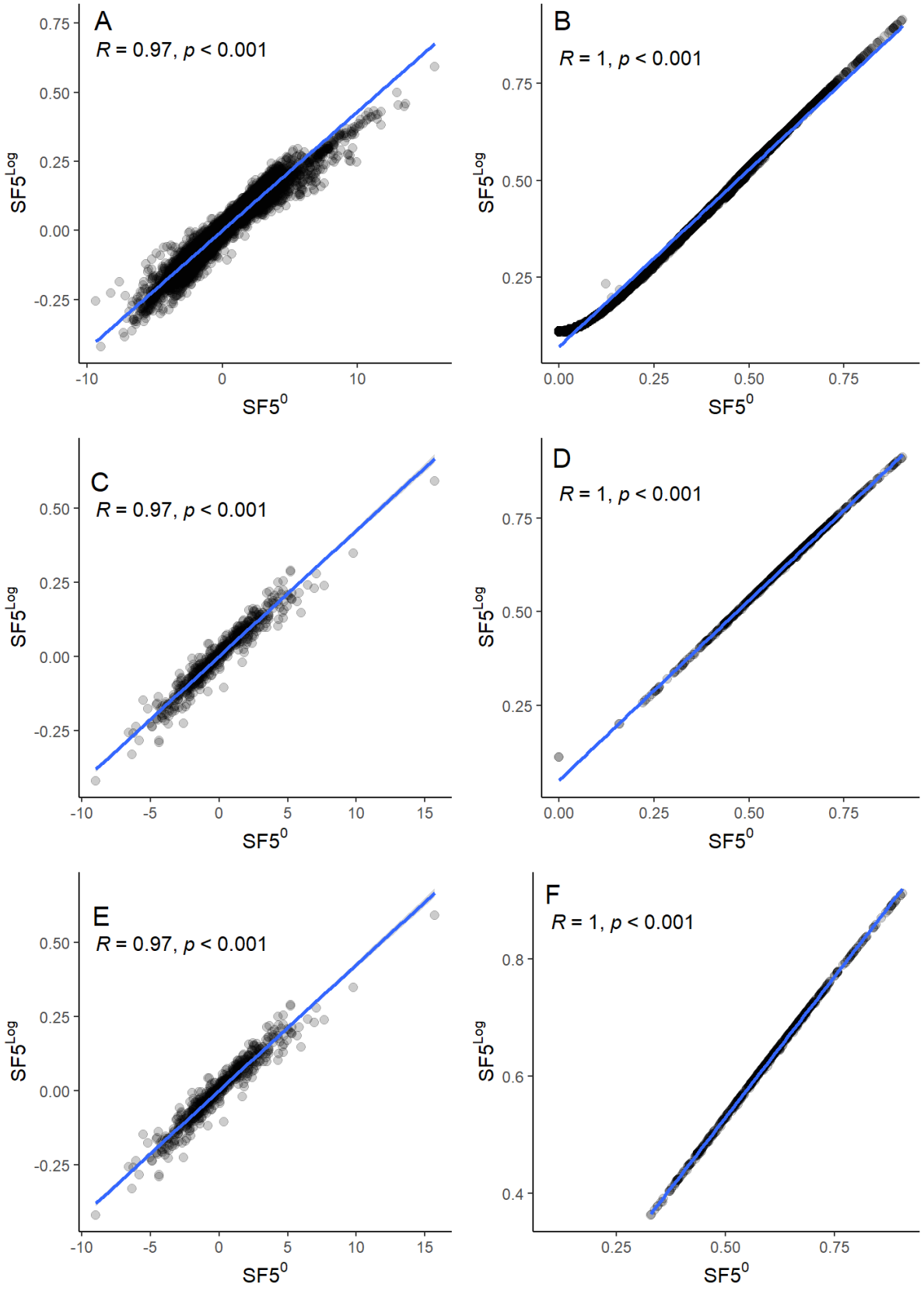
Table 7. Regression coefficient of progeny performance on sire estimated breeding values for SF5 using different transformations, models and extreme values filtering. Models and data transformation with the best predictive ability are shown in bold.

Transformation	Regression coefficient	Range	Model	Covariate	Filtering
$SF5^0$	0.88	0.67 - 1.10	1	*HCWT*	No
$SF5^0$	0.39	0.27 - 0.54	1		
$SF5^{Log}$	0.41	0.28 - 0.50	1	*HCWT*	Yes
$SF5^{GM}$	0.41	0.28 - 0.51	1		
$SF5^0$	0.40	0.25 - 0.67	2		
$SF5^{Log}$	0.44	0.30 - 0.69	2	*HCWT, ph24ll*	Yes
$SF5^{GM}$	0.44	0.28 - 0.69	2		
$SF5^0$	0.40	0.21 - 0.52	3		
$SF5^{Log}$	0.42	0.26 - 0.51	3	*HCWT, ph6temp*	Yes
$SF5^{GM}$	0.42	0.24-0.52	3		
$SF5^0$	0.39	0.30 - 0.50	4		
$SF5^{Log}$	0.41	0.30 - 0.47	4	*HCWT, CFAT*	Yes
$SF5^{GM}$	0.40	0.29 - 0.47	4		
$SF5^0$	0.41	0.32 - 0.57	5		
$SF5^{Log}$	0.42	0.31 - 0.52	5	*HCWT*	Yes
$SF5^{GM}$	0.42	0.31- 0.53	5		

Estimated breeding values (EBVs) acquired with the proposed model (Model 5) and $SF5^{Log}$ data transformation were compared against EBVs acquired with the basic model (Model 1) and $SF5^0$ data (raw phenotypes). In both cases data was filtered as described earlier (combined 1 and 2 filtering methods). Analyses were performed for each sire breed type separately, as it used in OVIS. The EBVs were highly correlated (0.96 – 0.97, Figure 5, 6, 7) indicating there was little re-ranking among sire breeding values.

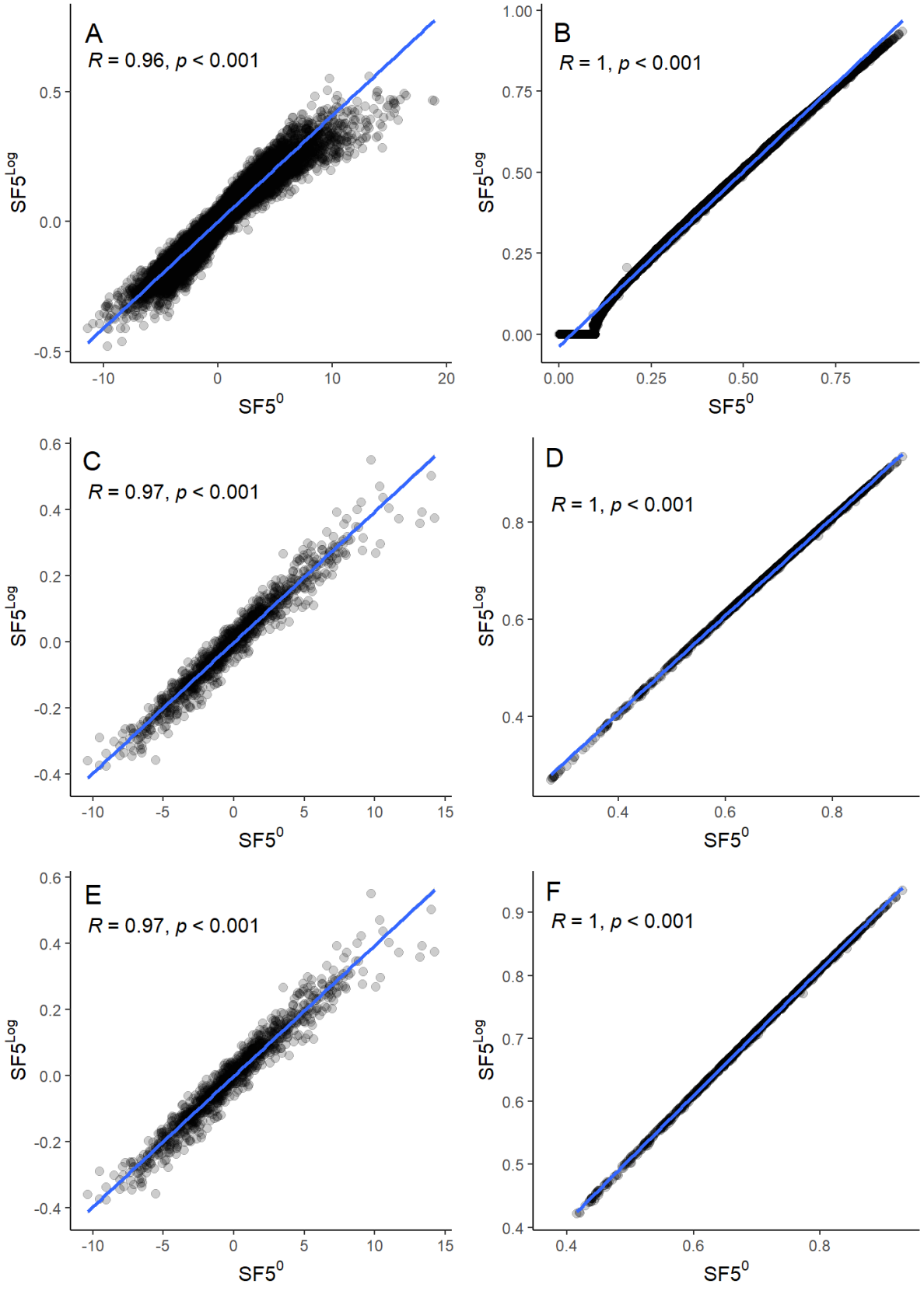
This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Figure 4.Correlations between estimated breeding values (EBVs) and accuracies with log2 transformed ($SF5^{Log}$) and raw shear force ($SF5^{0}$) data for: all Merino animals (A, B), all Merino sires (C, D), high accuracy Merino sires (E, F).



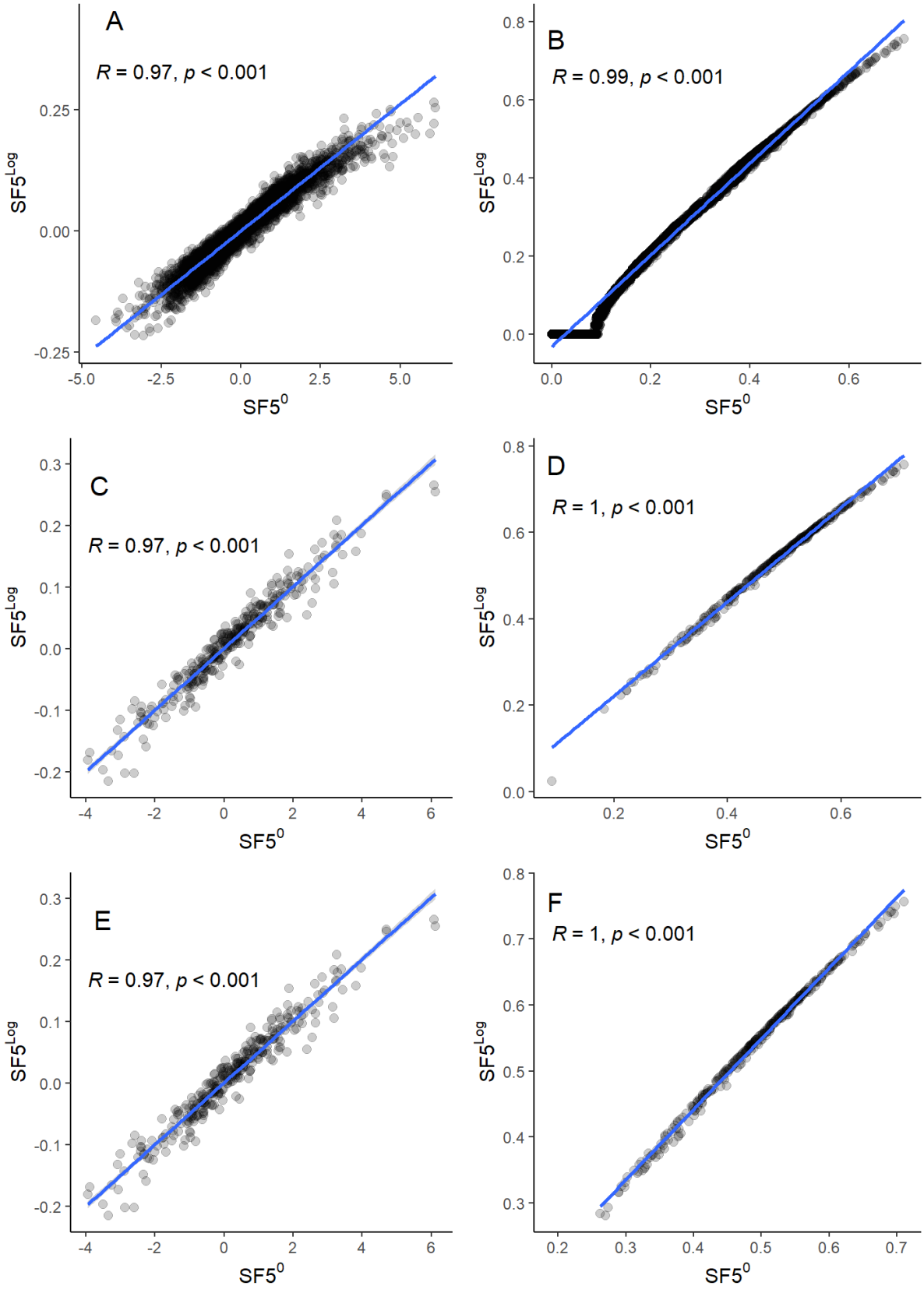
This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Figure 5. Correlations between estimated breeding values (EBVs) and accuracies with log2 transformed ($SF5^{Log}$) and raw shear force ($SF5^{0}$) data for: all terminal animals (A, B), all terminal sires (C, D), high accuracy terminal sires (E, F).



This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Figure 6. *Correlations between estimated breeding values (EBVs) and accuracies with log2 transformed ($SF5^{Log}$) and raw shear force ($SF5^{0}$) data for: all maternal animals (A, B), all maternal sires (C, D), high accuracy maternal sires (E, F).*



This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

To be consistent with current analysis in OVIS where Merino, terminal and maternal sire breeds are analysed separately, variance components were estimated using $SF5^{Log}$ and $SF5^{0}$ for each of the sire breed types (Table 8 and Table 9, respectively). Shear force was moderately heritable for the full data set and for Merino and terminal animals (0.32 and 0.26). Previous studies reported heritability estimates of five day aged shear force from 0.27 (Mortimer *et al.* 2014) to 0.38 ((Mortimer *et al.* 2010; Hopkins *et al.* 2011a). Heritability estimates for maternal animals which were the smallest subset of the data were the lowest (0.18). This can be attributed to lower additive variance in maternal animals (8.25 for $SF5^{0}$ compared to 16.05 in Merino and 25.41 in terminal). In general, $\mathrm{SF5^{Log}}$ improved heritability; all estimates were higher with $SF5^{Log}$ compared to $SF5^{0}$.

Table 8. Variance component estimates for different breeds using $SF5^{Log}$ data. Heritability (h^2), additive ($\hat{\sigma}_a$), residual ($\hat{\sigma}_\varepsilon$), and phenotypic ($\hat{\sigma}_p$) variance.

Breed	Records	Mean $SF5^{Log}$ (sd)	h^2	$\hat{\sigma}_a$	$\hat{\sigma}_\varepsilon$	$\hat{\sigma}_p$
all	27588	4.91 (0.48)	0.26 (0.02)	0.03 (0.002)	0.08 (0.002)	0.13 (0.006)
maternal	3507	4.89 (0.45)	0.18 (0.04)	0.02 (0.005)	0.09 (0.005)	0.11 (0.003)
Merino	7680	4.90 (0.48)	0.26 (0.03)	0.03 (0.004)	0.08 (0.004)	0.11 (0.002)
terminal	16401	4.92 (0.49)	0.32 (0.03)	0.04 (0.003)	0.08 (0.003)	0.13 (0.005)

Table 9. Variance component estimates for different breeds for $SF5^{0}$ data. Heritability (h^2), additive ($\hat{\sigma}_a$), residual ($\hat{\sigma}_\varepsilon$), and phenotypic ($\hat{\sigma}_p$) variance.

Breed	Records	Mean $SF5^{0}$ (sd)	h^2	$\hat{\sigma}_a$	$\hat{\sigma}_\varepsilon$	$\hat{\sigma}_p$
all	27588	31.94 (11.78)	0.24 (0.02)	19.80 (1.26)	55.05 (1.13)	83.19 (3.19)
maternal	3507	31.10 (10.45)	0.13 (0.04)	8.25 (2.48)	54.60 (2.63)	63.16 (1.80)
Merino	7680	31.79 (12.18)	0.23 (0.03)	16.05 (2.28)	52.61 (2.11)	68.71 (1.24)
terminal	16401	32.23 (11.95)	0.30 (0.02)	25.41 (2.00)	54.26 (1.72)	85.00 (2.96)

4.5 Correlations with other carcase traits

Estimates of genetic and phenotypic correlations between SF5 and other carcase traits were estimated using bivariate analyses for $SF5^{Log}$ and $SF5^{0}$ both for the full dataset and for different sire breed types. Genetic and phenotypic correlations are shown on Table 10. Genetic correlations comparison between different breeds for $SF5^{Log}$ and $SF5^{0}$ are shown on Figure 6. Comparison of genetic correlations of *CFAT* with $SF5^{Log}$ and $SF5^{0}$ within breeds showed that the genetic correlations estimated with $SF5^{Log}$ were less extreme; they ranged from -0.268 to 0.088, while the correlations estimated with $SF5^{0}$ were between -0.34 and 0.15. In both cases correlations between CFAT and lower than previously reported (-0.08, Mortimer *et al.* (2018)). Genetic correlations between SF5 and EMD with $SF5^{Log}$ are higher than the correlations estimated from $SF5^{0}$ and slightly higher than previously reported (Brito *et al.* 2017).Genetic correlations between $SF5^{Log}$ and $SF5^{0}$ and IMF were similar for both all data and each breed separately (-0.27 to -0.40) with the exception of Merino data the estimate between IMF and $SF5^{0}$ was 0.63. Results were in agreement with previous research where genetic correlation between SF5 and IMF was estimated to be between -0.62 and -0.27, indicating that higher

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

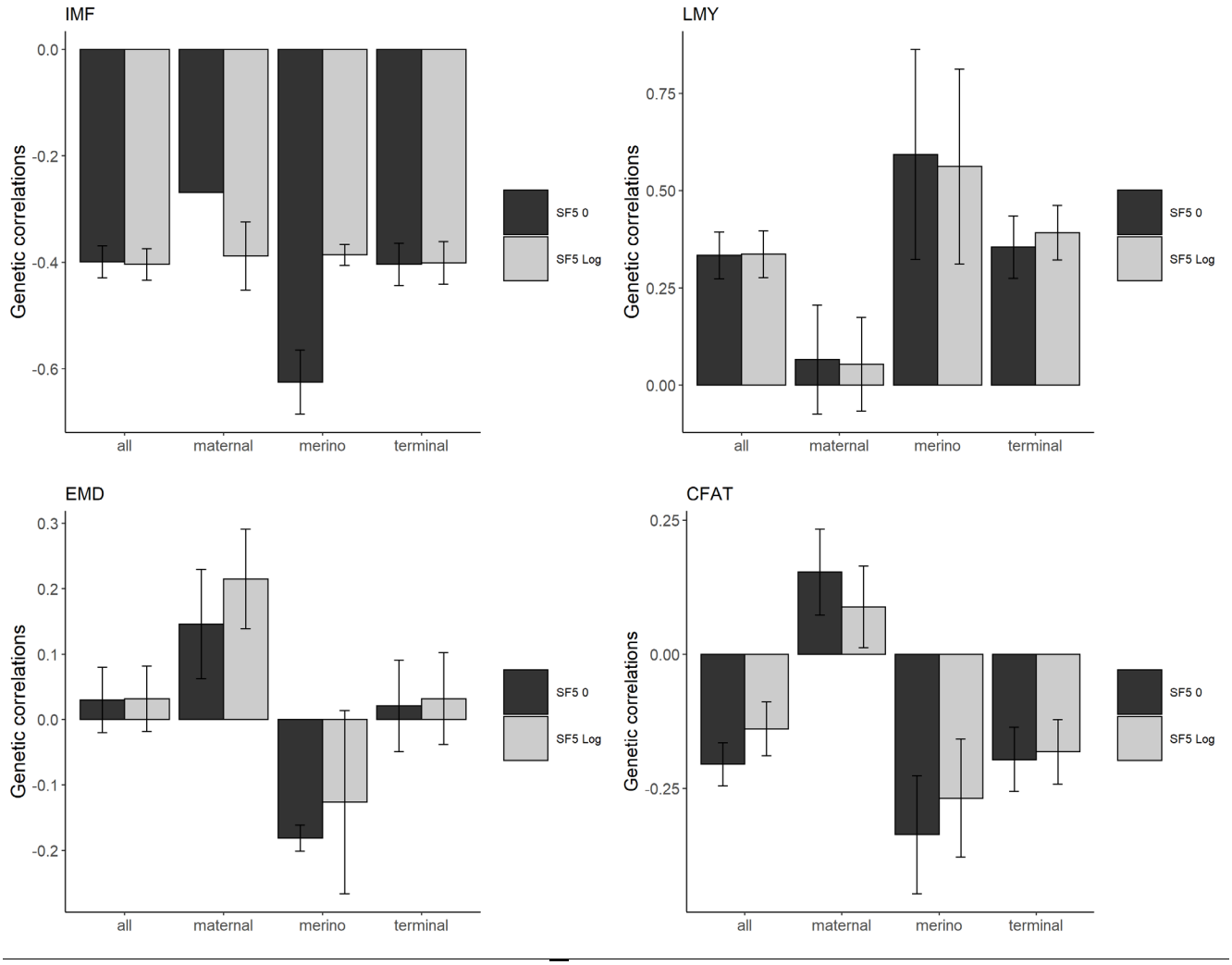
levels of intramuscular fat are genetically associated with more tender meat (Karamichou *et al.* 2006; Mortimer *et al.* 2014; Mortimer *et al.* 2018). Genetic correlations between LMY and SF5 for the full data set and terminal and maternal animals were lower (0.05 – 0.39) than previously reported (0.53, Mortimer *et al.* (2018)). LMY and SF5 correlations were higher for Merino animals (0.562 for $SF5^{Log}$ and 0.593 for $SF5^{0}$ respectively).

Table 10. Genetic and phenotypic correlations of $SF5^{Log}$ and $SF5^{0}$ and carcase and meat quality traits *for all data and each breed separately.*

		Genetic Correlations		Phenotypic Correlations	
Breed	**Trait**	***SF5^{Log}***	***SF5^{0}***	***SF5^{Log}***	***SF5^{0}***
all	*CFAT*	-0.14 (0.05)	-0.21 (0.04)	-0.09 (0.02)	-0.11 (0.04)
maternal		0.09 (0.19)	0.15 (0.20)	-0.04 (0.04)	-0.05 (0.03)
terminal		-0.18 (0.06)	-0.20 (0.06)	-0.08 (0.03)	-0.07 (0.02)
merino		-0.27 (0.11)	-0.34 (0.12)	-0.15 (0.02)	-0.05 (0.02)
all	*EMD*	0.03 (0.05)	0.03 (0.05)	0.09 (0.04)	0.08 (0.04)
maternal		0.22 (0.19)	0.15 (0.21)	0.02 (0.04)	0.02 (0.03)
terminal		0.03 (0.07)	0.02 (0.07)	-0.01 (0.03)	0.002 (0.02)
merino		-0.13 (0.14)	-0.18 (0.02)	0.01 (0.02)	0.01 (0.01)
all	*IMF*	-0.40 (0.03)	-0.40 (0.03)	-0.19 (0.01)	-0.28 (0.03)
maternal		-0.38 (0.16)	-0.27 (0.01)	-0.22 (0.04)	-0.23 (0.02)
terminal		-0.40 (0.04)	-0.40 (0.05)	-0.27 (0.05)	-0.22 (0.03)
merino		-0.39 (0.02)	-0.63 (0.06)	-0.30 (0.01)	-0.27 (0.02)
all	*LMY*	0.34 (0.06)	0.33 (0.06)	0.10 (0.01)	0.13 (0.06)
maternal		0.05 (0.30)	0.07 (0.35)	0.11 (0.08)	0.08 (0.11)
terminal		0.39 (0.07)	0.36 (0.07)	0.16 (0.03)	0.16 (0.04)
merino		0.56 (0.25)	0.59 (0.27)	0.17 (0.06)	0.16 (0.05)

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Figure 7.Genetic correlations between SF5 and carcase and meat quality traits for $SF5^{Log}$ and $SF5^{0}$. IMF: intramuscular fat, LMY: lean meat yield, EMD: eye muscle depth, CFAT: c-side fat.



This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

5 Conclusions

- Cold shortening impact on SF5 could not be defined in this analysis. Based on the available data a clear temperature threshold for cold shortening could not be defined and the relationship between shear force and temperature at pH6 appears to be linear with no cut-off point. Moreover there is a lot of variation in shear force and temperature at pH6 between different sires and contemporary groups.
- Filtering carcases with extreme shear force values improves variance components estimation and progeny performance predictability.
- Shear force model predictability improved with log transformation and accounting for temperature at pH6 or pH 24 hours after slaughter.
- Only one third of the animals have temperature records. To include the highest possible number of animals in the genetic evaluation, bivariate analysis and comparisons were carried out with log2 transformed ($SF5^{Log}$) data only and without including temperature.
- Genetic correlations of shear force and carcase and meat quality traits obtained with $SF5^{Log}$ and $SF5^{0}$ data are similar and in agreement with previous research, but for some traits $SF5^{Log}$ provided more consistent correlations for animals of different breeds.

6 References

Anonymous (1992) AUS-MEAT language (4th ed.) Sydney: Authority for Uniform Specification Meat and Livestock.

Brito L.F., McEwan J.C., Miller S., Bain W., Lee M., Dodds K., Newman S.-A., Pickering N., Schenkel F.S. & Clarke S. (2017) Genetic parameters for various growth, carcass and meat quality traits in a New Zealand sheep population. *Small Ruminant Research* **154**, 81-91.

Brown D.J., Tier B., Reverter A., Banks R.G. & Graser H.-U. (2000) OVIS: a mutliple trait breeding value estimation program for genetic evaluation of sheep. *International Journal of Sheep and Wool Science* **48**, 285-97.

Ertbjerg P. & Puolanne E. (2017) Muscle structure, sarcomere length and influences on meat quality: A review. *Meat Sci* **132**, 139-52.

Gardner G.E., Williams A., Siddell J., Ball A.J., Mortimer S., Jacob R.H., Pearce K.L., Hocking Edwards J.E., Rowe J.B. & Pethick D.W. (2010) Using Australian Sheep Breeding Values to increase lean meat yield percentage. *Animal Production Science* **50**, 1098-106.

Gilmour A.R., Gogel B.J., Cullis B.R., Welham S.J. & Thompson R. (2015) ASReml User Guide Release 4.1. In: *VSN International Ltd, Hemel Hempstead, UK*

Gutzke D.A., Franks P., Hopkins D.L. & Warner R.D. (2014) Why is muscle metabolism important for red meat quality? An industry perspective. *Animal Production Science* **54**, iii-v.

Hopkins D.L., Fogarty N.M. & Mortimer S.I. (2011a) Genetic related effects on sheep meat quality. *Small Ruminant Research* **101**, 160-72.

Hopkins D.L., Holman B.W. & van de Ven R.J. (2015) Modelling lamb carcase pH and temperature decline parameters: relationship to shear force and abattoir variation. *Meat Sci* **100**, 85-90.

Hopkins D.L. & Toohey E.S. (2006) Eating quality of conventionally chilled sheep meat. *Australian Journal of Experimental Agriculture* **46**, 897-901.

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Hopkins D.L., Toohey E.S., Lamb T.A., Kerr M.J., van de Ven R.J. & Refshauge G. (2011b) Explaining the variation in the shear force of lamb meat using sarcomere length, the rate of rigor onset and pH. *Meat Science* **88**, 794 - 6.

Hopkins D.L., Toohey E.S., Warner R.D., Kerr M.J. & van de Ven R. (2010) Measuring the shear force of lamb meat cooked from frozen samples: comparison of two laboratories. *Animal Production Science* **50**, 382-5.

Huisman A.E., Brown D.J. & Fogarty N.M. (2015) Ability of sire breeding values to predict progeny bodyweight, fat and muscle using various transformations across environments in terminal sire sheep breeds. *Animal Production Science* **56**, 95-101.

Karamichou E., Richardson R.I., Nute G.R., Gibson K.P. & Bishop S.C. (2006) Genetic analyses and quantitative trait loci detection, using a partial genome scan, for intramuscular fatty acid composition in Scottish Blackface sheep1. *Journal of Animal Science* **84**, 3228-38.

Legarra A., Robert-Granie C., Manfredi E. & Elsen J.M. (2008) Performance of genomic selection in mice. *Genetics* **180**, 611-8.

Mortimer S.I., Fogarty N.M., van der Werf J.H.J., Brown D.J., Swan A.A., Jacob R.H., Geesink G.H., Hopkins D.L., Hocking Edwards J.E., Ponnampalam E.N., Warner R.D., Pearce K.L. & Pethick D.W. (2018) Genetic correlations between meat quality traits and growth and carcass traits in Merino sheep1. *J Anim Sci* **96**, 3582-98.

Mortimer S.I., van der Werf J.H., Jacob R.H., Hopkins D.L., Pannier L., Pearce K.L., Gardner G.E., Warner R.D., Geesink G.H., Edwards J.E., Ponnampalam E.N., Ball A.J., Gilmour A.R. & Pethick D.W. (2014) Genetic parameters for meat quality traits of Australian lamb meat. *Meat Sci* **96**, 1016-24.

Mortimer S.I., van der Werf J.H.J., Jacob R.H., Pethick D.W., Pearce K.L., Warner R.D., Geesink G.H., Hocking Edwards J.E., Gardner G.E., Ponnampalam E.N., Kitessa S.M., Ball A.J. & Hopkins D.L. (2010) Preliminary estimates of genetic parameters for carcass and meat quality traits in Australian sheep. *Animal Production Science* **50**, 1135-44.

Muela E., Sañudo C., Campo M.M., Medel I. & Beltrán J.A. (2010) Effects of cooling temperature and hot carcass weight on the quality of lamb. *Meat Science* **84**, 101-7.

Muggeo V.M.R. (2003) Estimating regression models with unknown break-points *Statistics in Medicine* **22**, 3055 - 71.

Muggeo V.M.R. (2008) segmented: An R package to fit regression models with broken line relationships In: *R news*, pp. 20 - 5.

Pearce K.L., van de Ven R., Mudford C., Warner R.D., Hocking-Edwards J., Jacob R., Pethick D.W. & Hopkins D.L. (2010) Case studies demonstrating the benefits on pH and temperature decline of optimising medium-voltage electrical stimulation of lamb carcasses. *Animal Production Science*, 1107-14.

Perry D., Shorthose W.R., Ferguson D.M. & Thompson J.M. (2001) Methods used in the CRC program for the determination of carcass yield and beef quality. *Australian Journal of Experimental Agriculture* **41**, 953-7.

Purchas R.W. (2014) TENDERNESS MEASUREMENT. In: *Encyclopedia of Meat Sciences (Second Edition)* (eds. by Dikeman M & Devine C), pp. 452-9. Academic Press, Oxford.

Starkey C.P., Geensik G.H., Collins D., Hutton Oddy V. & Hopkins D.L. (2016) Do sarcomere length, collagen content, pH, intramuscular fat and desmin degradation explain variation in the tenderness of three ovine muscles? *Meat Science* **113**, 51 - 8.

Swan A.A., Brown D.J. & van der Werf J.H.J. (2016) Genetic variation within and between subpopulations of the Australian Merino breed. *Animal Production Science* **56**, 87.

Thompson J.M., Hopkins D.L., D'Souza D.N., Walker P.J., Baud S.R. & Pethick D.W. (2005) The impact of processing on sensory and objective measurements of sheep meat eating quality. *Australian Journal of Experimental Agriculture* **45**, 561-73.

Thompson J.M., Perry D., Daly B., Gardner G.E., Johnston D.J. & Pethick D.W. (2006) Genetic and environmental effects on the muscle structure response post-mortem. *Meat Sci* **74**, 59-65.

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.

Thomson J.M., Hopkins D.L., D'Sousa D., Walker P.J., Baud S.R. & Pethick D.W. (2005) The impact of processing on sensory and objective measurements of sheep meat eating quality. *Australian Journal of Experimental Agriculture* **45**, 561 - 73.

Van der Werf J.H.J., Kinghorn B.P. & Banks R.G. (2010) Design and role of an information nucleus in sheep breeding programs. *Animal Production Science*, 998 - 1003.

Warner R. (2016) Meat: Conversion of Muscle into Meat. In: *Encyclopedia of Food and Health* (eds. by Caballero B, Finglas PM & Toldrá F), pp. 677-84. Academic Press, Oxford.

This project is supported by funding from the Australian Government Department of Agriculture, Fisheries and Forestry as part of its Rural R&D for Profit programme in partnership with Research & Development Corporations, Commercial Companies, State Departments & Universities.