The effects of divergent selection for reproduction and sex on quantitative and qualitative slaughter traits in Merinos

S.W.P. Cloete[a,b#], C.S. Naudé[c], J.J.E. Cloete[a,d], A.J. Scholtz[b], A.C.M. Kruger[b] and C. Visser[c]

[a]*Department of Animal Sciences, Stellenbosch University, Matieland 7602, South Africa*

[b]*Western Cape Department of Agriculture, Directorate Animal Sciences: Elsenburg, Elsenburg, 7607, South Africa*

[c]*Department of Animal Science, University of Pretoria, Hatfield 0028, South Africa*

[d]*Western Cape Department of Agriculture, Cape Institute for Agricultural Training, Elsenburg, 7607, South Africa*

[#]Corresponding author: Tel.: +27 21 808 4747 or +27 82 542 5224

E-mail address: schalkc2@sun.ac.za

Highlights

- Meat traits were studied in Merinos divergently selected for lamb output.
- The High line was selected upwards and the Low line downwards.
- Overall, High line hoggets were heavier than their Low line contemporaries.
- High line hoggets had a lower ultimate pH and slightly darker meat.
- Heritability ranged from 0.25−0.29 for fat depth to 0.63 for carcass weight.

ABSTRACT

The impact of selection of sheep for reproduction on meat traits are not evident, while genetic parameters for meat traits is absent for South African pure breeds. Quantitative and qualitative meat traits were therefore studied in progeny of two Merino selection lines that were divergently selected for number of lambs weaned per ewe joined (NLW) since 1986. The historic divergent selection resulted in two lines (High (H) and Low (L)) differing widely for NLW. Slaughter data were recorded during the routine slaughter of surplus 14-month-old ram and ewe hoggets from these lines and assessed for selection line and sex. Single-trait heritability estimates were derived for meat traits by average information restricted maximum likelihood methods. Depending on the trait, data were available for between 340 and 576 animals that were recorded between 2015 and 2018. Hoggets from the H line were heavier than their L line contemporaries, with a slightly lower ultimate pH after 48 hours in the cooler and slightly darker meat. H line ewes had, on average, redder meat than the other selection line x sex groups. Single-trait heritability estimates amounted to 0.44 ± 0.16 for slaughter weight, 0.63 ± 0.15 for carcass weight, 0.34 ± 0.15 for dressing percentage, 0.25 ± 0.11 for fat depth at the 13th rib, 0.29 ± 0.11 for fat depth at the rump, 0.12 ± 0.11 for ultimate pH, 0.32 ± 0.12 for lightness, 0.11 ± 0.09 for redness, 0.04 ± 0.06 for yellowness, 0.05 ± 0.08 for cooking loss and 0.06 ± 0.07 for drip loss. Parameter estimates for initial pH and shear force of the meat went to the boundary of parameter space and were not estimable. It was concluded that selection for NLW did not compromise any of the meat traits and that most quantitative meat traits were heritable and variable, making selection for improvement of these traits feasible. Additional research is indicated on the qualitative meat traits studied.

Keywords: Meat pH, meat colour, shear force, heritability

1. Introduction

Despite being relatively small in magnitude in terms of gross value of production, compared to chickens and cattle, sheep production contributes markedly to the South African agriculture industry (Cloete and Olivier, 2010). The adaptability of sheep to arid and marginal environments, as well as value added to the cropping industry, contributes to the popularity of sheep in the South African agricultural landscape (Cloete et al., 2014).

Meat and apparel wool are the most important sheep products in South Africa (Cloete and Olivier, 2010). The modern red meat consumer considers meat quality as the most important characteristic but also demands healthier products that are environmentally friendly, promote sustainability and comply with animal welfare guidelines (Webb and Casey, 2010). Meat price relative to the wool price as well as the importance of lamb and meat production from wool breeds contributes to the complexity of the overall objective and profit of the sheep industry (Cloete et al., 2008; Van der Merwe et al., 2020).

Reproduction is a key component in Merino breeding in South Africa (Olivier, 1999). It has been shown that reproduction rate, expressed as number of lambs weaned per ewe mated (NLW), showed a marked response to selection in South African Merinos (Cloete et al., 2004c). Results from literature, however, suggest that meat characteristics could be compromised in lambs originating from prolific breeds (Greeff, 1992; Schoeman et al., 1993). Provisional results indicated that selection for NLW did not compromise quantitative carcass traits or qualitative meat traits (Hoffman et al., 2003; Cloete et al., 2004b; Cloete et al., 2005). However, these inferences were based on small sample sizes, which were also slaughtered at a relatively late age of 18 to 19 months. Therefore, based on the time lapse since the previous studies as well as the late slaughter age, these provisional results were revisited by assessing the impact of continued selection for NLW.

Up to the early 2000's, limited research was performed on genetic parameters for meat quality traits despite the high economic value of marketable lambs. This is reflected in the review by Safari et al. (2005) on genetic parameters in sheep, where the authors concluded that meat quality traits were most commonly represented by five or fewer heritability estimates, sometimes exhibiting considerable variation. Recently overseas researchers have published updated genetic parameters for meat traits, often involving industry-level databases (Brown et al., 2016; Brito et al., 2017). This has not yet happened in the South African sheep industry, as no mainstream breed includes meat traits as part of its recording protocol (Schoeman et al., 2010). There is therefore limited information available on genetic parameters for meat traits in local sheep breeds (Cloete et al*.,* 2012). The most comprehensive heritability estimates in South Africa were derived from a combination of crossbred and purebred genetic resources (Naudé et al., 2018).

Against this background, the present study was designed to firstly investigate the effect of selection line in a local Merino population divergently selected for NLW on quantitative and qualitative slaughter and meat quality traits of hoggets. Furthermore, to the knowledge of the authors, heritability has not yet been estimated for any of the pure breeds contained within the South African ovine genetic resource (described by Cloete et al., 2014), and specifically not for South African Merinos. A secondary aim was thus to use the available data to derive provisional heritability estimates for the resource flock studied.

2. Material and Methods

2.1 Animals and location

Data of between 340 and 576 (depending on trait; see Table 1) hoggets born from 2015 to 2018 were used to compare Merinos in two separate lines that were divergently selected for reproduction (number of lambs weaned per ewe mated, NLW) since 1986. The experimental animals were maintained in the same flock but separated on sex during the course of the experiment at the Elsenburg Research farm. Elsenburg is situated approximately 10 km north of Stellenbosch. The elevation of the site is 177 m and the average long-term precipitation is 606 mm per annum, 78% of which is recorded between April and September. The formation of the selection lines, the selection strategy implemented as well as realised genetic gains was described by Cloete et al. (2004c). The selection lines are commonly referred to as the High (H) line for the line selected for NLW and the Low (L) line for the line selected in the downwards direction. In short, the selection strategy involved that ewe and ram progeny of ewes rearing more than one lamb per joining (*i.e.* that reared twins at least once) were preferred as replacements in the H line. Descendants of ewes that reared less than one lamb per joining (*i.e.* that were barren or lost all lambs born at least once) were preferred as replacements in the L line. It should be noted that there were external sires from industry sources (n = 4 in the H line and n = 3 in the L line) during the period data were recorded. These sires were introduced to link the flock with industry (Cloete et al., 2014; 2020) and to curb inbreeding (Jorgensen et al., 2020).

Table 1

Descriptive statistics for the quantitative and qualitative slaughter traits recorded on Merino hoggets of the High- and Low reproduction lines

Trait	Number of records	Mean ± SD	Coefficient of variation (%)	Range
Quantitative traits:				
Slaughter weight (kg)	469	38.9 ± 8.4	21.6	20.0 – 69.5
Carcass weight (kg)	446	15.6 ± 3.6	23.1	8.1 – 26.7
Dressing percentage (%)	340	40.3 ± 4.0	9.9	31.3 – 50.7
Fat depth (13th rib) (mm)	564	1.01 ± 0.91	90.1	0.1 – 5.78
Fat depth (rump) (mm)	564	1.77 ± 1.34	75.7	0.2 – 7.68
Qualitative traits:				
Initial pH	574	6.58 ± 0.35	5.3	5.41 – 7.39
Ultimate pH	470	5.91 ± 0.33	5.6	5.05 – 6.96
Lightness (L*)	575	34.5 ± 3.4	9.9	24.1 – 46.8
Redness (a*)	576	11.9 ± 2.3	19.3	6.2 – 19.9
Yellowness (b*)	576	10.0 ± 1.9	19.0	4.2 – 15.5
Cooking loss (%)	571	30.5 ± 4.9	16.1	15.2 – 41.6
Drip loss (%)	522	1.29 ± 0.51	39.5	0.5 – 3.6
Shear force (N)	491	40.5 ± 13.5	33.3	11.6 – 79.9

Ewes of both lines were managed as a single flock except at mating during January-February when they were mated in single-sire groups within lines. The ewe flock as well as the hoggets used in this study was subjected to the same level of husbandry (e.g. parasite control, general managerial practices) during this period as described in previous literature (Cloete and Scholtz, 1998; Cloete et al., 2004c). The ewe flock was joined annually during January-February to 6-8 rams (H Line) or 3-5 rams (L Line) in single-sire groups for the lambing season to occur from June-July of the same year. All the ewe and offspring flocks were kept on similar grazing with no concentrate supplementation provided at any stage. Animals were provided with roughage supplementation in the form of lucerne (*Medicago sativa*) hay when needed during the typically dry summer in a Mediterranean environment. A fairly typical health program for the area was followed. Individual lambs were identified with their dams within 24 hours of birth during lambing in winter. This allowed lambs to be traced back to the sire used to ensure complete pedigree information. The sex, dam age and birth type of lambs were recorded simultaneously. The lambs were maintained to yearling age when they were subjected to performance recording for live weight and wool traits during May of the year following their lambing year. Surplus ewe and ram hoggets not needed for replacements were available for slaughter. Pasture utilised during the growing-out phase included dryland and irrigated lucerne and kikuyu (*Pennisetium clandestinum*), as well as dryland oats (*Avena sativa*), cultivated as fodder crops.

The flock was maintained, managed and recorded under the ethical clearance number R12/57 of the Western Cape Department of Agriculture. Ethical approval for use of the data for postgraduate studies was granted by the Ethics Committee of the Faculty of Natural and Agricultural Sciences, University of Pretoria (Ethics number: EC 160922 – 073).

2.2 Slaughter procedures and recordings

The sheep were mostly slaughtered as hoggets within 3 months after yearling performance recording. It was attempted to slaughter the hoggets at a target live weight of at least 32 kg. However, being pasture-fed without concentrate supplementation, some animals did reach this weight in the allotted time and were slaughtered at a lower weight. On-farm weight records included slaughter weight at an average slaughter age (± SD) of 431 ± 50 days, or just over 14 months (n = 576 individuals). Unfortunately on-farm slaughter weight was not recorded for lambs born in 2015 while cold carcass weight was not recorded for 2016 hoggets. Only data points of 340 hoggets born in 2017 and 2018 were thus available to calculate dressing percentage, while slaughter weights of 469 hoggets born from 2016 to 2018 were recorded. Hoggets were weighed and transported to Swartland Abattoir in Malmesbury or Tomi's Abattoir in Hermon on the day prior to slaughter. The hoggets were held overnight in lairage for ~17 hours before slaughter. In lairage, hoggets had no access to feed but had free access to water. The hoggets were slaughtered according to standard South African techniques for this species. The hoggets were rendered unconscious by electrical stunning (5 seconds at 200 volts), they were then exsanguinated and carcasses were suspended and allowed to bleed out (Cloete et al., 2004a, 2004b). No electrical stimulation was applied to the carcasses.

Qualitative traits recorded in the abattoir were carcass pH at 45 minutes post-slaughter (initial pH) and 48 hours post-slaughter (ultimate pH) measured on the *M. longissimus lumborum* on the right side of the carcass 2.5 cm from the midline. The pH meter, a CRISON handheld model 25 was equipped with a thermometer that allowed for automatic temperature adjustment. Before each session, the pH metre was calibrated using standard buffers (pH 4.0 and pH 7.0) provided by the manufacturer. Additionally, the quantitative traits cold carcass weight, dressing percentage as well as fat depth at two sites were recorded after 48 hours of cold storage. The first site was at the 13th rib and the second site was between the 3rd and 4th lumbar vertebrae. These measurements were made 2.5 cm from the midline, using an electronic calliper in a cut made parallel to the spinal column (Bruwer et al., 1987).

The *Longissimus lumborum* muscle on the left side of the carcass was excised between the 13th rib and the 4th lumbar vertebrae, and was taken to the laboratory in a cool box and used for various physical meat-quality tests, namely: colour, drip loss, cooking loss and shear force. Each LL muscle sample was cut into 3 – 4 pieces of 25 mm thickness and allowed to bloom for 30 minutes at room temperature (Honikel, 1998). Meat surface colour was then measured using a digital calibrated handheld Colour-guide 45°/0° colorimeter (aperture size 11 mm; illuminant/observer of 100 D65/10°) (BYK-Gardner GmbH, Gerestried, Germany). Calibration of the colorimeter was done using the standards provided (BYK-Gardner). Three measurements were taken on the bloomed surface to determine the following CIE (Commission International De l'Eclairage, 1976) values: L* (lightness; 0 =

black; 100 = white), a* (red-green range; positive = red; negative =green) and b* (blue-yellow range; positive = yellow; negative = blue) values.

In order to calculate cooking loss, a sample piece (25 mm thick) was weighed on a digital scale and inserted into a thin-walled plastic bag. These samples were placed in a water bath (80°C) and cooked for 60 minutes in the bags. The bags were then removed from the water bath, and the exuded water drained and samples were submerged in cold water. The samples were allowed to cool for 24 hours at 4°C and were then removed from the bags, blotted dry with paper towels and weighed. The cooking loss was calculated as the difference from original sample weight and expressed as a percentage. Drip loss was determined by suspending a 25 mm thick sample piece, which had been weighed, from a wire in an inflated and sealed thin-walled plastic bag. The bags were hung in a refrigerator at 4°C for 24 hours. The samples were then removed from the bags and blotted dry using paper towels to remove excess water before weighing on a digital scale. The drip loss was expressed as the percentage of weight lost over a 24 hour period.The shear force of the cooked samples was then measured instrumentally using the Warner-Bratzler shear force method (Honikel, 1998). Three 2.5 cm cores, 1.27 cm in diameter, were cut parallel to the meat fibres, using a cylindrical cutting tool; from the cooked meat samples after cooking loss had been determined. An Instron universal testing machine (Instron model 4444/H1028, Appollo Scientific cc, South Africa) fitted with a Warner-Bratzler attachment with a 1 mm thick triangular blade with a semi-circular cutting edge which would cut the core sample perpendicular to the grain, was used. The Instron machine was set to operate with a load cell of 2.000 kN at a speed of 200mm/min. The shear force values so obtained were expressed in Newton.

2.3 Statistical analyses

All data were analysed with ASREML (Gilmour *et al*., 2016), using an average information algorithm operating on sparse matrices during Restricted Maximum Likelihood analyses (Gilmour et al., 1995). The software allows for the prediction of means in unbalanced designs in various forms of mixed linear models. A series of preliminary single-trait analyses involving fixed and interaction effects was conducted to provide guidance as to the operational model required for each trait. Based on these analyses, the fixed effects fitted were narrowed down to selection line (H or L), year of birth (2015 to 2018), sex (ram or ewe), dam age (2 to 6+ years) and birth type (single or pooled multiples), as well as two-factor interactions of selection line with all other effects as well as birth year x sex. In addition, slaughter age was fitted as a linear covariate for all traits while muscle temperature was fitted as a linear covariate for the corresponding pH measurement to account for the known relationship of meat pH with muscle temperature (Van de Ven *et al*., 2014). These analyses were used to obtain operational fixed effect models prior to the inclusion of a random animal effect for the estimation of preliminary heritability estimates. The pedigree file used for estimating heritability included 10277 animals, the progeny of 377 sires and 2208 dams. Given that the number of records barely reached a threshold for the estimation of genetic variances, as well as a lack of dams and maternal grand-dams with data, it was not attempted to partition variances into direct and maternal effects. Sizeable maternal variances at the relatively high average age of 14.2 months at recording were also considered as unlikely.

3. Results and Discussion

3.1 Descriptive statistics

On average, 13.1% of 306 ram hoggets and 29.4% of 163 ewe hoggets did not reach a target slaughter weight of 32kg by the end of their second spring (Chi^2=17.7; P<0.01). The lower percentage of ewes meeting the target was expected, based on the known effect of sex on slaughter weight and slaughter age (Van der Merwe et al., 2020). Slaughter was motivated by the unlikely prospect of further weight gains under the Mediterranean climate conditions at the experimental site once the season progressed to summer.

Values for the coefficient of variation (CV) of weight traits were somewhat over 20%, just below 10% for dressing percentage and above 70% for fat depth (Table 1). The CV values of initial and ultimate pH as well as lightness were below 10, between 10 and 20% for redness and cooking loss and above 30% for drip loss and shear force. These CVs were consistent or just above literature values with ranges of 11 to 18% for slaughter weight, 10 to 25% for carcase weight, 6 to 12% for dressing percentage, 35 to 97% for fat depth, 8 to 11% for lightness, 13 to 20% for redness and 34 to 36% for shear force (Greeff et al., 2008; Mortimer et al., 2014; Brito et al., 2017; Naudé et al., 2018). Although the high CVs of 75% or higher for fat depth were inside the literature ranges, it warrants further discussion. It is known that the Merino is a relatively lean breed with a greater likelihood of fat depth records close to zero (Cloete et al., 2012). Other factors possibly contributing were the facts that study took place on natural pastures without any supplementation while some hoggets were slaughtered before reaching the target slaughter weight. Naudé et al. (2018) reported slightly higher CVs of 97% for fat depth at the 13^{th} rib and 81% at the rump in their across-breed study.

3.2 Significance of effects

Selection line affected slaughter weight and carcass weight (P < 0.01), but not dressing percentage and fat depth (Table 2). Selection line also interacted with birth year in the case of carcass weight (P < 0.05). All quantitative slaughter traits were affected by birth year and sex, while sex also interacted (P < 0.05) with birth year for all traits except dressing percentage. Slaughter weight was the only trait that depended on dam age (P < 0.05), while birth status impacted on the weight traits and fat depth (P < 0.05). The regressions of all traits on slaughter age were significant. Among the qualitative meat traits, ultimate pH and lightness was influenced by selection line (P < 0.05; Table 3). Selection line also interacted with sex for redness (P < 0.01). All traits were affected by birth year (P < 0.01). Sex influenced lightness, redness, drip loss and shear force (P < 0.05). It also interacted (P < 0.01) with birth year for all traits barring ultimate pH and shear force (P = 0.06). All qualitative meat traits were independent of dam age and the only trait affected by birth type was lightness (P < 0.05). The regressions of initial pH, cooking loss and drip loss on slaughter age were also significant.

Table 2

Significance of fixed effects, two-factor interactions and linear covariates for the quantitative slaughter traits recorded on Merino hoggets of the High- and Low reproduction lines

Effect	Slaughter weight (kg)	Carcass weight (kg)	Dressing %	Fat depth (13^{th} rib) (mm)	Fat depth (rump) (mm)
Line (L)	**	**	0.14	0.76	0.46
Year (Y)	**	**	**	**	**
L x Y	0.45	*	0.61	0.86	0.21
Sex (S)	**	**	**	**	**
S x Y	**	**	0.93	*	*
S x L	0.38	0.78	0.67	0.98	0.06
Dam age (A)	**	0.28	0.47	0.18	0.22
Birth type (B)	**	**	0.41	*	**
L x B	0.51	0.39	0.18	0.17	0.74
<u>Regressions:</u>					
Slaughter age	**	**	0.20	**	**

* – P<0.05; ** – P<0.01

Table 3

Significance of fixed effects, two-factor interactions and linear covariates for the qualitative slaughter traits recorded on Merino hoggets of the High- and Low reproduction lines

Effect	pH_i	pH_u	L*	a*	b*	CL	DL	SF
Line (L)	0.82	**	**	0.06	0.52	0.41	0.39	0.78
Year (Y)	**	**	**	**	**	**	**	**
L x Y	0.11	0.06	0.39	0.84	0.62	0.41	0.16	0.78
Sex (S)	0.26	0.82	**	**	0.06	0.49	**	*
S x Y	**	0.06	**	**	**	**	**	0.06
S x L	0.67	0.53	0.21	**	0.73	0.59	0.79	0.29
Dam age (A)	0.08	0.66	0.55	0.47	0.46	0.21	0.48	0.88
Birth type (B)	0.37	0.70	*	0.70	0.72	0.06	0.25	0.54
L x B	0.13	0.06	0.63	0.38	0.70	0.27	0.13	0.81
<u>Regressions:</u>								
Slaughter age	**	0.24	0.32	0.62	0.66	**	*	0.52
Temperature[#]	0.55	0.06	–	–	–	–	–	–

Trait definitions: pH_i – Initial pH; pH_u – Ultmate ph; L* - Lightness; a* - Redness; b* - Yellowness; CL – Cooking loss; DL – Drip loss; SF – Shear force; [#]Carcass temperature associated with the pH record; – Effect not fitted; * - P<0.05; ** - P<0.01

3.3 *The effect of selection line*

Hoggets from the H line were 5.6% heavier than their L line contemporaries at slaughter ($P < 0.01$; Table 4). The comparable difference in carcass weight amounted to 15.0%. These differences in live weight are consistent with results of previous slaughter trials on the divergently selected lines (Cloete et al., 2004b; 2005). Genetic trends in hogget weight also suggested that H line progeny should be heavier than their L line contemporaries at yearling age (Cloete et al., 2005). This result should not be surprising, based on the known positive genetic correlation of hogget weight with reproduction rate in general, but also specifically with number of lambs weaned (Safari et al., 2005; 2007). A similar positive genetic correlation was also previously reported for the mating weight of mature ewes in the flock studied (Cloete et al., 2004c). However, slaughter weight was also affected by a significant ($P < 0.01$) interaction of selection line with birth year (Figure 1). It was noted that the carcases of H line progeny was respectively 26.8 and 11.8% heavier than L line contemporaries in 2015 and 2017. The 2017 line difference was in close correspondence with a previous value of 12% reported by Cloete et al. (2005). The comparable line difference was much smaller in 2018 and not significant ($P \sim 0.20$). Closer inspection indicated that this interaction could be related to the usage of external sires in the respective selection lines. There were three external rams used in the H line during 2015, all of which had positive within flock breeding values ranging from 0.88 to 2.14 kg for carcase weight. No external rams were used in the L line at this stage. The industry rams in the H line could arguably contribute to the larger than expected line difference in favour of the H line in 2015 (Figure 1). Two external sires, one in each line, both with slightly positive breeding values for carcase weight were used in 2017, suggesting that the impact of external genetics on the 2017 results was minimal, hence the correspondence with previous results. In contrast, two external rams were used in the L line during 2018. One of these had a positive breeding value of 1.53 kg for carcase weight, while the other had a lowly positive breeding value. These rams could have inflated the L line mean for 2018 to be comparable to the H line, also contributing to the observed interaction. It was interesting that this interaction was not noted for live weight or dressing percentage (Table 2). The fact that slaughter weight was not recorded during 2015 with its large external sire influence in the H line probably contributed to this result. Likewise, dressing percentage was only recorded in 2017 and 2018, when line differences in carcase weights were substantially reduced relative to previous years (Figure 1).

In accordance with the present study, previous results also did not report significant differences for fat depth between selection lines (Cloete et al., 2005). The average pH of meat from the H line was lower than that of their L line contemporaries, while their meat was also darker ($P < 0.01$; Table 4). This result was unexpected, as darker meat is generally associated with a high ultimate pH (Greeff et al., 2008; Brito et al., 2017; Naudé et al., 2018). It is notable that dark-cutting, high pH meat is generally accepted to be indicative of chronic long-term stress (Lawrie, 1998). In this respect it has been suggested that the hypothalamus-pituitary-adrenal axis of sheep in the H line was adapted to better cope with stress compared to the L line (Hough et al., 2015). Behavioural observations also indicated that H line progeny found flock-isolation in a contrived arena test less stressful than L line contemporaries, as indicated by fewer urination and defecation events as well as a willingness to approach a stationary human situated between the tested animal and its flock mates closer in comparison to L line contemporaries (Cloete et al., 2017). A later, more comprehensive study reported that the line difference in urination and defecation events persisted while H line progeny also bleated less than L line contemporaries (Cloete et al., 2020). Interestingly the line difference in the distance from the human operator was reduced to a tendency (P < 0.10) in the latter study, with a similar selection line x birth year interaction as reported for carcass weight. This interaction could also be related to the introduction of external genetics, as in the present study (Cloete et al., 2020).

Table 4

Predicted means (±SE) depicting the effects of selection line (High or Low) on the quantitative and qualitative slaughter traits recorded on Merino hoggets of the High- and Low reproduction lines

Trait	High selection line	Low selection line
Quantitative traits:		
Slaughter weight (kg)	39.5 ± 0.3^b	37.4 ± 0.8^a
Carcass weight (kg)	16.1 ± 0.2^b	14.0 ± 0.5^a
Dressing percentage (%)	41.2 ± 0.2	40.1 ± 0.6
Fat depth (13th rib) (mm)	1.10 ± 0.04	1.03 ± 0.10
Fat depth (rump) (mm)	1.94 ± 0.06	1.82 ± 0.16
Qualitative traits:		
Initial pH	6.55 ± 0.02	6.54 ± 0.04
Ultimate pH	5.86 ± 0.02^a	5.98 ± 0.05^b
Lightness (L*)	33.8 ± 0.2^b	35.0 ± 0.4^b
Redness (a*)	12.2 ± 0.1	11.5 ± 0.2
Yellowness (b*)	9.9 ± 0.1	10.1 ± 0.2
Cooking loss (%)	29.8 ± 0.2	29.6 ± 0.5
Drip loss (%)	1.33 ± 0.02	1.30 ± 0.06
Shear force (N)	41.3 ± 0.7	39.9 ± 1.9

^{a,b} – Different superscripts denote significant differences (P<0.05) between selection lines

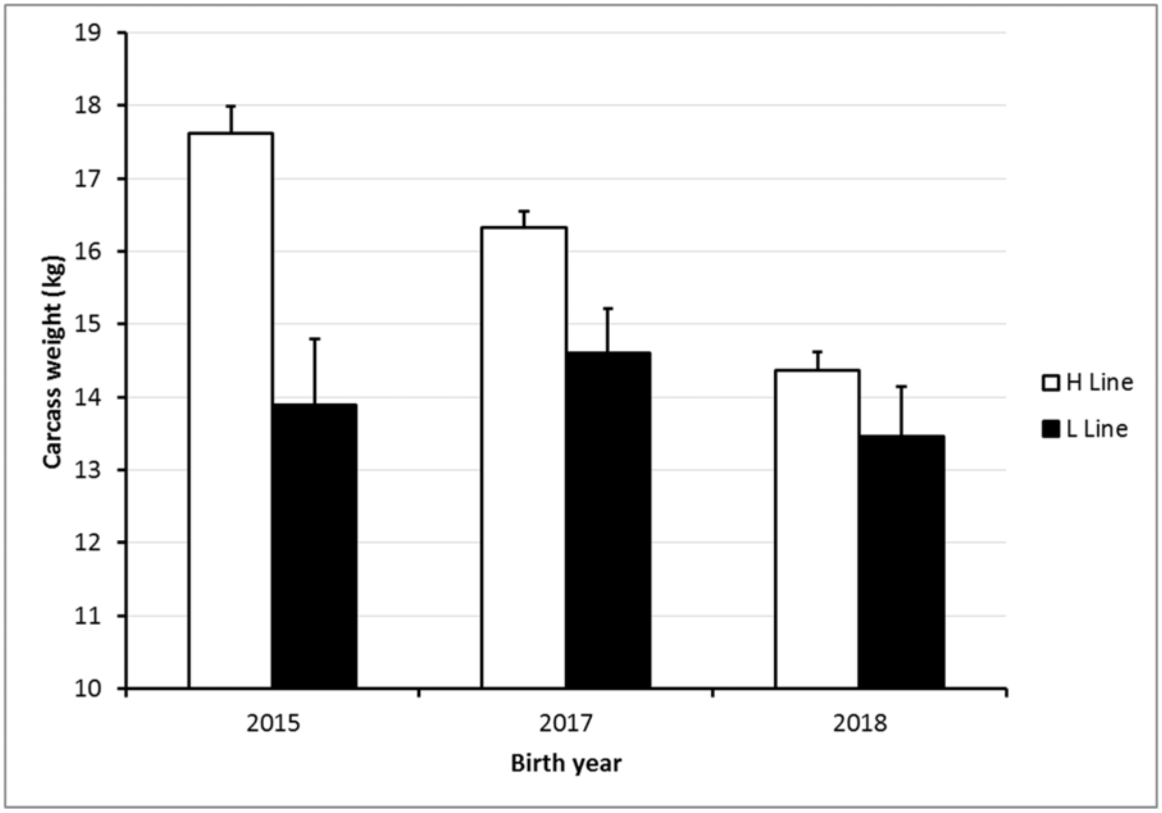

Figure 1. Predicted means (positive error bar representing SEs) depicting the interaction between selection line (H or L Line) and birth year for carcass weight

It is not clear at present why the well-known relationship of a high pH and dark colour does not seem to apply to the H line and further research is suggested. It is noteworthy that the values of lightness in both lines were still acceptable. Previous studies on the genetic resource did not uncover line differences for either ultimate pH (Hoffman et al., 2003; Cloete et al., 2005) or lightness (Cloete et al., 2005). The latter study, however, reported that meat from the H line was redder than that of the L line. A similar tendency was reported in this study ($P = 0.06$) but selection line interacted ($P < 0.05$) with sex for redness. With a predicted mean of 12.9 ± 0.02, H line ewe hoggets had redder ($P < 0.05$) meat than H line rams (11.3 ± 0.01), L Line rams (11.4 ± 0.02) and L Line ewes (11.7 ± 0.04). No significant differences were found among the latter three groups. It thus seems that the line difference for redness was mostly driven by a more vividly red colour in the meat of H line ewe hoggets in the present study. The underlying biology of this result is not known at present.

The other traits were independent of selection line ($P > 0.10$). These results are consistent with previous results reported by Hoffman et al. (2003) for cooking loss and drip loss and Cloete et al. (2005) for yellowness, cooking loss, drip loss and shear value. Hoffman et al. (2003) reported that the meat of H line hoggets was tougher than that of their L line contemporaries. However, it should be noted only 10 animals of each line was sampled in the latter study and inferences should be made with caution.

3.4 The effect of sex

Sex interacted (P < 0.05) with birth year for the vast majority of traits analysed (Tables 2 and 3). This interaction was not unexpected, as ewe and ram hoggets grazed in separate flocks for at least 7 to 8 months prior to slaughter. It is understandably challenging to provide exactly the same conditions for animals grazing in separate flocks. Similar results are common in the sheep literature (Matebesi et al., 2009). However, ram hoggets were overall heavier with a higher carcass weight than ewes (Table 5). These observations are consistent with trends generally found in the literature (Kirton et al., 1982; Cloete et al., 2004a; 2004b; Cloete et al., 2005; Okeudo and Moss, 2008; Van der Merwe et al., 2020). As the mature body weight of females is generally lower than that of males, females reach mature weight earlier than males (Hossner, 2005). Okeudo and Moss (2008) found that the growth rate of rams was 11.5 g/d more than that of ewes. This difference in the rate of live weight gain resulted in rams reaching slaughter weight earlier than ewes.

Table 5

Predicted means (±SE) depicting the effects of sex (ram or ewe) on the quantitative and qualitative slaughter traits recorded on Merino hoggets of the High- and Low reproduction lines

Trait	Rams	Ewes
Quantitative traits:		
Slaughter weight (kg)	41.2 ± 0.5^{b}	35.7 ± 0.7^{a}
Carcass weight (kg)	15.6 ± 0.2^{b}	14.5 ± 0.4^{a}
Dressing percentage (%)	38.4 ± 0.3^{a}	42.8 ± 0.5^{b}
Fat depth (13^{th} rib) (mm)	0.86 ± 0.06^{a}	1.27 ± 0.09^{b}
Fat depth (rump) (mm)	1.60 ± 0.09^{a}	2.16 ± 0.14^{b}
Qualitative traits:		
Initial pH	6.58 ± 0.02	6.51 ± 0.04
Ultimate pH	5.93 ± 0.03	5.91 ± 0.04
Lightness (L*)	34.8 ± 0.2^{b}	34.0 ± 0.4^{a}
Redness (a*)	11.4 ± 0.1^{a}	12.3 ± 0.2^{a}
Yellowness (b*)	10.1 ± 0.1	9.9 ± 0.2
Cooking loss (%)	29.6 ± 0.3	29.8 ± 0.5
Drip loss (%)	1.28 ± 0.03^{a}	1.35 ± 0.06^{b}
Shear force (N)	39.5 ± 0.7^{a}	41.6 ± 1.2^{b}

^{a,b} – Different superscripts denote significant (P<0.05) differences between sexes

Ewe lambs recorded a higher dressing percentage and an increased fat depth compared to rams. These results are consistent with those generally found in literature (Kirton et al., 1982; Teixeira et al., 1996; Cloete et al., 2004a; 2004b; Cloete et al., 2005a; Van der Merwe et al., 2020). In contrast, Peña et al. (2005) observed that sex had no effect on dressing percentage. This apparent discrepancy may be explained by the relatively low live weight of sheep (19 – 25 kg) slaughtered in their study. The meat of ewe hoggets was darker and redder than that of rams (Table 5). Cloete et al. (2008) and Van der Merwe et al. (2020) similarly reported higher lightness values for rams than for ewes. Ewe meat also had a slightly higher drip loss than ram meat. The meat of ewe hoggets had a lower shearing value than that of rams (Table 5). The more tender meat produced by ewes are in accordance with results reported by Bruwer et al. (1987), Koohmaraie (1994) and Hoffman et al. (2003).

3.5 The effect of birth type

Single-born hoggets were heavier ($P < 0.01$) than multiples at slaughter (40.1 ± 0.6 vs. 36.9 ± 0.5 kg), as dressed carcases (15.8 ± 0.4 vs. 14.3 ± 0.3 kg) and single carcases had a thicker fat cover at the 13th rib (1.10 ± 0.03 vs 1.03 ± 0.02 mm) as well as the rump (2.04 ± 0.12 vs 1.72 ± 0.10 mm). Multiple-born carcases also had slightly lighter ($P < 0.05$) meat than carcases of singles (34.1 ± 0.3 vs. 34.7 ± 0.2). All the other traits were independent of birth type ($P > 0.05$). The impact of birth/rearing type on live weight and fat depth has previously been reported in scientific literature (Greeff et al., 2008; Brown et al., 2016) and is well-known. Cloete et al. (2008) also reported that multiple lambs were, on average lighter and leaner than singles.

3.6 The effects of dam age and slaughter age

Slaughter weight was the only trait that was affected by dam age (Table 2). Scrutiny of the means indicated that the progeny of 2-year-old dams were lighter at 36.5 ± 0.6 than those of other dam age classes, ranging from 38.4 ± 0.7 kg for 4-year old dams to 39.9 ± 0.7 kg for 3-year-old dams. No significant differences were found among dam age groups older than 2 years. Brown et al. (2016) fitted dam age as linear and quadratic covariates in their industry-based data set. There results support the contention that slaughter weight reacted in a second-degree polynomial fashion in response to changes in dam age. Significant ($P < 0.05$) regressions of slaughter traits on slaughter age amounted to 0.118 ± 0.008 kg for slaughter weight, 0.045 ± 0.004 kg for carcass weight, 0.0075 ± 0.0010 mm for fat depth at the 13th rib, 0.0100 ± 0.0015 mm for fat depth at the rump, -0.0040 ± 0.0004 for initial pH, -0.0224 ± 0.0050 % for cooking loss and 0.0015 ± 0.0006 % for drip loss. Previous results similarly reported that older lambs were generally heavier than younger ones (Brown et al., 2016).

3.7 Heritability estimates

All quantitative meat traits had heritability estimates in excess of double the corresponding standard error, amounting to 0.44 ± 0.16 for slaughter weight, 0.63 ± 0.15 for carcass weight, 0.34 ± 0.15 for dressing percentage, 0.25 ± 0.11 for fat depth at the 13th rib and 0.29 ± 0.11 for fat depth at the rump. Earlier ovine heritability estimates summarised by Safari et al. (2005) averaged 0.21 to 0.33 for post-weaning weight, 0.20 for carcass weight, 0.42 for dressing percentage and 0.25 to 0.26 for fat depth. Corresponding recent literature estimates for mixed breed populations ranged from 0.22 to

0.60 for slaughter weight, 0.19 to 0.54 for carcass weight and 0.21 to 0.50 for fat depth (Mortimer et al., 2010; 2014; Brown et al., 2016; Brito et al., 2017; Naudé et al., 2018). Brito et al. (2017) estimated the heritability of dressing percentage as 0.25. The corresponding range for Merinos were 0.38 to 0.41 for slaughter weight, 0.35 to 0.37 for carcass weight, 0.21 to 0.25 for dressing percentage and 0.20 to 0.29 for fat depth (Greeff et al., 2008; Mortimer et al., 2017). Given the size of the data set used in the present study, the derived estimates are a fair reflection of literature values, although the estimates reported above were mostly among the higher values.

Among the qualitative meat traits, only lightness was moderately heritable at 0.32 ± 0.12. Estimable heritability estimates for the other traits amounted to 0.12 ± 0.11 for ultimate pH, 0.11 ± 0.09 for redness, 0.04 ± 0.06 for yellowness, 0.05 ± 0.08 for cooking loss and 0.06 ± 0.07 for drip loss. Comparable estimates derived from the early literature by Safari et al. (2005) amounted to 0.18 for pH, 0.16 for lightness, 0.04 for redness and 0.05 for yellowness. More recent estimates for mixed breed populations ranged from 0.08 to 0.47 for pH, 0.18 to 0.31 for lightness, 0.06 to 0.15 for redness and 0.06 to 0.13 for yellowness (Mortimer et al., 2010; 2014; Brito et al., 2017; Naudé et al., 2018). Corresponding values for Merinos were 0.15 to 0.22 for pH, 0.14 to 0.18 for lightness, 0.07 to 0.10 for redness and 0.08 to 0.10 for yellowness (Greeff et al., 2008; Mortimer et al., 2017). These estimates were broadly consistent with corresponding values in the present study. Naudé et al. (2018) reported a higher heritability estimate of 0.34 for cooking loss than the value of 0.05 reported here. The genetic variance for shearing value went to the boundary of parameter space and could not be estimated. However, it is notable that previous heritability estimates ranged from 0.27 to 0.48 in the studies of Mortimer et al. (2010; 2014) and Brito et al. (2017) for mixed breeds. Mortimer et al. (2017) reported a heritability of 0.19 for shear force in Merinos. These results suggest that this trait was indeed heritable, particularly in multi-breed populations.

4. Conclusions

This study confirmed that divergent selection for and against NLW did not compromise quantitative or qualitative meat traits in the study material. Moreover, despite a relatively small database available there was strong evidence that most meat traits were heritable and variable. Selection for improved meat traits should thus be achievable. To achieve industry-wide gains may prove to be challenging though, as no meat traits are formally included in the South African sheep recording system. The best way to achieve gains at the industry level might be to include it in a comprehensively recorded genomic reference population that is well linked to industry genetic resources.

Conflict of interest declaration

The authors declare no conflict of interest that could have influenced the outcome of the research reported herein.

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References

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 Rumin. Res. 154, 81-91. https://doi.org/10.1016/j.smallrumres.2017.07.011

Brown, D.J., Swan, A.A., Gill, J.S., Ball, A.J., Banks, R.G., 2016. Genetic parameters for liveweight, wool and worm resistance traits in multi-breed Australian meat sheep. 1. Description of traits, fixed effects, variance components and their ratios. Anim. Prod. Sci. 56, 1442-1448. https://doi.org/10.1071/AN14787

Bruwer, G.G., Grobler, I., Smit, M., Naudé, R., 1987. An evaluation of the lamb and mutton carcase grading system in the Republic of South Africa. 4. The influence of age, carcase mass and fatness on meat quality characteristics. S. Afr. J. Anim. Sci. 17, 95-103.

Cloete, J.J.E., Cloete, S.W.P., Hoffman, L.C., 2005. Behaviour of Merinos divergently selected for multiple rearing ability in response to external stimuli. Small Rumin. Res. 60, 227-236. https://doi.org/10.1016/j.smallrumres.2004.12.009

Cloete, J.J.E., Hoffman, L.C., Cloete, S.W.P., 2008. Carcass characteristics and meat quality of progeny of five Merino dam lines, crossed with Dormer and Suffolk sires. S. Afr. J. Anim. Sci. 38, 355-366. Ajol.info/index.php/sajas/issue/view/472 (Accessed online on 10 June 2020)

Cloete, J.J.E., Hoffman, L.C., Cloete, S.W.P., Fourie, J.E., 2004a. A comparison between the body composition, carcass characteristics and retail cuts of South African Mutton Merino and Dormer sheep. S. Afr. J. Anim. Sci. 34, 44-50. Doi:10.4314/sajas.v34i1.4040 (Accessed online on 10 June 2020)

Cloete, J.J.E., Hoffman, L.C., Cloete, S.W.P., Fourie, J.E., 2004b. Slaughter traits of Merino sheep divergently selected for multiple rearing ability. S. Afr. J. Anim. Sci. 34, 189-196.

Cloete, J.J.E., Hoffman, L.C., Cloete, S.W.P., 2008. Carcass characteristics and meat quality of progeny of five Merino dam lines, crossed with Dormer and Suffolk sires. S. Afr. J. Anim. Sci. 38, 355-366.

Cloete, J.J.E., Hoffman, L.C., Cloete, S.W.P., 2012. A comparison between slaughter traits and meat quality of various sheep breeds: Wool, dual-purpose and mutton. Meat Sci. 91, 318-324. https://doi.org/10.1016/j.meatsci.2012.02.010

Cloete, J.J.E., Scholtz, A.J., Cloete, S.W.P., 2017. Genetic parameters for arena behaviour of lambs from Merinos divergently selected for lambs weaned per ewe mated. In: Proc. Assoc. Advmt. Anim. Breed. Genet. 22, 577-580. http://www.aaabg.org/aaabghome/AABG22papers/135Cloete22577.pdf

Cloete, S.W.P., Burger, M., Scholtz, A.J., Cloete, J.J.E., Kruger A.C.M. & Dzama, K., 2020. Arena behaviour of Merino weaners is heritable and affected by divergent selection for number of lambs weaned per ewe mated. *Applied Animal Behaviour Science*, in press. https://doi.org/10.1016/j.applanim.2020.105152.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J., Van Wyk, J.B., 2004c. Genetic and phenotypic trends and parameters in reproduction, greasy fleece weight and liveweight in Merino lines divergently selected for multiple rearing ability. Aus. J. Exp. Agric. 44, 745-754. https://doi.org/10.1071/EA02225

Cloete, S.W.P., Olivier, J.J., 2010. South African Sheep and Wool Industry. In: The International Sheep and Wool Handbook. Ed: Cottle, D.J., Nottingham University Press, Manor Farm, Thrumpton, Nottingham NG11 0AX, United Kingdom, 95-112.

Cloete, S.W.P., Olivier, J.J., Sandenbergh, L., Snyman, M.A., 2014. The adaption of the South African sheep industry to new trends in animal breeding and genetics: A review. S. Afr. J. Anim. Sci. 44, 307-321. http://dx.doi.org/10.4314/sajas.v44i4.1

Cloete, S.W.P., Scholtz, A., 1998. Lamb survival in relation to lambing and neonatal behavior in medium wool Merino lines divergently selected for multiple rearing ability. Aust. J. Exp. Agric. 38, 801-811. https://doi.org/10.1071/EA98095

Commission Internationale de l'Eclairage, 1976. 2nd edn, Colometry CIE, Vienna.

Gilmour, A.R., Cullis, B.R., Harding, S.A., Thompson, R., 2016. ASReml Update: What's new in Release 2.00 VSN International Ltd, Hemel Hempstead, HP1 1ES, UK.

Gilmour, A.R., Thompson, R., Cullis, B.R., 1995. Average Information REML: an efficient algorithm for variance parameter estimation in linear mixed models. Biometrics 51, 1440-1450.

Greeff, J.C., 1992. Evaluation of the Finnish Landrace x Merino and the Merino as dam lines in crosses with five sire lines: slaughter and carcass traits of ram lambs. S. Afr. J. Anim. Sci. 22, 207-210. https://www.sasas.co.za/wp-content/uploads/2012/09/Greeff22Issue1_1.pdf

Greeff, J.C., Safari, E., Fogarty, N.M., Hopkins, D.L., Brien, F.D., Atkins, K.D., Mortimer, S.I., Van der Werf, J.H.J., 2008. Genetic parameters for carcass and meat quality traits and their relationships to live weight and wool production in hogget Merino rams. J. Anim. Breed. Gen. 125, 205-215. https://doi.org/10.1111/j.1439-0388.2007.00711.x

Hoffman, L.C., Schmidt, D., Muller, M.M., Cloete, J.J.E., Cloete, S.W.P., 2003. Sensory and objective mutton quality characteristics of SA Merino sheep selected for and against reproductive fitness. S. Afr. J. Anim. Sci. 33, 52-64. https://www.ajol.info//index.php/sajas/article/view/3738

Honikel, K.O., 1998. Reference methods for the assessment of physical characteristics of meat. Meat Sci. 49, 447-457. https://doi.org/10.1016/S0309-1740(98)00034-5

Hossner, K.L., 2005. Hormonal regulation of farm animal growth. CABI Publishing. https://www.cabi.org/bookshop/book/9780851990804/

Hough, D., Storbeck, K., Cloete, S.W.P., Swart, A.C., Swart, P., 2015. Relative contribution of P450c17 towards the acute cortisol response: Lessons from sheep and goats. Mol. Cell. Endocrinol. 408, 107-113. https://doi.org/10.1016/j.mce.2015.01.018

Jorgensen, P., Nel, C.L., Scholtz, A.J., Cloete, S.W.P., 2020. Pedigree analysis of the Elsenburg Merino flock. Agriprobe 17(1), 56-60.

Kirton, A.H., Clarke, J.N., Hickey, S.N., 1982. A comparison of the composition and carcass quality of Kelly and Russian castrate, ram, wether and ewe lambs. Proc. N. Z. Soc. Anim. Prod. 42, 117-118.

Koohmaraie, M., 1994. Muscle proteinases and meat aging. Meat Sci. 36, 93-104. https://doi.org/10.1016/0309-1740(94)90036-1

Lawrie, R.A., 1998. Lawrie's Meat Science. 7th ed. Woodhead Publ. Ltd. Cambridge, England.

Matebesi, P.A., Van Wyk, J.B., Cloete, S.W.P., 2009. Genetic parameter estimation of 16-month live weight and objectively measured wool traits in the Tygerhoek Merino flock. S. Afr. J. Anim. Sci. 39, 73–82. scielo.org.za/pdf/sajas/v39n3/v39n3a02.pdf (Accessed online on 10 June 2020)

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., Ponnampalami, 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 sheep. J. Anim. Sci. 96, 3582–3598. doi: 10.1093/jas/sky232.

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., Ponnampalami, 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. Anim. Prod. Sci. 50, 1135–1144. https://doi-org.ez.sun.za/10.1071/AN10126

Mortimer, S.I., van der Werf, J.H.J., Jacob, R.H., Hopkins, D.L., Pannier, L., Pearce, K.L., Gardner, G.E., Warner, R.D., Geesink, G.H., Hocking Edwards, J.E., Ponnampalami, 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, 1016–1024. https://dx.doi.org/10.1016/j.meatsci.2013.09.007

Naudé, C.S., Visser, C., Hoffman, L.C., Cloete, J.J.E., Cloete, S.W.P., 2018. The genetics of meat traits in South African sheep. In: Proc. 11th Wld. Cong. Gen. Appl. Livest. Prod. http://www.elsenburg.com/sites/default/files/attachments/2018-04/CloeteJJE.pdf (Accessed online on 9 June 2020)

Okeudo, N.J., Moss, B.W., 2008. Production performance and meat quality characteristics of sheep comprising four sex-types over a range of slaughter weights produced following commercial practice. Meat Sci. 80, 522-528. https://doi.org/10.1016/j.meatsci.2008.02.003

Olivier, J.J., 1999. The South African Merino Performance Testing Scheme. Proc. Assoc. Advmt. Anim. Breed. Genet. 13, 119-124.

Peña, F., Cano, T., Domenech, V., Alcalde, M.J., Martos, J., Garcia-Martinez, A., Herrera, M., Rodero, E., 2005. Influence of sex, slaughter weight and carcass weight on ''non carcass" and carcass quality in Segureña lambs. Small Rumin. Res. 60, 247–254. https://doi.org/10.1016/j.smallrumres.2004.12.011

Safari, E., Fogarty, N.M., Gilmour, A.R., 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. Livest. Prod. Sci. 92, 271-289. https://doi.org10.1016/j.livprodsci.2004.09.003

Safari, E., Fogarty, N.M., Gilmour, A.R., Atkins1, K.D., Mortimer, S.I., Swan, A.A., Brien, F.D., Greeff, J.C., Van der Werf, J.H.J., 2007. Genetic correlations among and between wool, growth and reproduction traits in Merino sheep. J. Anim. Breed. Genet. 124, 65–72.

Schoeman, S.J., Cloete, S.W.P., Olivier, J.J., 2010. Returns on investment in sheep and goat breeding. Livest. Sci. 130, 70-82. https://doi.org/10.1016/j.livsci.2010.02.012

Schoeman, S.J., De Wet, R., Van der Merwe, C.A., 1993. Assessment of the reproductive and growth performance of two sheep composites, developed from the Finnish Landrace, compared to the Dorper. S. Afr. J. Anim. Sci. 23, 207-210. https://www.ajol.info/index.php/sajas/article/view/138468 (Accessed online on 9 June 2020)

Teixeira, A., Delfa, R., Treacher, T., 1996. Carcass composition and body fat depots of Galego Bragançano and crossbred lambs by Suffolk and Merino Precoce sire breeds. Anim. Sci. 63, 389-394. https://core.ac.uk/download/pdf/153402910.pdf

Van de Ven, R.J., Pearce, K.L., Hopkins, D.L., 2014. Post-mortem modelling of pH and temperature in related lamb carcases. Meat Sci. 96, 1034–1039.

Van der Merwe, D.A., Brand, T.S., Hoffman, L.C., 2020. Slaughter characteristics of feedlot-finished premium South African lamb: effects of sex and breed type. Foods (Special issue: Sheep and Goat Meat Processing and Quality) 9, 648. https://doi.org/10.3390/foods9050648

Webb, E.C., Casey N.H., 2010. Physiological limits to growth and the related effects on meat quality. Livest. Sci. 130, 33-40. https://doi.org/10.1016/j.livsci.2010.02.008