GENETIC RESPONSES IN COMPONENT AND COMPOSITE REPRODUCTION TRAITS IN MERINO EWES DIVERGENTLY SELECTED FOR NUMBER OF LAMBS WEANED

S.W.P. Cloete[1,2], J.B. van Wyk[3] and J.J. Olivier[2]

[1]Department of Animal Sciences, University of Stellenbosch, Private Bag X1, Matieland, 7602 South Africa
[2]Directorate Animal Sciences: Elsenburg, Private Bag X1, Elsenburg, 7607 South Africa
[3]Department of Animal, Wildlife and Grassland Sciences, University of the Free State, PO Box 339, Bloemfontein, 9300 South Africa

SUMMARY

This study reports phenotypic and genetic parameters and trends for reproduction traits in a Merino flock divergently selected for number of lambs weaned per ewe joined. Three component traits (ewes conceived per ewe joined, lambs born and average lamb weaning weight per ewe reared) and three composite traits (number of lambs born and weaned as well as total weight of lamb weaned, all per ewe joined) were assessed. Most traits were variable and heritable and should respond to selection. Genetic trends suggested divergence between the lines in all traits assessed. Composite trait selection for number of lambs weaned resulted in genetic trends in the desired direction in those component traits considered here.

INTRODUCTION

It is generally accepted that reproduction traits are economically important in sheep. It has been suggested that a trait closely resembling lamb output per ewe joined, termed as net reproduction rate, most closely resembles the breeding objective strived for (Olivier 1999). However, selection decisions are complicated by the composite nature of this trait. Snowder and Fogarty (2009) argued that selection for such a composite trait will ensure that the contributing component traits remain in balance. However, approaches followed to select for reproduction vary in different sheep producing countries (Brien *et al.* 2014). Selection focuses on ewe records and number of lambs weaned in Australia and South Africa. In contrast, in New Zealand selection was based on lamb records, including ewe litter size and lamb survival as separate traits. Bunter and Brown (2015) contended that selection based on a balanced index, including reproduction rate as well as direct and maternal components of lamb weaning weight could potentially yield better and more predictable genetic gains. Against this background, data from a South African resource flock divergently selected for number of lambs weaned per ewe joined were used to study genetic and phenotypic parameters and trends for composite as well as component reproduction traits.

MATERIALS AND METHODS

Animals and selection procedures. Two lines of Merino sheep were divergently selected from the same base population from 1986 to the present, solely using maternal ranking values for number of lambs reared per joining. The selection regime resulted in two lines differing appreciably in reproduction (Cloete *et al.* 2004), termed the High (H) line for the line selected in the upward direction and the Low (L) line for the line selected in the downward direction. Details of the origin of the lines and the procedures for the selection of replacements have been reported elsewhere (Cloete *et al.* 2004; 2009). Only data recorded from 1987 to 2007 were used in this study. Outside sires were since introduced to the flock, to link this genetic resource with the broader South African Merino industry (Cloete *et al.* 2014). The lines are managed as a single flock, except at mating.

Location and data recording. The resource flock is being kept at the Elsenburg Research Farm near Stellenbosch. The climate, pastures grown as well as the management of the animals at joining

in single-sire groups and at lambing were described by Cloete *et al.* (2004; 2009). The composite reproduction traits number of lambs born per ewe joined (NLB_{EJ}), number of lambs weaned per ewe joined (NLW_{EJ}) and total weigh of lamb weaned (pre-corrected for lamb age and sex) per ewe joined (TWW_{EJ}) were recorded (Cloete *et al.* 2004). The component traits number of ewes lambed per ewe joined (EL_{EJ}), number of lambs born per ewe lambed (NLB_{EL}) and average lamb weaning weight per ewe reared (AWW_{ER}) were derived additionally.

   Statistical analyses. The data were analysed for fixed effects to obtain an operational model, fitting the effects of line (H or L), lambing year (1987-2007) and ewe age group (2-7+ years), as well as interactions. Random effects for each trait included additive animal (ewe) effects, ewe permanent environmental (PE) effects to accommodate repeated records and service sire PE (SS). All analyses were conducted in ASREML (Gilmour *et al.* 2015). Fixed effects significant in analyses to determine an operational model were used in downstream analyses. After the appropriate random effects for each trait were determined with Log Likelihood tests, bivariate analyses were conducted to derive correlations between traits for additive genetic, ewe PE and SS effects based on significance in univariate analyses. Genetic trends were constructed from within-line regressions of animal solutions from single-trait analyses excluding selection line (and its interactions with year) on birth year. The pedigree file included 6167 animals, the progeny of 300 sires and 1444 dams.

RESULTS AND DISCUSSION
   Reproduction traits were all highly variable, coefficients of variation ranging from 37-73 % (Table 1). Lamb AWW_{ER}, in contrast, was less variable. These results are consistent with results in the literature (Cloete *et al.* 2004; Safari *et al.* 2005; Bunter and Brown 2015) although the observed coefficients of variation were on the higher end of the ranges reported.

Table 1. Descriptive statistics for the traits analysed on the ewes forming part of the study, namely ewes lambed per ewe joined (EL_{EJ}), number of lambs born per ewe lambed (NLB_{EL}), number of lambs born per ewe joined (NLB_{EJ}), number of lambs weaned per ewe joined (NLW_{EJ}), weight of lamb weaned per ewe joined (TWW_{EJ}) and average weaning weight per ewe reared (AWW_{ER})

Trait	N	Mean	s.d.	CV	Minimum	Maximum
EL_{EJ}	3790	0.86	0.35	40.7	0	1
NLB_{EL}	3256	1.38	0.51	37.0	1	3
NLB_{EJ}	3790	1.19	0.67	56.3	0	3
NLW_{EJ}	3790	0.90	0.66	73.3	0	3
TWW_{EJ}	3790	19.8	14.1	71.2	0	64.8
AWW_{ER}	2756	22.5	4.4	19.6	9.3	46.6

   All traits were affected (P<0.01) by selection line and year (Table 2). Only NLB_{EL} was not affected by interactions between line with year or age, although line x year approached significance. Ewe age affected all traits, except AWW_{ER}. EL_{EJ} and AWW_{ER} were affected by the line x age interaction. Cloete *et al.* (2003) also reported that the composite reproduction traits were independent of this interaction. Least squares means for the component traits EL_{EJ} and NLB_{EL} and the composite trait NLW_{EJ} (Figure 1) all indicated observed divergence between the selection lines. No distinct line differences were observed in the early years of the experiment, but consistent significant differences in favour of the H Line for NLB_{EL} were observed from 1995 (P<0.05). Significant divergence for EL_{EJ} was first observed in 1999 (P<0.05). However, the H Line clearly and consistently outperformed (P<0.05) the L line for NLW_{EJ} from 1993. It is notable that this line difference in NLW_{EJ} were found prior to obvious divergence in the component traits reported here.

Table 2. Significance, using type III p-values, for the fixed effects fitted in the full model to the traits analysed in the study, namely EL_{EJ}, NLB_{EL}, NLB_{EJ}, NLW_{EJ}, TWW_{EJ} and AWW_{ER} (see Table 1 for trait abbreviations)

Effect	Trait					
	EL_{EJ}	NLB_{EL}	NLB_{EJ}	NLW_{EJ}	TWW_{EJ}	AWW_{ER}
Selection line (SL)	**	**	**	**	**	**
Year (Y)	**	**	**	**	**	**
Ewe age (A)	**	**	**	**	**	0.678
SL x Y	**	0.052	**	**	**	**
SL x A	**	0.378	0.223	0.370	0.739	**

* - P<0.05; ** P<0.01; Actual significance for P>0.05
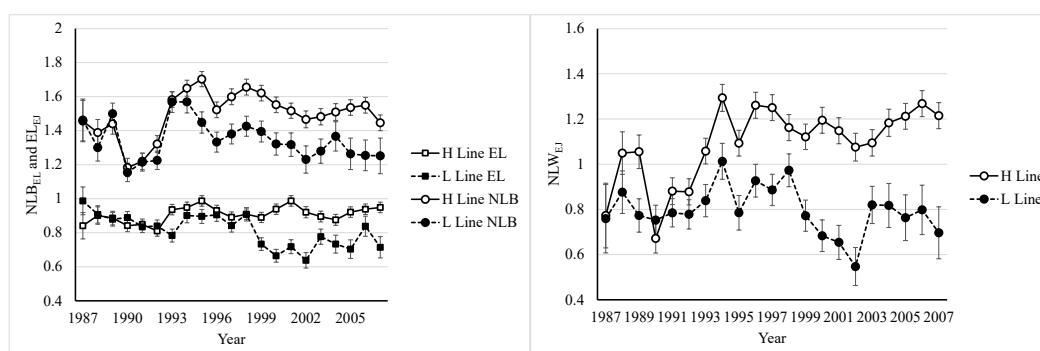
Figure 1. Least squares means (±s.e.) depicting the selection line x year interaction for the component traits EL_{EJ} and NLB_{EL} (left) and the composite trait NLW_{EJ} (right)

All reproduction traits were lowly heritable (Table 3), with estimates below 0.10 except for NLB_{EL} and NLB_{EJ}. The heritability of EL_{EJ} was not significantly different to zero. All traits were affected by animal PE. These results are not presented, but the derived estimates ranged from 0.04±0.02 for NLB_{EL} to 0.14±02 for EL_{EJ}. All traits except for NLB_{EL} were affected by SS. These estimates were small at 0.04±0.01 for EL_{EJ} and 0.02±0.01 for NLB_{EJ}, NLW_{EJ}, TWW_{EJ} and AWW_{ER}. These results were consistent with results reported in the literature (Cloete *et al.* 2004; Safari *et al.* 2005; 2007; Bunter and Brown 2015). Genetic correlations were favourable and significant, except for correlations of all traits with AWW_{ER}, where the estimates were still favourable but commonly smaller than the corresponding s.e. Animal PE and SS correlations among reproduction traits were mostly similar to genetic correlations. However, these correlations became negative with AWW_{ER} for the reproduction traits EL_{EJ}, NLB_{EJ} and NLW_{EJ}. The exception in this respect was PE correlations of TWW_{EJ} with AWW_{ER}. Previous studies also reported favourable genetic correlations among reproduction traits (Cloete *et al.* 2004; Safari *et al.* 2005; 2007; Bunter and Brown 2015) and potentially small or unfavourable correlations with AWW_{ER} (Bunter and Brown 2015).

Linear estimates of genetic trends for the respective traits are reported in Table 4. In terms of composite traits, both lines responded in the expected direction from the selection pressure applied. Expressed relative to the overall least squares mean for the first year with data (1987), the responses in the composite traits were larger in magnitude compared to component traits. Not surprisingly, the responses in the composite traits were consistent in direction and magnitude with previous results in the same resource flock (Cloete *et al.* 2004). The latter authors related the asymmetry in the responses of the H and L lines to an attempt to select against natural selection in the L Line, as well as to a reduced selection differential stemming from the reduced lamb output in the latter line.

Table 3. Phenotypic variance components (σ^2_P) and (co)variance ratios for EL_{EJ}, NLB_{EL}, NLB_{EJ}, NLW_{EJ}, TWW_{EJ} and AWW_{ER} (see Table 1 for trait abbreviations)

Component and trait	Trait					
	EL_{EJ}	NLB_{EL}	NLB_{EJ}	NLW_{EJ}	TWW_{EJ}	AWW_{ER}
σ^2_P	0.117	0.229	0.406	0.399	174.97	17.99
(Co)variance ratios*						
EL_{EJ}	**0.02±0.02**	0.78±0.43	0.78±0.23	0.64±0.32	0.57±0.10	0.16±0.58
NLB_{EL}	0.03±0.03	**0.13±0.03**	1.00±0.05	0.76±0.20	0.66±0.18	0.30±0.22
NLB_{EJ}	0.71±0.01	0.88±0.02	**0.10±0.02**	0.83±0.11	0.72±0.12	0.12±0.27
NLW_{EJ}	0.54±0.01	0.47±0.02	0.64±0.01	**0.04±0.02**	0.96±0.03	0.34±0.37
TWW_{EJ}	0.56±0.01	0.32±0.05	0.57±0.01	0.94±0.01	**0.06±0.02**	0.37±0.44
AWW_{ER}	-0.01±0.03	-0.40±0.02	-0.52±0.02	-0.59±0.01	0.26±0.02	**0.06±0.03**

* Heritability in bold on the diagonal, genetic correlations above the diagonal and phenotypic correlations below the diagonal

Table 4. Genetic trends for EL_{EJ}, NLB_{EL}, NLB_{EJ}, NLW_{EJ}, TWW_{EJ} and AWW_{ER} (see Table 1 for trait abbreviations) expressed relative to trait means in 1987

Trait	High Line*		Low Line*	
	Regression ± s.e.	As % of mean	Regression ± s.e.	As % of mean
EL_{EJ}	0.0047±0.0004	0.50	-0.0028±0.0001	-0.30
NLB_{EL}	0.0114±0.0002	0.76	-0.0035±0.0002	-0.23
NLB_{EJ}	0.0186±0.0002	1.33	-0.0053±0.0003	-0.38
NLW_{EJ}	0.0159±0.0001	1.96	-0.0064±0.0002	-0.79
TWW_{EJ}	0.430±0.004	2.35	-0.147±0.005	-0.81
AWW_{ER}	0.065±0.001	0.29	-0.042±0.001	-0.19

* All regressions were significant (P<0.01)

CONCLUSIONS

This study suggested that composite trait selection for NLW_{EJ} resulted in genetic responses in the desired direction in the component traits studied, as suggested by Snowder and Fogarty (2009). The present study did not include a measure of lamb survival or ewe rearing ability. It is thus important that further studies should also consider these traits (Bunter and Brown, 2015).

REFERENCES

Brien F.D., Cloete S.W.P., Fogarty N.M., Greeff J.C., Hebart M.L., Hiendleder S., Hocking Edwards J.E., Kelly J.M., Kind K.L., Kleeman D.O., Plush K.L. and Miller, D.R. (2014) *Anim. Prod. Sci.* **54**: 667.

Bunter K.L. and Brown D.J. (2015) *Proc. Assoc. Advmt. Anim. Breed. Genet.* **21**: 201.

Cloete S.W.P, Gilmour A.R., Olivier J.J. and Van Wyk J.B. (2003) *S. Afr. J. Anim. Sci.* **33**: 43.

Cloete S.W.P., Gilmour A.R., Olivier J.J and van Wyk J.B. (2004) *Anim. Prod. Sci.* **44**: 745.

Cloete S.W.P., Misztal I. and Olivier J.J. (2009) *J. Anim. Sci.* **87**: 2196.

Cloete S.W.P., Olivier J.J., Sandenbergh L. and Snyman M.A. (2014) *S. Afr. J. Anim. Sci.* **44**: 308.

Gilmour A.R., Gogel B.J., Cullis B.R., Welham S.J. and Thompson R. (2015) ASREML - User Guide Release 4.1. VSN International Ltd, Hemel Hempstead, HP11ES, UK.

Olivier J.J. (1999) *Proc. Assoc. Advmt. Anim. Breed. Genet.* **13**: 119.

Safari E., Fogarty N.M. and Gilmour A.R. (2005) *Livest. Prod. Sci.* **92**:271.

Safari E., Fogarty N.M., Gilmour A.R., Atkins K.D., Mortimer S.I., Swan A.A., Brien F.D., Greeff J.C. and van der Werf J.H.J. (2007) *Aust. J. Agric. Res.* **58**: 177.

Snowder G.D. and Fogarty N.M. (2009) *Anim. Prod. Sci.* **49:** 9.