Studies on the behavioural and genetic aspects of ewe rearing ability and lamb survival in South African sheep flocks

by

S.W.P. Cloete

Dissertation submitted to the Faculty of Natural and Agricultural Sciences,
Department of Animal, Wildlife and Grassland Sciences,
University of the Free State,
in partial fulfilment of the requirements for the degree

PHILOSOPHIAE DOCTOR

Promoter:	Professor G.J. Erasmus
Co-promoters:	Professor J.B. van Wyk Professor S.J. Schoeman

Bloemfontein, November 2002

CONTENTS

Chapter 4: Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and South African Mutton Merino flocks.

Chapter 5: Observations on neonatal progress of Dormer and South African Mutton Merino lambs.

Chapter 6: Ease of birth relation to pelvic dimensions, litter weight and conformation in sheep.

Chapter 12: Genetic and environmental parameters for lambing and neonatal behaviour in Merino lines divergently selected for ewe multiple rearing ability.

Chapter 13: Genetic parameters and trends for birth weight, birth coat score and weaning weight in Merino lines divergently selected for ewe multiple rearing ability.

Preface:

This dissertation reports research work that took place over the period from 1989 to 2002. It is organized as scientific papers. Some of these papers have been published over the period from 1992 to 2002 in various local and overseas journals, while some are still under consideration. Papers already published were replicated with the permission of the relevant scientific journals holding the copyright. I am grateful to the editors of these journals for granting me permission to do this. Changes to such papers were thus limited to the standardization of style and format.

Because of the nature of the thesis, some duplication is unavoidable. Readers may feel bored when they read for the umpteenth time how the lines that were divergently selected for maternal rearing ability were set up, or how the models for genetic analyses looked in matrix notation. Quite a number of references were also duplicated. All I can offer in this respect is my condolences. Because of the time span involved, readers will also find that methods used for statistical appraisal differ between individual papers.

The results were obtained from projects undertaken under the auspices of the Elsenburg Agricultural Centre near Stellenbosch in South Africa. Permission to use the data is gratefully acknowledged.

Prof. Gert Erasmus acted as promoter for this study, while Prof. Japie van Wyk and Prof. Fanie Schoeman were co-promoters. I want to thank these colleagues for their constructive involvement. Apart from the inputs by Japie to the dissertation as such, I am extremely grateful for his assistance in administrative matters. I am notoriously weak in this department.

I am grateful to my colleagues at the Elsenburg Animal Production Division, as well as the students under my supervision, for their support and their patience with me during the course of the study.

This work would be impossible without extensive technical support. I want to express my heartfelt gratitude to all the technical personnel involved (Jaco Fourie, Lizette du Toit, Jan ten Hoope, Farida Martin and Ansie Scholtz) for their dedicated and unselfish service. A special word of thanks to Ansie, for the capturing of all the behavioural data and extensive assistance with the final compilation of the dissertation.

All those involved in the pelvimetry and lambing behaviour studies also deserves a very special word of thanks. I have to especially mention the inputs of Jan ten Hoope, Jasper Cloete, Jaco Fourie, Piet Lombard, Farida Martin and Ansie Scholtz in this respect.

I am grateful to Buks Olivier for his inputs in the papers forthcoming from this research.

I appreciate the assistance I received from Arthur Gilmour with regard to the usage of ASREML.

I want to thank Revenna Barnard for the re-typing of papers already published.

I appreciate the inputs of Tino Herselman with regard to the simulation study reported in Chapter 17. Jasper Cloete did most of the actual simulation runs, and Tertius Brand made some useful suggestions.

The study was partially funded by grants received from the South African wool industry, for which I am extremely grateful.

My late parents afforded me the opportunity to study. This is a gift that I will cherish for the rest of my life.

I gratefully acknowledge the excellent support of my family during the study. I am also thankful for their patience with me during periods of continued absence. My wife, Alta, provided me with subsistence and support during observation periods. Without her continued dedication it would have been impossible for me to undertake this research.

Schalk jr. provided assistance with the observations over an extended period from a very early age.

This dissertation is dedicated to my friend, the late Kevin Haughey, who played a major role in the launching of the research program on lamb survival and ewe rearing ability.

Soli Deo Gloria!

Chapter 1

General introduction

Lamb mortality is seen as a major source of reproductive failure in sheep flocks, and has been the topic of numerous reviews (Alexander, 1984; 1988; Le Neidre *et al.*, 1990; Lindsay *et al.*, 1990; Haughey, 1991). In South Africa, attention was focused on the intensification of the lambing operation to reduce lamb mortality (Brand *et al.*, 1985). Although lamb mortality was reduced ($P < 0.05$) in the latter study, the reduction was only marginal (from 21.9 % to 17.5 %). The main reduction was achieved in deaths from birth to three days, where lamb mortality was nearly halved. The proportion of lambs that succumbed during this time interval was, however, too low at 17.6 % of the total deaths to make a substantial impact on overall lamb rearing performance. The costs of intensification involved extra labour and additional concentrate feeding, making it uneconomic.

To obtain a clearer picture of the levels and causes of lamb mortality on commercial and experimental farms, a major investigation was launched during 1987 and 1988. It was estimated that lamb mortality on individual properties ranged from approximately 10 % to more than 40 % (Haughey, 1989). The majority of deaths were associated with an incompatibility between dam and offspring. The two major classifications involved were parturient deaths and lambs that succumbed showing lesions indicative of starvation, mismothering and/or exposure. Together, these classifications accounted for 84 % of all lambs autopsied. Infection, lethal congenital malformation, ante-parturient deaths and primary predation accounted for the remainder of the lambs, making the contribution of these classifications of minor importance. The findings of the latter investigation by Haughey (1989) led to a number of recommendations:

1) The levels and causes of reproduction failure in commercial sheep flocks in the major sheep producing areas were the first topic worthy of investigation. The contribution of rearing failure to overall failure should also receive attention.

2) The study of rearing failure in relation to maternal pelvic size was also recommended. Results in the literature indicated that repeated rearing failure of Australian sheep flocks were related to small maternal pelvic size in three out of four flocks (Haughey *et al.*, 1985).

3) Breeding studies to investigate the improvement of rearing ability by means of genetic selection were proposed next. At that time, this was a brave suggestion, since indications were that essentially no genetic variation existed for lamb survival (Yapi *et al.*, 1992). Subsequent analyses on local sheep flocks served to confirm this contention (cf. Snyman *et al.*, 1998; Olivier *et al.*, 1998).

4) A number of management studies were proposed. These included the effects of stocking density as well as the period that ewes remained on or near their birth site on the separation of ewes from their lambs, and subsequent lamb mortality (Alexander *et al.*, 1983).

5) Studies on the behaviour of flocks during lambing were recommended. It was suggested that such studies would enable a better understanding of the complexities associated with lamb mortality under typical South African conditions.

Many of the studies reported in this dissertation stemmed from these recommendations. I hope that readers will indeed gain a better understanding of factors associated with lamb mortality among its pages.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay, D.R., Pearce, D.T. (Eds.), Reproduction in Sheep. Australian Academy of Science in Conjunction with Australian Wool Corporation, Canberra, Australia, pp. 199 - 209.

Alexander, G., 1988. What makes a good mother? *Proceedings of the Australian Society for Animal Production* 17: 25 - 41.

Alexander, G., Stevens, D., Mottershead, B.E., 1983b. Problems in the accurate recording of lambing data. *Australian Journal of Experimental Agriculture and Animal Husbandry* 23: 361 - 368.

Brand, A.A., Cloete, S.W.P., De Villiers, T.T., 1985. Factors that influence mortality amongst lambs in the Elsenburg Dormer and SA Mutton Merino flocks. *South African Journal of Animal Science* 15: 155 - 161. (in Afrikaans.)

Haughey, K.G., 1989. Studies on causes of perinatal lamb mortality in the Western Cape and pelvic dimensions of ewes relative to their lifetime rearing performance. Report on activities during a visiting research fellowship 1987-1988, Department of Agriculture and Water Supply, Private Bag, Elsenburg.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Haughey, K.G., George, J., McGuirk, B.J., 1985. The repeatability of rearing performance of Merino and Dorset Horn ewes and its relationship with mature pelvic size. *Australian Journal of Experimental Agriculture* 25: 541 - 549.

Le Neidre, P., Poindron, P., 1990. Physiological and sensory basis of the mother young relationship in sheep. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.), Reproductive Physiology of Merino sheep. School of Agriculture, University of Western Australia, Perth, pp. 179 - 190.

Lindsay, D.R., Nowak, R., Putu, I.G., McNeil, D., 1990. Behavioural interactions between the ewe and her young at parturition. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.), Reproductive Physiology of Merino Sheep. School of Agriculture, University of Western Australia, Perth, pp. 191 - 205.

Olivier, W.J., Snyman, M.A., Erasmus, G.J., Van Wyk, J.B. (1998) Genetic parameter estimates of fitness traits in South African Merino sheep. *Livestock Production Science* 56: 71-77.

Snyman, M.A., Erasmus, G.J., Van Wyk, J.B. 1998. The possible genetic improvement of reproduction and survival rate in Afrino sheep using a threshold model. *South African Journal of Animal Science* 28:120-124.

Yapi, V.V., Boylan, W.J., Robinson, R.A., 1992. Heritability and repeatability estimates and correlations of lamb mortality with birth weight and litter size. *World Review of Animal Production* 27: 55 - 60.

PART 1

Background

Chapters 2 and 3

CHAPTER 2

REPRODUCTIVE PERFORMANCE OF COMMERCIAL MERINO, DOHNE MERINO AND SA MUTTON MERINO FLOCKS IN THE SOUTHERN CAPE

A.J.Fourie[a] and S.W.P.Cloete[b]

[a]Bredasdorp-Napier Co-operative,
Swellendam Road, Bredasdorp 7280,
Republic of South Africa
[b]Elsenburg Agricultural Centre,
Private Bag Elsenburg 7607,
Republic of South Africa

Published in:
South African Journal of Animal Science (1993) 23: 104 – 110

Reproduced with permission of:
South African Journal of Animal Science

Reproductive performance of commercial Merino, Dohne Merino and SA Mutton Merino flocks in the Southern Cape

A.J Fourie
Bredasdorp-Napier Co-operative, Swellendam Road, Bredasdorp, 7280 Republic of South Africa

S.W.P. Cloete
Elsenburg Agricultural Centre, Private Bag, Elsenburg, 7607 Republic of South Africa

Received 29 May 1992; accepted 10 December 1992

Abstract: Data of 23 189 Merino ewes (8 farms), 7 692 Dohne Merino ewes (3 farms) and 2 399 SA Mutton Merino ewes (1 farm) were recorded for the 1988 - 1991 lambing seasons. The udders of ewes present at lamb marking were inspected to differentiate between barren (unlambed), lambed and lost (lambed ewes suckling no progeny), and wet (lambed and suckling ≥ 1 lamb) ewes, using the 'wet and dry' technique. The lambs present at lamb marking were counted, and information regarding number of ewes mated and managerial inputs was recorded. The mean number of lambs marked as a percentage of ewes joined (Lm/Ej) was 87.7% for Merino flocks, ranging between 62.8 - 103.3%. Figures for Dohne Merino flocks were found to be similar, ranging between 75.6 - 113.2% Lm/Ej, with a mean of 92.6%, while Lm/Ej was 112.7% in the SA Mutton Merino flock. Between 72.2% (Merino) and 80.4% (SA Mutton Merino) of joined ewes suckled ≥ 1 lamb at lamb marking. Mean fecundity (estimated number of lambs born as a percentage of ewes lambed) was estimated at 121.6% for Merino ewes, 122.7% for Dohne Merino ewes and 140.2% for SA Mutton Merino ewes. Significant ($P \leq 0.05$) differences in Lm/Ej occurred between Merino and Dohne Merino ewes stocked on different farms. It was attempted to relate these differences to managerial practices (flock size at mating, mating period percentage of rams, the use of vasectomized rams, the use of ultrasonic scanning, and management at lambing). Increasing flock sizes tended to be associated with a decline in Lm/Ej. Reproductive efficiency within flocks was independent of the other managerial practices. Ewes which failed to suckle ≥ 1 lamb to lamb marking during 1988 - 1990 were ear notched (marked). The mean levels of reproductive failure in marked ewes (groups with < 40 marked ewes were excluded) were compared with those of contemporaries without a history of reproductive failure within lambing years and farms. In 15 groups of Merino ewes where this procedure was followed, the number of ewes dry (the total of the unlambed and lambed and lost categories) as a percentage of ewes present at lamb marking (Ed/Epm) was 33.7% compared to 24.2% for the 15 groups of contemporaries of these ewes ($P \leq 0.05$). In four groups of Dohne Merino ewes, Ed/Epm was 32.8% for marked ewes and 21.5% for their contemporaries ($P = 0.06$). It was concluded that there was scope for the improvement of the reproductive efficiency of local woolled sheep flocks. Selection against reproductive failure by using the simple 'wet and dry' technique appears to be a low-input method for the improvement of reproductive performance in commercial sheep flocks, at least in the current flock. Results from the literature suggest that such selection will also benefit future generations.

Keywords: Management, repeated failure, reproductive performance, sheep.

Introduction

More than two decades ago, Hofmeyr and Boyazuglo (1965) reported that the national sheep population weaned 65 lambs per 100 ewes mated. More recently, de Klerk *et al.* (1983) estimated the proportion of lambs born per ewe mated to be 74% for woolled sheep and 71% for Merinos. Preweaning lamb mortalities will reduce these figures even further, suggesting that high levels of reproductive failure occur in local sheep flocks. Since these studies were based on survey information, the precise level of reproductive failure in commercial flocks remains unknown. Programmes aimed at reducing reproductive failure require aetiological information in order to succeed.

The purpose of this study was to acquire objective information on the reproductive efficiency of commercial Merino, Dohne Merino and SA Mutton Merino ewes in the Bredasdorp district. It was also attempted to relate managerial aids employed by Merino farmers to the level of performance in their flocks. Lastly, the contribution of repeated reproductive failure to flock performance was investigated in a sub-sample of Merino and Dohne Merino ewes. The potential use of selection for ewe rearing performance was assessed in this part of the study. Preliminary conclusions for a sub-sample of Merino ewes were previously published (Fourie and Cloete, 1990).

Material and Methods

Location and climate

The investigation was conducted on 12 commercial farms in the Bredasdorp, Klipdale, Protem and Napier districts and the Strandveld area of the Bredasdorp district in the Southern Cape. The area is situated between latitude 20 - 21°E, and longitude 34 - 35°S. The climate is temperate with a mean annual precipitation of 390 - 450 mm. Most of the rain is recorded in winter, with 58 - 65% of the total rainfall being recorded from April to September. Occasionally, good summer rains also occur. The mean minimum and maximum temperatures vary between 5 - 8°C and 16 - 18°C in winter and between 15 - 18°C and 26 - 28°C in summer, respectively (Agrometeorology, 1989). The districts are situated in a cropping/pasture region, and sheep are mainly dependent on dryland lucerne pasture and winter cereal crop residues (mainly wheat and barley stubble lands). Dryland medics, clovers and oats are occasionally produced as winter pastures. Frost seldom causes mentionable damage to pastures and crops.

Animals

Of the 12 farms included, 8 were stocked with Merinos, 3 with Dohne merinos and 1 with SA Mutton Merinos (see Table 1). In total, the study included joining records of 23 189 Merino ewes, 7 692 Dohne Merino ewes and 2 339 SA Mutton Merino ewes over the period 1988 - 1991.

Table 1 Description of data relative to breed, farm, year, lambing season and number of ewes joined.

Breed	Farm	District	No. of times recorded	Lambing season and year	Number of ewes joined/season	
					Mean	Range
Merino	1	Bredasdorp	4	March '88, May '89, July '90 – '91	972	920 – 1 006
	2	Bredasdorp	4	March '88 – '91	1 453	1 351 – 1 528
	3	Bredasdorp	3	March '88 – '90	1 221	1 119 – 1 401
	4	Bredasdorp	4	March '88 – '91	751	660 – 843
	5	Napier	3	March '88 – '90	563	519 – 638
	6	Protem	3	March '88 – '90	390	382 – 398
	7	Protem	4	March '88 – '91	420	394 – 446
	8	Klipdale	7	March, July '88 – '91[a]	326	253 – 427
Dohne Merino	1	Bredasdorp	4	March '88 – '91	487	325 – 564
	2	Napier	3	March '88 – '90	820	478 – 1 139
	3	Strandveld	3	March '88 – '90	1 095	1 059 – 1 121
SA Mutton Merino	1	Strandveld	4	March '88 –'91	585	368 – 755

[a] – Exluding the July 1990 lambing season for which no data were available

Data recorded

Each farm was visited at lamb marking, which took place 4 - 6 weeks after lambing. The udders of all ewes present at lamb marking were visually appraised and manually palpated, using the simple 'wet and dry' technique (Luff, 1980; Haughey, 1991). Ewes were allocated to three groups, namely ewes which had not lambed (barren ewes), ewes which had lambed but lost all the progeny born (lambed and lost ewes), and ewes which had suckled ≥ 1 lamb to lamb marking (wet ewes). The number of ewes in each category and lambs present at lamb marking were recorded. Details regarding the number of ewes mated, duration of mating, ram percentage, mating regime, the use of vasectomized rams for synchronization (Signoret, 1990), and flock sizes at mating were recorded for each farm. Management system at lambing, the use of ultrasonic scanning (Herbst, 1990) and flock size at lambing were also recorded. Data were available for all farms over the period 1988 - 1990, but in 1991 data were not recorded for 5 farms (3 stocked with Merinos and 2 with Dohne Merinos, *cf.* Table 1).

Ewe deaths were calculated as the difference between ewes joined and ewes present at lamb marking. An estimate was also made of the number of lambs born, by expressing the number of lambs present at lamb marking as a percentage of the number of wet ewes, to obtain an indication of fecundity. This figure was then applied to all the lambed ewes (lambed and lost ewes as well as wet ewes) to estimate the number of lambs born. Ewe deaths, ewes which lambed, the estimated number of lambs born, wet ewes at lamb marking and lambs present at lamb marking were expressed as percentages of ewes joined on a within-flock basis. The calculated number of lambs born and the lambed and lost ewes were similarly expressed as percentages of ewes lambed. These calculations were used as minimum estimates of fecundity and lamb mortality, respectively (Haughey, 1991).

In most flocks, ewes falling into the barren and lambed and lost categories were differentially ear notched in 1988 - 1990. In subsequent years, these ewes were used to obtain information on the importance of repeated reproductive failure by a minority of ewes to overall flock performance. Since this study deals with reproductive failure in its totality, ear-notched ewes were designated to two groups only, *viz.* wet (suckled ≥ 1 lamb) or dry (failed to suckle a lamb). The percentage of ear-notched ewes failing to suckle a lamb in subsequent seasons was then expressed on a 'per ewe present at lamb marking' basis, and compared to the same parameter in contemporaries without a previous record of rearing failure (i.e. not ear-notched). These ewes also included maidens without previous lamb rearing experience.

Statistical analyses

Reproduction figures within farms, years, and seasons were used as replications within breeds. Means, standard deviations and ranges in reproductive efficiency were calculated for the respective breeds. Data for the Merino and Dohne Merino breeds were normally distributed, and no transformation was made. Between-group comparisons were analysed by standard one-way analysis of variance procedures (Snedecor and Cochran, 1967), with pair-wise comparisons performed by the protected l.s.d. procedure. It should be stated that management regimes, in general, were confounded with property within breeds, making it difficult to discern between the managerial skill of the farmer and the practices followed on the farm. The results with regard to the influence of a number of management practices (mating regime, the use of vasectomized rams, ultrasonic scanning, lambing management) should be seen against this background. *Chi*^{2} procedures (Snedecor and Cochran, 1967) were used to compare the proportions of dry (lambed and lost and barren categories) ewes amongst previously marked ewes within groups with contemporaries without a previous history of reproductive failure. Analysis of variance was used to compare the mean performance of marked ewes with unmarked contemporaries across farms and years and within breeds.

Results and Discussion

Mean levels of performance

Flock size at mating ranged between 253 and 1 528 breeding ewes (Table 2). Mean levels of ewe deaths ranged between 0.53 and 2.8% for the three breeds with the highest level of 5.9% deaths occurring in a Merino flock. Under Australian conditions, mean levels of ewe deaths were reported to be somewhat higher, namely 4.4 - 5.3% in Western Australian ewe flocks (Knight *et al.*, 1975), 4 - 5% for autumn and spring lambing ewes in New South Wales (Plant, 1984), and 7.3% for Merino flocks in Queensland (Jordan *et al.*, 1989). In the last study, a mean level of 15.7% was reported for ewe losses in lambing seasons with limited grazing, with a death rate as high as 36% occurring in one flock.

The number of ewes lambed as a percentage of ewes joined (El/Ej) exceeded 80% in all three breeds (Table 2), with the lowest figure (65.1%) being observed in a Merino flock. In the Dohne Merino flocks and the SA Mutton Merino flock under observation, El/Ej exceeded 81% on all occasions. In the study of Knight *et al.* (1975), the failure of mated ewes to lamb was found to be a major source of reproductive wastage, ranging from 20.1 - 26.4%. A further 2.2 - 4.4% of available ewes failed to mate, to bring reproductive losses owing to barrenness to *ca.* 25% of ewes mated. Plant (1984) similarly reported a mean percentage of 27% barren ewes in autumn lambing flocks. In other studies, El/Ej tended to be higher, e.g. > 90% in the study of Jordan *et al.* (1989), whereas only 4% (ranges 1 - 14%) of ewes were barren in the study of Kelly (1982) in New Zealand.

The number of ewes which suckled at least one lamb as a percentage of ewes joined (Ew/Ej) ranged between 72 and 80% for the respective breeds (Table 2). In general, roughly three ewes suckled ≥ 1 lamb at lamb marking for every four ewes joined.

Table 2 Means, standard deviations and ranges in reproductive efficiency of commercial Merino, Dohne Merino and SA Mutton ewe flocks in the Bredasdorp and Napier districts.

	Breed		
Parameter	**Merino**	**Dohne Merino**	**SA Mutton Merino**
Number of replicates (farms)	32 (8)	10 (3)	4(1)
Flock size (n)			
Mean	724	792	585
Range	253 - 1 528	325 - 1 121	368 – 755
Traits expressed per ewe joined (%)			
Ewe deaths (Ed/Ej)			
Mean ± *SD*	2.8 ± 1.7	2.0 ± 1.9	0.53 ± 0.51
Range	0 - 5.9	0.5 - 7.1	0 - 1.2
Ewes lambed (El/Ej)			
Mean ± *SD*	81.4 ± 6.8	86.2 ± 3.3	92.0 ± 2.1
Range	65.1 – 94.2	81.6 – 91.7	88.9 – 93.4
Ewes wet (Ew/Ej)			
Mean ± *SD*	72.2 ± 7.7	75.3 ± 5.2	80.4 ± 1.3
Range	52.3 – 87.8	69.5 – 85.2	79.1 – 82.0
Lambs born (Lb/Ej)			
Mean ± *SD*	98.9 ± 10.0	105.9 ± 10.5	128.9 ± 7.8
Range	78.1 – 109.6	89.8 – 121.7	121.9 – 139.7
Lambs present at lamb marking (Lm/Ej)			
Mean ± *SD*	87.7 ± 10.2	92.6 ± 11.9	112.7 ± 8.2
Range	62.8 – 103.3	75.6 – 113.2	104.7 – 124.2
Traits expressed per ewe lambed (%)			
Lambs born (Lb/El)			
Mean ± *SD*	121.6 ± 7.7	122.7± 10.7	140.2 ± 11.5
Range	100.3 – 133.8	108.4 – 136.3	131.2 – 157.0
Ewes lambed and lost (El/El)			
Mean ± *SD*	11.3 ± 4.0	13.7 ± 3.7	12.5 ± 1.5
Range	20.3 – 4.1	21.6 – 5.6	14.0 – 11.0

Plant (1984) correspondingly reported that 53% and 68% of autumn and spring lambing ewes, respectively, eventually reared ≥ 1 lamb. The number of lambs born as a percentage of ewes joined (Lb/Ej) ranged between 99 and 129% for the breeds included in the present study. Fecundity (the number of lambs born as a percentage of ewes lambed; Lb/El) was similarly estimated at 122 - 140%. Since these results serve merely to establish minimum performance levels in the flocks investigated, it will not be discussed in detail. It should be mentioned that average levels of performance in the study of Knight *et al.* (1975) were somewhat lower than in the present study. Kelly (1982) reported a mean figure of 141.2% for Lb/El in sheep flocks in New

Zealand. This figure is somewhat higher than our estimates for Merino and Dohne Merino ewes, but in correspondence with the figure for SA Mutton Merino ewes.

There was remarkable correspondence between the three breeds investigated, regarding the number of ewes which lambed and lost all progeny as a percentage of ewes lambed (El/El) (Table 2). From these results, a minimum level of *ca.* 12 - 14% could be estimated for lamb mortality in these flocks. Although this estimate accords fairly well with previous reports of Hofmeyr and Boyazuglo (1965) and Haughey (1989), it does not make provision for the differential mortality figures for multiple lambs when compared to singles (Hight and Jury, 1970; Dalton *et al.,* 1980). It is also reasonable to assume that at least some of the ewe deaths that occurred between joining and lamb marking were associated with lamb deaths owing to dystocia, mastitis, pregnancy toxaemia, or other causes. Results published by Plant (1984) and Jordan *et al.* (1989), nonetheless suggest higher mean percentages of lambed and lost ewes in their investigations. In the study of Jordan *et al.* (1989), it was reported that up to a mean of 58.9% of lambed ewes lost all progeny born up to lamb marking in lambing seasons with limited grazing. Fiss *et al.* (1991) similarly concluded that preweaning death loss is the most important factor affecting productivity in Canadian sheep flocks.

The number of lambs marked as a percentage of ewes joined (Lm/Ej) in the highest producing Merino flock was 64% higher when expressed relative to the lowest producing Merino flock (Table 2). In the Dohne Merino breed, the corresponding value was found to be 50%. This variation is, however, small compared to the four- to fivefold variation in Lm/Ej reported by Plant (1984). In the study of Jordan *et al.* (1989), Lm/Ej similarly ranged between 10 and 115% and mean values for good, average and poor seasons at lambing were 89.2, 71.0 and 52.7%, respectively. The average levels of performance in our study were somewhat better than those reported in Australia (Knight *et al.,* 1975; Plant, 1984; Jordan *et al.,* 1989), but (with the exception of the SA Mutton Merino flock) lower than the mean level of 120.4% for Lm/Ej reported in New Zealand (Kelly, 1982). The difference between Australian and New Zealand results could be related to differences in breed structure and breeding objectives between the two countries. Australian studies mainly involved

Merino sheep, kept predominantly for wool production, whereas dual-purpose and crossbred ewes were used in the New Zealand study.

Influence of farm on reproduction

Since all farms were represented during 1988 - 1990, data for these years were used to investigate the influence of farm on reproduction. Lower ($P \leq 0.05$) means for Lm/Ej in Merinos were observed on farms 2 and 6 compared to the other six farms (Table 3). The poorer performances on these farms could be attributed to lower values for El/Em. Ewes kept on farm 6 also had a lower ($P \leq 0.05$) Ew/Ej than the other flocks. Ewes kept on farm 2 similarly had a lower ($P \leq 0.05$) Ew/Ej than ewes on the highest producing farms. Although the mean fecundity figures on the respective farms did not differ significantly ($P > 0.25$), the lowest absolute mean value was observed on farm 2. In Dohne Merino ewes, Lm/Ej was lower ($P \leq 0.01$) on farm 3 compared to the other farms (Table 3). This difference was largely associated with a lower ($P \leq 0.05$) fecundity on farm 3.

Mean reproductive performance of groups of Merino ewes to the managerial regime under which they reproduced. The mean performance of 20 groups of ewes where vasectomized rams were introduced *ca.* 14 days prior to mating, was similar to results obtained for 12 groups of ewes mated without the use of vasectomized rams. Since most groups were joined in a period of low sexual activity for South African Merino sheep (Boshoff *et al.,* 1975), it was reasoned that, apart from the synchronization of oestrus, the presence of vasectomized rams could stimulate ewes in anoestrus to resume normal oestrous cycles, thus beneficially influencing conception rate. It is impossible to speculate with regard to the level of synchronization achieved in the flocks where vasectomized rams were used (Signoret, 1990), but it clearly did not contribute to a higher biological efficiency. The reproductive performance of 19 groups of ewes subjected to real-time ultrasonic scanning did not differ significantly from that of 13 groups in which no scanning took place. Bowman *et al.* (1989) and Herbst (1990) stressed the importance of ultrasonic scanning as a tool to select for multiple birth rate in sheep. The effect of this indirect advantage of scanning could not be assessed in the present investigation, but it did not contribute markedly to the variation observed between farms.

Table 3 Influence of farm on the mean (± *SE*d) reproductive performance of Merino and Dohne Merino ewes in 1988 - 1990.

Breed and farm	**No. of obser–vations**	**Parameter[1] (%)**					
		Ed/Ej	**El/Ej**	**Ew/Ej**	**Lb/El**	**El/El**	**Lm/Ej**
Merino							
1	3	3.6	86.5^{c}	$74.4^{c,d}$	124.6	14.0	92.8^{b}
2	3	3.9	$77.5^{a,b}$	67.1^{b}	114.2	13.4	75.9^{a}
3	3	4.9	$82.9^{b,c}$	$71.6^{b,c}$	124.1	13.6	88.9^{b}
4	3	3.3	87.5^{c}	81.3^{c}	119.4	7.0	97.1^{b}
5	3	1.3	$83.5^{b,c}$	$75.4^{c,d,e}$	119.2	9.6	89.9^{b}
6	3	3.3	71.8^{a}	60.9^{a}	120.8	15.3	73.6^{a}
7	3	2.9	86.3^{c}	$77.3^{d,e}$	123.5	10.3	95.5^{b}
8	5	1.7	$82.4^{b,c}$	$73.3^{c,d}$	128.1	11.0	93.9^{b}
*SE*d		1.2	2.9	3.3	5.7	2.9	5.1
Dohne Merino							
1	3	1.8	87.9	77.8	129.7^{b}	11.7	100.8^{b}
2	3	1.6	86.2	75.4	130.0^{b}	12.5	98.0^{b}
3	3	0.9	85.0	71.2	109.2^{a}	16.2	77.7^{a}
*SE*d		0.5	3.1	4.1	4.5	3.1	5.7

[1] Ed/Ej = Ewe deaths/Ewe joined; El/Ej = Ewes lambed/Ewe joined;
Ew/Ej = Ewes wet/Ewe joined; Lb/El = Lambs born/Ewe lambed (calculated);
El/El = Ewes lambed and lost/Ewe lambed; Lm/Ej = Lambs marked/Ewe joined.
$^{a-e}$ Denote significance in columns within breeds ($P \leq 0.05$).

The length of the mating period (28 - 60 days), percentage of rams (2 - 4%) and flock size at mating (60 - 320 ewes) were unrelated to El/Ej in 25 groups of Merino ewes and 10 groups of Dohne Merino ewes subjected to flock mating. Mating performance in sheep depends on many factors like ram age (Croker and Lindsay, 1972), paddock size (Allison and Davis, 1976a), ewe age and live mass (Allison and Davis, 1976b) and ram serving capacity (Kilgour, 1980). The percentage of rams used in the present study was well above the minimum of *ca.* 1%, generally considered as sufficient for flock mating (Allison and Davis, 1976a; Fowler, 1982).

Correlations of number of ewes mated with Lm/Ej were –0.33 ($P \approx 0.05$) in 32 groups of Merino ewes and –0.65 ($P \leq 0.05$) in 10 groups of Dohne Merino ewes. Rohloff *et al.* (1982) correspondingly found that flock size decreased with an increase in lamb drop in high performance New Zealand flocks. The relationship between flock size and Lm/Ej was evidently not sufficiently strong to predict flock performance accurately. In Merino ewes, Lm/Ej was also correlated with flock size at lambing (r =

-0.55; $P \leq 0.05$). This correlation was associated with corresponding relations of flock size at lambing with El/Ej, Lb/El and El/El.

Repeated reproductive failure of marked ewes

Fifteen groups of Merino ewes and four groups of Dohne Merino ewes, containing ≥ 40 ewes marked because of prior reproductive failure (6.7 - 29.5% of the total number of ewes present at lamb marking), were compared on the basis of the number of ewes dry as a percentage of ewes present at lamb marking (Ed/Epm) with contemporaries with no history of reproductive failure. Using *Chi*^{2} procedures within farms and years, it was evident that Ed/Epm values in marked ewes were higher ($P \leq 0.10$) than in their unmarked contemporaries in 10 groups (67%) of Merino ewes and two groups of Dohne Merino ewes (Table 4).

Table 4 Performance (ewes dry/ewes present at lamb marking) of ewes marked because of previous reproductive failure in relation to their contemporaries.

			Marked ewes (M)		**Contemporaries ©**			
Breed	**Farm**	**Year**	**No**	**Ed/Ep[a] (%)**	**No**	**Ed/Ep (%)**	**Difference (M – C)**	**Significance[b]**
Merino	1	1989	113	33.6	816	22.7	10.9	*
		1990	75	30.7	835	21.9	9.1	0.10
	2	1989	196	38.3	1 169	35.6	2.7	NS
		1990	261	31.8	1 045	23.0	8.8	**
		1991	327	50.5	1 143	39.4	11.1	**
	3	1989	111	37.8	1 211	23.0	14.8	**
		1990	243	26.3	826	20.6	5.7	0.10
	4	1989	65	33.8	661	13.5	20.3	**
		1990	49	26.5	677	13.9	13.5	*
		1991	89	20.2	717	18.7	1.5	NS
	5	1990	77	26.0	553	24.1	1.9	NS
	6	1989	85	57.6	307	44.0	13.6	*
		1990	108	29.6	258	31.0	-1.4	NS
	7	1991	40	52.5	358	22.1	30.4	**
	8	Jul 1991	41	9.8	382	11.5	-1.7	NS
Dohne Merino								
	1	1989	96	42.7	411	25.5	17.2	**
		1990	40	25.0	488	11.9	13.1	*
	2	1989	122	31.1	703	24.0	7.1	NS
		1990	74	32.4	1 055	24.6	7.8	NS

[a] Ewes dry/Ewes present at lamb marking.

[b] NS – Not significant ($P > 0.10$); 0.10 – significant ($P \leq 0.10$); * - significant ($P \leq 0.05$); ** - significant ($P \leq 0.01$).

When groups of marked Merino ewes were compared with groups of unmarked contemporaries across farms and years by analysis of variance, the mean (± *SE*) Ed/Epm in the former groups (33.7 ± 4.1%) was higher ($P \leq 0.05$) than in the latter groups (24.2 ± 4.1%). A similar tendency ($P = 0.06$) was obtained in Dohne Merino ewes (32.8 ± 4.9 *vs*. 21.5 ± 4.0). From these results it appears that overall flock reproduction would benefit from the culling of ewes which fail to rear ≥ 1 lamb to lamb marking.

Following the reasoning of Lush (1956) as outlined by Turner and Young (1969), the difference in performance between the marked ewes and their unmarked contemporaries should give an indication of the repeatability of reproductive failure in the groups of ewes concerned. The repeatability of reproductive failure was thus estimated at 0.095 for Merino ewes and 0.113 for Dohne Merino ewes. As the reproductive failure in maiden ewes entering the breeding flocks were not previously determined, these figures cannot be regarded as 'true' repeatability estimates. These figures can nonetheless be related to the difference of *ca.* 0.14 lambs weaned/ewe joined found between Merino ewes rearing no lambs at two years of age and contemporaries rearing one lamb in a subsequent study by Cloete and Heydenrych (1987). Piper *et al.* (1982) and Haughey *et al.* (1985) reported that the repeatability of ewe rearing ability (which is part of Ed/Epm) was in the order of 0.10. These results support the contention that repeated reproductive failure in a comparatively small number of ewes add to unsatisfactory performance in the flock as a whole. In studies on rearing failure it was found that a minority of ewes (*ca.* 27%) was involved in roughly 60% of all cases of rearing failure in Australian and South African sheep flocks (Haughey *et al.*, 1985; Cloete and Haughey, 1988).

Conclusions

The mean levels of reproductive performance in the commercial flocks recorded were satisfactory, particularly in comparison to Australian results. Mean figures of 72.2 to 80.4% mated ewes rearing ≥ 1 lamb to lamb marking do, however, suggest ample scope for further improvement. Despite significant differences in reproductive efficiency found between farms within the Merino and Dohne Merino breeds, it was impossible to relate these differences conclusively to specific managerial practices. The managerial skills of the shepherds employed on the respective farms could not be ascertained in this study, but it appears to be of paramount importance. Ewes which were marked because of previous reproductive failure, generally performed poorer than contemporaries without a history of reproductive failure. The culling of such ewes would enhance reproduction in the current flock. Selection for twinning and against reproductive failure in Australia resulted in a marked improvement in overall reproductive efficiency (Atkins, 1980). It is reasonable to assume that the combination of selection for twinning (using ultrasonic scanning) and against reproductive failure (using the 'wet and dry' technique) would lead to similar benefits in South Africa. These methods can be implemented in large commercial flocks with the keeping of minimal records.

Acknowledgement

We thank the participating farmers for their inputs and for the opportunity to use their results in this investigation.

References

Agrometeorology, 1989. Climate statistics for the Winter Rainfall Region up to 1989. Soil and Irrigation Research Institute, Department of Agriculture and Water Supply.

Allison, A.J., Davis, G.H., 1976a. Studies of mating behaviour and fertility of Merino ewes. I. Effects of number of ewes joined per ram, age of ewe and paddock size. *New Zealand Journal of Experimental Agriculture* 4: 239.

Allison, A.J., Davis, G.H., 1976b. Studies of mating behaviour and fertility of Merino ewes. II. Effects of age of ewe, live weight and paddock size on duration of oestrus and ram-seeking activity. *New Zealand Journal of Experimental Agriculture* 4: 269.

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of the Australian Society of Animal Production* 13: 174.

Boshoff, D.A., Gouws, D.J., Nel, J.A., 1975. Die reproduksiepatroon van vyf skaaprasse onder ekstensiewe toestande. *Suid-Afrikaanse Tydskrif vir Veekunde* 5: 37.

Bowman, P.J., Fowler, D.G., Wysel, D.A., White, D.H., 1989. Evaluation of a new technology when applied to sheep production systems. Part II – Real-time ultrasonic scanning of ewes in mid-pregnancy. *Agricultural Systems* 29: 287.

Cloete, S.W.P., Haughey, K.G., 1988. Preliminary note on mature pelvic dimensions and rearing efficiency in Merino ewes. *South African Journal of Animal Science* 18: 171.

Cloete, S.W.P., Heydenrych, H.J., 1987. The repeatability of reproduction rate in the Tygerhoek Merino flock. *South African Journal of Animal Science* 17: 15.

Croker, K.P., Lindsay, D.R., 1972. A study of the mating behaviour of rams when joined at different proportions. *Australian Journal of Experimental Agriculture and Animal Husbandry* 12: 13.

Dalton, D.C., Knight, T.W., Johnson, D.L., 1980. Lamb survival in sheep breeds on New Zealand hill country. *New Zealand Journal of Agricultural Research* 23: 167.

De Klerk, C.H., Düvel, G.H., Terblance, E. le F., 1983. ’n Ondersoek na wolskaapboerdery in die Republiek van Suid-Afrika. Suid-Afrikaanse Instituut vir Landbouvoorligting, Universiteit van Pretoria.

Fiss, C.F., Kemp, R.A., Sullivan, P.G., 1991. Factors affecting productivity of sheep flocks in Ontario. *Canadian Journal of Animal Science* 71: 13.

Fourie, A.J., Cloete, S.W.P., 1990. Reproductive efficiency of breeding ewes in commercial Merino flocks in the Bredasdorp district. *Proceedings of the World Merino Conference* Volume 2: 2 - 4 May 1990, Pretoria. Paper 5.1.

Fowler, D.G., 1982. Mating activity and reproductive performance in Merino flocks where ram percentages are 1.0, 0.5 and 0.25. *Australian Journal of Experimental Agriculture and Animal Husbandry* 22: 268.

Haughey, K.G., 1989. Studies on causes of perinatal lamb mortality in the Western Cape and pelvic dimensions of ewes relative to their lifetime rearing performance. Report on activities during a visiting research fellowship 1987 - 1988, Department of Agriculture and Water Supply, Private Bag, Elsenburg.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78.

Haughey, K.G., George, J.M., McGuirk, B.J., 1985. The repeatability of rearing performance of Merino and Dorset Horn ewes and its relationship with mature pelvic size. *Australian Journal of Experimental Agriculture* 25: 541.

Herbst, I.A., 1990. Ultrasonic scanning of ewes to determine pregnancy status and the incidence of multiple births. *Proceedings of the World Merino Conference.* Volume 2: 2 - 4 May 1990, Pretoria. Paper 20.1.

Hight, G.K., Jury, K.E., 1970. Hill country sheep production. II. Lamb mortality and birth weights in Romney and Border Leicester x Romney flocks. *New Zealand Journal of Agricultural Research* 13: 735.

Hofmeyr, J.H., Boyazuglo, J.G., 1965. Verslag oor die opname by Merino-boere. Ongepubliseerde rapport. Departement Landbou-tegniese Dienste, Pretoria.

Jordan, D.S., Orr, D.M., McMeniman, N.P., Dunlop, I.B., Evenson, C.J., 1989. The magnitude of reproductive wastage to lamb marking in 30 flocks in South-West Queensland. *Australian Veterinary Journal* 66: 202.

Kelly, R.W., 1982. Reproductive performance of commercial sheep flocks in South Island districts. I. Flock performance and sources of wastage between joining and tailing. *New Zealand Journal of Agricultural Research* 25: 175.

Kilgour, R.J., 1980. Serving capacity of rams and flock fertility. *Proceedings of the Australian Society of Animal Production* 13: 46.

Knight, T.W., Oldham, C.M., Smith, J.F., Lindsay, D.R., 1975. Studies in ovine infertility in agricultural regions in Western Australia: analysis of reproductive wastage. *Australian Journal of Experimental Agriculture and Animal Husbandry* 15: 183.

Luff, A., 1980. Final report of the Sheep Fertility Service. NSW Department of Agriculture, Australia.

Lush, J.L., 1956. Query. *Biometrics* 12: 84.

Piper, L.R., Hanrahan, J.R., Evans, R., Bindon, B.M., 1982. Genetic variation in individual and maternal components of lamb survival of Merinos. *Proceedings of the Australian Society of Animal Production* 14: 29.

Plant, J.W., 1984. Is research aimed at industry problems? In: Reproduction in sheep. Eds. Lindsay, D.R. and Pearce, D.T., Australian Acadamy of Science in conjunction with Australian Wool Corporation, Canberra, Australia, 1984, 394.

Rohloff, R.M., Davis, G.H., Hinch, G.N., 1982. Characteristics of high performance flocks in Otago and Southland. *Proceedings of the New Zealand Society of Animal Production* 42: 19.

Signoret, J.P., 1990. The influence of the ram effect on the breeding activity of ewes, and its underlying physiology. In: Oldham, C.M., Martin, G.B. and Purvis, I.W., (Eds.), Reproductive physiology of Merino sheep. School of Agriculture, University of Western Australia, 1990, 59.

Snedecor, G.W., Cochran, W.G., 1967. Statistical methods. Iowa State University Press, Ames, USA.

Turner, Helen N., Young, S.S.Y., 1969. Quantitative genetics in sheep breeding. Ithaca, New York, USA.

CHAPTER 3

REARING PERFORMANCE OF MERINO, SA MUTTON MERINO AND DORMER EWES IN RELATION TO LIVE MASS, REPRODUCTION AND PELVIC DIMENSIONS

S.W.P. Cloete

Elsenburg Agricultural Centre,
Private Bag, Elsenburg 7607,
Republic of South Africa

Published in:
Journal of the South African Veterinary Association (1994) 65: 10 – 17

Reproduced with permission of:
Journal of the South African Veterinary Association

Rearing performance of Merino, SA Mutton Merino and Dormer ewes in relation to live mass, reproduction and pelvic dimensions

S.W.P. Cloete

Elsenburg Agricultural Centre, Private Bag, Elsenburg, 7607, Republic of South Africa

Received June 1993; accepted January 1994

Abstract: Live mass, reproduction and pelvic dimensions (determined mainly by radiographic pelvimetry at more than 4 years of age) were obtained for ewes of the Langgewens Merino flock (n = 102), ewes of the Tygerhoek Merino flock (n = 434) and ewes of the Elsenburg SA Mutton Merino (n = 130) and Dormer flocks (n = 130). Ewes were classified as "good" or "poor" according to their rearing ability (ewes rearing/ewes lambed – Er/El) and rearing performance (lambs reared/lambs born – Lr/Lb) averaged over at least 4 lambings in 4 to 5 lambing opportunities. Good ewes tended to be lighter than poor ewes at 18 months (Merino) or weaning (SA Mutton Merino and Dormer). This tendency was also reflected in live mass at the time of radiography, being significant ($P \leq 0.01$) in Tygerhoek Merinos. Good and poor ewes were similar with regard to fecundity (lambs born/ewes lambed) and lambing percentage (lambs born/ewes joined), but differed ($P \leq 0.01$) markedly with regard to rearing percentage (lambs reared/ewes joined), Er/El and Lr/Lb. Poor ewes constituted 6.9 to 21.7% of the available ewes in the respective flocks, and were involved in 38.9 to 56.9% of all cases of rearing failure. Good ewes had smaller ($P \leq 0.07$) transverse pelvic diameters than poor ewes in the Langgewens Merino and Elsenburg Dormer flocks, while rearing performance was independent of transverse diameter in the other two flocks. Good ewes generally had larger conjugate pelvic diameters than poor ewes, significantly ($P \leq 0.05$) so in the case of the 2 Merino flocks. The area of pelvic inlet of good ewes was larger ($P \leq 0.05$) than that of poor ewes in the Tygerhoek Merino flock and the Elsenburg SA Mutton Merino flock. Phenotypic correlations of conjugate diameter and pelvic area with Er/El and Lr/Lb were, however, too low ($r < 0.20$) for accurate predictions. Pooled repeatability estimates (± *SE*s) for Er/El and Lr/Lb (obtained from the regression of subsequent performance on records at 2 and 3 years of age) amounted to 0.06 ± 0.01 and 0.08 ± 0.03 respectively. It was concluded that conjugate diameter and the area of the pelvic inlet were positively related to flock rearing performance, despite the fact that rearing failure can also be caused by numerous other factors.

Key words: Sheep, lamb mortality, rearing failure, pelvic dimensions, repeatability.

Introduction

Failure of lambs to survive to weaning is seen as an important cause of reproductive inefficiency in sheep flocks (Alexander, 1984; Haughey, 1991). The vast majority of lamb deaths are expected during the perinatal period, defined as the period shortly before, during and within 7 d of birth (Haughey, 1991). Birth problems were implicated in some 60% of 560 lambs that died during the perinatal period in the western and southern Cape Province (Haughey, 1989). Studies on dystocia in sheep demonstrated that ewes with known histories of malpresentations, assistance at birth and stillbirths, had markedly smaller pelvic outlets than contemporaries with good rearing records (Fogarty and Thompson, 1974; McSporran and Fielden, 1979; Quinlivan, 1971). Selection for increased lamb survival was found to result in larger pelvic dimensions and lower percentages of dystocia in the Marshall Romney strain

(Knight *et al.*, 1988). Repeated rearing failure was related to pelvic size on a flock basis in 2 out of 3 Australian sheep flocks (Haughey *et al.*, 1985).

This study concentrated on ewe rearing performance in 4 experimental flocks in the western and southern Cape Province. These flocks differed considerably in fecundity. Rearing performance was related to pelvic dimensions in an attempt to determine the contribution of ewe pelvic size to repeated rearing failure. Preliminary results, involving a small sample of 72 Merino ewes, have been reported previously (Cloete and Haughey, 1988).

Material and Methods

Animals and locations

In order to assess rearing performance, the more fertile ewes from 4 sheep flocks on 3 experimental farms in the winter rainfall area of South Africa were used. Ewes were 5 – 6 years old, and had lambed at least 4 times from 4 or 5 opportunities:

1) Merino ewes (*n* = 102) from a flock maintained on Langgewens, near Moorreesburg. The ewes were born in the period 1983 to 1986, and formed the base population of a selection experiment for number of lambs reared/ewes joined. The ewes were randomly allocated to 2 selection groups in 1988. In subsequent years, these ewes were mated to rams divergently selected on maternal ranking values.
2) Merino ewes (*n* = 434) from the Tygerhoek experimental farm near Riviersonderend were obtained from a selection experiment involving the improvement of clean fleece mass by direct and indirect (for secondary: primary wool follicle ratio – S:P ratio) selection relative to an unselected control group (Heydenrych *et al.*, 1984). Selection on S:P ratio ceased in 1981, but ewes in both selection groups were selected predominantly on clean fleece mass for the period under consideration. These ewes were born during the period from 1981 to 1986.
3) SA Mutton Merino ewes (*n* = 130) were obtained from the Elsenburg stud. The early history of this study was described by Vosloo (1967). The ewes under consideration were born in the period 1980 to 1988.
4) Dormer ewes (*n* = 130) from the Elsenburg stud. The history of this flock has been described by Van der Merwe (1976) and by Van Wyk (1992). The ewes under consideration were born during the period 1980 to 1988.

Selection in the Elsenburg flocks was based mainly on fecundity and conformation at 18 months, although preweaning growth was also taken into consideration. Parturition, lambing behaviour and management of these flocks were recently studied by Cloete (1992).

Data recorded

Records were kept of live mass, pelvic dimensions and reproductive parameters on individual ewes. Live body mass of ewes was recorded at weaning (SA Mutton Merino and Dormer ewes), 18 months (Merino ewes) and at radiographic examination or at slaughter (all ewes). Pelvic dimensions were estimated by radiography in the majority of ewes. In a small number of SA Mutton Merino (n = 12) and Dormer (n = 15) ewes, the dissected pelves were measured after slaughtering since the radiographic equipment in use at that stage was inadequate for accurate measurements on these breeds. All ewes were older than 4 years at radiographic examination or when slaughtered. The radiographic technique (method C) described by Haughey and Gray (1982) was used with regression equations reported by Cloete and Haughey (1990). Pelvic dimensions included the transverse diameter (the distance between the ilia of the pelvis), conjugate diameter (the distance between the sacral promontory and the pecten of the pubis) and the area of the pelvic inlet (the product of the transverse and conjugate diameter).

Reproduction traits included fecundity (lambs born/ewes lambed – (Lb/El), lambing percentage (lambs born/ewes joined – Lb/Ej), rearing percentage (lambs reared/ewes joined – Lr/Ej), ewe rearing ability (ewes rearing at least one lamb/ewes lambed – Er/El) and rearing performance (lambs reared/lambs born – Lr/Lb). Lambs reared to weaning were recorded, except in the Langgewens Merino flock, where survival to lamb marking at approximately 6 weeks of age was noted. No detailed information regarding the cause of death of individual lambs was available for lambs that died prior to lamb marking or weaning. The above mentioned parameters were averaged across lambing opportunities for statistical assessment. Year of birth (previously specified) and birth type (singles or pooled multiples) were known for individual ewes.

Classification of ewes as "good" or "poor" mothers

In order to relate the other parameters to rearing performance, ewes were very broadly classified as good or poor mothers (Cloete and Haughey, 1988; Haughey *et al.*, 1985). The group of ewes with a poor rearing performance failed to rear a lamb at 2 or more lambings, or reared 50% or fewer of lambs born. Ewes with a good performance only failed to rear a lamb at a maximum of one lambing, and reared more than 50% of lambs born. This classification is not entirely satisfactory, as it was done without taking the effects of year of birth, year of lambing, parity and litter size into account. It is, however, seen as the broadest classification to be able to relate rearing performance to live mass and pelvic dimensions.

Statistical analysis

The data were unbalanced, and analysed according to least squares procedures (Harvey, 1990). The fixed models fitted to all 4 data sets included the effects of year of birth, birth type (single or multiple) and rearing classification (good or poor). In case of the Tygerhoek ewes, selection group (clean fleece mass, S : P ratio or control) was also included as a fixed effect in the model. The original models fitted to live mass, pelvic dimension and reproduction data included all fixed effects and 2-factor interactions. Interactions were unimportant, and excluded from the final runs. Reproduction parameters were analysed directly by analysis of variance. This approach was considered valid, since the distribution was largely normalised by the fact that average performance across 4 or 5 lambings was assessed. Live mass at 18 months, or weaning was included as a covariate in analyses on pelvic dimensions where appropriate.

Subsequent reproduction was regressed on rearing ability of lambed ewes rearing at least one lamb compared to no lambs at 2 or 3 years of age in the case of Tygerhoek ewes. This procedure was followed to obtain an indication of the repeatability of rearing performance. Repeatability estimates were derived from the difference between groups of ewes classified according to their performance in a reference year (Turner and Young, 1969). These estimates were pooled for performance at 2 and 3 years, using described procedures (Turner and Young, 1969). The other flocks did not include sufficient numbers for a similar exercise.

Results

Significant ($P \leq 0.05$) differences in live mass, pelvic dimensions and reproduction were obtained in some cases between ewes with different birth years and birth types. Selection group also exerted a significant influence on live mass and pelvic dimensions in the Tygerhoek ewes. This report will, however, emphasise results with relevance to the relationship between rearing performance and the other traits.

Live mass and reproduction of good and poor ewes

Good ewes tended to weigh less than poor ewes at weaning or at 18 months of age. (Table 1). These differences approached significance in the case of Tygerhoek Merino ($P = 0.19$) and Elsenburg Dormer ($P = 0.06$) ewes. A similar tendency was observed for live mass at the time of radiography, with a significant ($P \leq 0.01$) difference for Tygerhoek Merino ewes.

No difference in Lb/El and Lb/Ej was observed between good and poor ewes, although poor SA Mutton Merino ewes tended to have a higher fecundity ($P = 0.14$) (Table 1). The large differences in Lr/Ej, Er/El and Lr/Lb were expected, since it was the basis of classification as good or poor. Ewes classified as good did, however, rear roughly twice as many lambs as their contemporaries classified as poor. It was similarly clear that repeated rearing failure in a minority of ewes was important in all flocks. In the Tygerhoek Merino flock and the Elsenburg SA Mutton Merino flock, for instance, poor ewes constituted respectively 21.7 and 17.7% of the ewes analysed. Yet these ewes were involved in respectively 56.9 and 53.2% of all cases of rearing failure.

In the Langgewens Merino flock and the Elsenburg Dormer flock, rearing performance was generally better than in the other 2 flocks. In spite of being fewer than 10% of the total number of ewes in these flocks, poor ewes were responsible for respectively 39.5 and 38.9% of all cases of rearing failure in these flocks.

Table 1. Least squares means (± *SE*s) for live mass and reproduction parameters for Merino, Dormer and SA Mutton Merino ewes classified on the rearing ability and rearing performance as "good" and "poor" mothers

Breed	**Merino**				**SA Mutton Merino**		**Dormer**	
Location:	**Langgewens**		**Tygerhoek**		**Elsenburg**		**Elsenburg**	
Classification:	**Good**	**Poor**	**Good**	**Poor**	**Good**	**Poor**	**Good**	**Poor**
Number of ewes:	95	7	340	94	107	23	118	12
Live mass (kg):								
weaning	-	-	-	-	30.2 ± 0.8	31.1 ± 0.6	30.6 ± 0.3	32.4 ± 1.0
18 months	42.7 ± 0.5	44.5 ± 1.7	48.5 ± 0.2	49.2 ± 0.5	-	-	-	-
radiography	49.8 ± 0.8	51.9 ± 2.4	50.5^{2} ± 0.3	52.4^{1} ± 0.6	74.1 ± 1.5	74.7 ± 2.4	71.7 ± 1.2	76.0 ± 3.5
Reproduction								
Lambs born/ewes lambed	1.30 ± 0.03	1.26 ± 0.10	1.33 ± 0.01	1.33 ± 0.03	1.85 ± 0.05	1.97 ± 0.08	1.71 ± 0.04	1.77 ± 0.10
Lambs born/ewes joined	1.22 ± 0.03	1.20 ± 0.10	1.22 ± 0.01	1.24 ± 0.03	1.76 ± 0.06	1.80 ± 0.04	1.61 ± 0.04	1.61 ± 0.12
Lambs weaned/ewes joined	1.08^{1} ± 0.03	0.56^{2} ± 0.09	0.97^{1} ± 0.01	0.55^{2} ± 0.02	1.32^{1} ± 0.05	0.75^{2} ± 0.07	1.26^{1} ± 0.03	0.73^{2} ± 0.09
Ewes rearing/ewes lambed	0.94^{1} ± 0.01	0.47^{2} ± 0.04	0.90^{1} ± 0.01	0.50^{2} ± 0.01	0.90^{1} ± 0.02	0.55^{2} ± 0.03	0.93^{1} ± 0.01	0.60^{2} ± 0.03
Lambs reared/lambs born	0.89^{1} ± 0.02	0.46^{2} ± 0.05	0.80^{1} ± 0.01	0.45^{2} ± 0.02	0.75^{1} ± 0.02	0.44^{2} ± 0.03	0.79^{1} ± 0.02	0.45^{2} ± 0.04

^{1,2} Denote significance ($P \le 0.01$) within flocks

Phenotypic correlations for live mass and pelvic dimensions

Phenotypic correlations between transverse and conjugate diameters were low in Merino ewes, barely reaching significance in the Tygerhoek ewes (Table 2). Both dimensions were highly correlated ($r > 0.63$) with pelvic area, as expected. The phenotypic correlations of live mass at 18 months with pelvic dimensions were significant ($P \leq 0.05$), exceeding 0.22 in all cases. Live mass at radiography was correlated with all pelvic dimensions, except conjugate diameter in the Langgewens ewes.

Table 2: Phenotypic correlation matrices$^+$ for pelvic dimensions and live mass in Langgewens (n = 102) and Tygerhoek (n = 434) Merino ewes

Trait	Trait				
	Pelvic dimensions			Live mass (kg)	
	Transverse diameter (cm)	Conjugate diameter (cm)	Pelvic area (cm^2)	Weaning	Radiography
Transverse diameter (cm)		-0.067	0.635^{**}	0.274^{**}	0.299^{**}
Conjugate diameter (cm)	0.133^{*}		0.702^{**}	0.225^{*}	0.042
Pelvic area (cm^2)	0.652^{**}	0.739^{**}		0.357^{**}	0.236^{*}
Live mass (kg): weaning	0.409^{**}	0.320^{**}	0.469^{**}		0.524^{**}
radiography	0.359^{**}	0.300^{**}	0.425^{**}	0.390^{**}	

$^+$ Values for Langgewens above diagonal

$^+$ Values for Tygerhoek below diagonals

*Significant ($P \leq 0.05$)

** Significant ($P \leq 0.01$)

The phenotypic correlation between transverse and conjugate diameters were similarly low in the SA Mutton Merino and Dormer ewes (Table 3). Both dimensions were correlated ($r > 0.46$) with pelvic area. Pelvic dimensions were virtually uncorrelated with live mass in Dormer ewes, while mass was correlated with conjugate diameter and pelvic area in the SA Mutton Merino ewes.

Pelvic dimensions of good and poor ewes

Live mass at 18 months (Merino ewes) or weaning (SA Mutton Merino ewes) was used as covariate, in order to adjust pelvic dimensions for differences in skeletal size. In Dormer ewes, where live mass and pelvic dimensions were uncorrelated, this was considered unnecessary. The regressions of pelvic dimensions on live mass as covariate, were significant ($P \leq 0.05$) where it was fitted, with the exception of transverse diameter in the SA Mutton Merino ewes.

Table 3: Phenotypic correlation matrices$^+$ for pelvic dimensions and live mass in Elsenburg SA Mutton Merino (n = 130) and Dormer (n = 130) ewes

	Trait				
	Pelvic dimensions			**Live mass (kg)**	
Trait	**Transverse diameter (cm)**	**Conjugate diameter (cm)**	**Pelvic area (cm^2)**	**Weaning**	**Radiography**
Transverse diameter (cm)		-0.140	0.622**	0.091	0.081
Conjugate diameter (cm)	-0.075		0.680**	0.295**	0.198*
Pelvic area (cm2)	0.469**	0.834**		0.299**	0.209*
Live mass (kg): weaning	0.112	-0.059	-0.003		0.355**
Radiography	0.017	-0.068	-0.053	0.337**	

$^+$ Values for SA Mutton Merinos above diagonal

$^+$ Values for Dormers below diagonal

* Significant ($P \leq 0.05$)

**Significant ($P \leq 0.01$)

Transverse diameter of good Langgewens Merino ewes tended to be lower (P = 0.07) than in poor ewes (Table 4). Good Dormer ewes had smaller ($P \leq 0.05$) transverse diameters than poor ewes, with an opposite tendency observed in the SA Mutton Merino ewes. The conjugate diameter of good ewes was larger ($P \leq 0.05$) than in poor ewes for the Merino ewes. Similar tendencies were observed in the Dormer and SA Mutton Merino ewes. The pelvic area of good ewes, similarly tended to be larger than in their poor contemporaries, significantly ($P \leq 0.05$) so in the Tygerhoek Merinos and Elsenburg SA Mutton Merinos. The exception in this regard was in the Dormer ewes, where no difference was observed. In this case, a difference ($P \leq 0.05$) in favour of poor ewes, for transverse diameter, was largely cancelled by an opposite tendency in conjugate diameter.

Phenotypic correlations of conjugate diameter and pelvic area with rearing ability and rearing performance were generally positive, but below 0.20 in all cases. Regressions of Er/El and Lr/Lb on ewe conjugate diameter were not significant in the Elsenburg SA Mutton Merino and Dormer ewes. Similar regressions for the Langgewens Merino ewes approached significance ($P \leq 0.18$), and corresponded with those derived for the Tygerhoek Merino ewes (0.048 ± 0.013 Er/El and 0.054 ± 0.014 Lr/Lb per cm increase in conjugate diameter). The only tendency ($P = 0.15$) towards curvilinearity was obtained for Lr/Lb in the Tygerhoek flock. An increase of one cm^2 in pelvic area was associated with respective increases of 0.003 ± 0.001 Er/El ($P \geq 0.05$) and 0.004 ± 0.001 Lr/Lb ($P \leq 0.01$) in the Tygerhoek Merino ewes. Some evidence of a curvilinear response was correspondingly found ($P \leq 0.15$). In the Elsenburg SA Mutton Merinos, both Er/El and Lr/Lb increased ($P \leq 0.05$) by respectively 0.005 ± 0.002 and 0.006 ± 0.002 units per cm^2 in pelvic area. Quadratic regression coefficients were not significant ($P > 0.40$) in this case.

Table 4: Least squares means (± *SE*s) for pelvic dimensions in Merino, Dormer and SA Mutton Merino ewes classified on the basis of their rearing ability as "good" and "poor" mothers

	Pelvic dimension		
Breed, location and classification	**Transverse diameter (cm)**	**Conjugate diameter (cm)**	**Pelvic area (cm^2)**
Merino			
Langgewens			
Good mothers	8.65 ± 0.05	11.74^a ± 0.08	101.5 ± 0.8
Poor mothers	8.93 ± 0.15	11.19^b ± 0.24	99.8 ± 2.4
Tygerhoek			
Good mothers	8.59 ± 0.02	11.65^1 ± 0.04	100.1^a ± 0.4
Poor mothers	8.62 ± 0.04	11.40^2 ± 0.07	98.3^b ± 0.8
Dormer			
Good mothers	10.09^b ± 0.04	11.70 ± 0.08	118.3 ± 0.9
Poor mothers	10.34^a ± 0.11	11.57 ± 0.25	119.8 ± 2.6
SA Mutton Merino			
Good mothers	10.15 ± 0.07	12.18 ± 0.10	123.4^a ± 1.2
Poor mothers	9.99 ± 0.11	11.96 ± 0.16	119.1^b ± 1.9

^{a,b}Significant ($P \leq 0.05$) within flocks

^{1,2}Significant ($P \leq 0.01$) within flocks

Subsequent performance of ewes classified according to their rearing performance at 2 or 3 years

Lambed Tygerhoek Merino ewes that failed to rear a lamb at 2 years, tended ($P = 0.07$) to perform more poorly than contemporaries that reared at least one lamb as far as Lr/Ej was concerned (Table 5). In 3-year-old ewes, this difference was significant ($P \leq 0.01$), amounting to 0.122 Lr/Ej.

Subsequent rearing ability (Er/El) and rearing performance (Lr/Lb) of ewes that lost all progeny born at 2 or 3 years, were poorer ($P \leq 0.05$) than those of ewes that reared at least one lamb (Table 5). When results for an initial age of 2 and 3 years were pooled, repeatability estimates amounted to 0.063 ± 0.010 for rearing ability and 0.083 ± 0.029 for rearing performance.

Table 5: Subsequent performance of lambed Tygerhoek Merino ewes classified according to their rearing performance at 2 or 3 years

Age and subsequent reproduction	**Classification**		**Significance**
	Reared ≥ lamb	**Failed to rear a lamb**	
2 Years:			
Number of ewes	305	105	
Lambs weaned/ewes joined	0.905 ± 0.020	0.835 ± 0.034	0.07
Ewes rearing/ewes lambed	0.837 ± 0.014	0.783 ± 0.024	*
Lambs reared/lambs born	0.760 ± 0.014	0.700 ± 0.024	*
3 Years:			
Number of ewes	376	95	
Lambs weaned/ewes joined	0.883 ± 0.020	0.761 ± 0.039	**
Ewes rearing/ewes lambed	0.833 ± 0.014	0.758 ± 0.029	*
Lambs reared/lambs born	0.758 ± 0.015	0.640 ± 0.029	**

*Significant ($P \leq 0.05$)

**Significant ($P < 0.01$)

Discussion

Live mass and reproduction

There appear to be grounds for suspecting that poor ewes may have had a larger skeletal size than good ewes (Table 1). Poor ewes also tended to be heavier than good ewes, significantly so in the Tygerhoek Merinos. The latter observation was previously ascribed to a better condition in the poor ewes, since they reared fewer lambs (Cloete and Haughey, 1988). Based on the means for earlier live mass in this investigation differences in skeletal size cannot be ruled out with certainty. Contrary to the present findings, New Zealand Romney ewes with a history of dystocia were lighter than ewes with a history of eutocia (McSporran and Fielden, 1979).

Fecundity (Lb/El) and lambing percentage (Lb/Ej) were largely similar in good and poor ewes of all flocks. The marked differences in rearing percentage (Lr/Ej) and rearing ability (Er/El) between these groups did thus not appear to stem from differences in prolificacy. The possible exception in this regard may be SA Mutton Merino ewes, where poor ewes tended to have a higher fecundity.

Differences between breeds were not assessed statistically. It is nonetheless clear that large differences were observed with regard to Lb/El and Lb/Ej. It is also notable that Lb/El in SA Mutton Merino ewes were higher than in Dormers on the same property. Yet this difference was largely eliminated at weaning as was reported previously (Cloete, 1992).

Correlations amongst live mass and pelvic dimensions

For practical purposes, transverse and conjugate diameters were uncorrelated in all flocks (Table 2 and 3). A similar conclusion was reached by several other researchers (Cloete and Haughey, 1988; Fogarty and Thompson, 1974; Haughey *et* al., 1985; Kilgour and Haughey, 1993; McSporran and Fielden, 1979). The high correlations of both diameters with the area of the pelvic inlet were expected, and consistent with reports in literature (Cloete and Haughey, 1988; Fogarty and Thompson, 1974; Kilgour and Haughey, 1993; McSporran and Fielden, 1979; Quinlivan, 1971).

Correlations of all pelvic dimensions with live mass at 18 months, in Merino ewes were significant (Table 2). It thus appears that pelvic dimensions are related to skeletal size in this breed. A similar conclusion was reached for correlations of weaning mass with conjugate diameter and pelvic area in SA Mutton Merinos. Dependency of pelvic dimensions on live mass was also reported in other studies (Cloete and Haughey, 1988; Fogarty and Thompson, 1974; Knight *et al.*, 1988; McSporran and Fielden, 1979) although correlations were not consistently significant in the studies of Fogarty and Thompson (1974) and McSporran and Fielden (1979). Live mass was recorded at the same time as pelvic measurements in the latter studies and that of Knight *et al.* (1988). It is important to note that correlations of live mass at radiography with pelvic dimensions, were generally lower than when an early measurement of live mass was taken. Cloete and Haughey (1988) related this observation to the confounding effect of body condition, which may also be a factor influencing body mass at the time of radiographic examination, whereas earlier live mass was likely to be more directly related to skeletal size. The exception in this regard were the Dormer ewes in this study, where pelvic dimensions were independent of live mass at any stage.

Rearing performance and pelvic dimensions

Ewes classified as good mothers on their rearing performance had smaller ($P \leq 0.08$) transverse diameters than their contemporaries classified as poor in the Langgewens Merino flock and the Elsenburg Dormer flock. In the study of Quinlivan (1971) the mean transverse diameter of 5 ewes with histories of assistance and malpresentations, were larger in absolute terms than that of 6 ewes with good lifetime records (9.46 *vs* 9.22 cm), but no significance could be established. In most other studies, transverse diameter was largely unrelated to rearing performance (Cloete and Haughey, 1988; Fogarty and Thompson, 1974; Haughey *et al.*, 1985). In the Dorset Horn flock reported by Haughey *et al.* (1985), ewes with good lamb rearing ability, had a larger mean transverse diameter than poor contemporaries. Marshall Romney ewes, which were selected for rearing ability, similarly had larger transverse diameters than control Romneys in the study by Knight *et al.* (1988). The results found in the Langgewens Merino flock and the Elsenburg Dormer flock could possibly be related to sampling, since the proportion of poor ewes was low. Results obtained for the Tygerhoek Merino flock and the Elsenburg SA Mutton Merino flock were in accordance with literature findings.

Ewes with good lifetime rearing records, consistently had larger conjugate diameters than contemporaries with poor records, although differences failed to reach significance in the Elsenburg flocks. Literature reports indicate that assistance at birth, malpresentations and dystocia were commonly associated with ewes with small conjugate diameters (Fogarty and Thompson, 1974; McSporran and Fielden, 1979; Quinlivan, 1971). On a flock basis, rearing performance has also been found to be positively associated with conjugate diameter (Cloete and Haughey, 1988; Haughey *et al.*, 1985; Knight *et al.*, 1988).

Ewes that suffer from malpresentations and dystocia, are commonly found to have smaller pelvic inlets than contemporaries not experiencing these problems (Fogarty and Thompson, 1974; McSporran and Fielden, 1979; Quinlivan, 1971). Rearing performance was found to be associated with pelvic area on a flock basis in 2 out of 3

Australian sheep flocks (Haughey *et al.*, 1985). Marshall Romney ewes were similarly found to have larger pelvic areas than control Romneys, after allowance had been made for live mass difference between strains (Knight *et al.*, 1988). A Merino flock, selected for rearing ability, was furthermore recently reported to have larger pelvic dimensions than an unselected control flock (Kilgour and Haughey, 1993). Rearing performance was also related to pelvic area in this investigation, differences being significant ($P \leq 0.05$) in the Tygerhoek Merino and Elsenburg SA Mutton Merino ewes. The exception in this respect was the Elsenburg Dormer ewes, where pelvic size was completely independent of rearing performance. Albeit speculative, this observation could possibly be related to the fact that the Dormer ewes were found to be less likely to experience difficult births than the SA Mutton Merinos on the same property (Cloete, 1992). Further work is, however, required to verify this assessment.

It seems reasonable to expect that rearing performance and conjugate diameter will be positively related in most sheep flocks. Phenotypic correlations of conjugate diameter with ewe rearing ability and rearing performance were, however, too low to predict rearing performance of an individual with a great deal of accuracy. In the review of Haughey (1991), it was suggested that the genetic correlation between conjugate diameter and rearing performance is markedly higher. Regression of Er/El and Lr/Lb on conjugate diameter and pelvic area, were in broad agreement with those reported by Haughey *et al.* (1985). Conjugate diameter and pelvic area were, however also curvi-linearly related to Lr/Lb in the latter study. Quadratic regression coefficients only approached significance ($P = 0.15$) in analyses on the Tygerhoek Merino ewes in the present investigation.

Repeated rearing failure and selection possibilities

Despite constituting only 7 to 22% of available ewes in the respective flocks, ewes classified as poor on rearing performance were involved in 38.9 to 56.9% of all cases of rearing failure. Repeated rearing failure in a minority of ewes was similarly found to contribute largely to unsatisfactory flock performance in other sheep flocks (Cloete and Haughey, 1988; Haughey *et al.*, 1985.

The possibility of using early records to select for improved rearing performance in the current flock was investigated with records of ewes from the Tygerhoek Merino flock. Lambed ewes that reared at least one lamb at 2 or 3 years of age, had better ($P \leq 0.07$) subsequent records for Lr/Ej, Er/El and Lr/Lb than contemporaries that failed to rear a lamb. Although repeatability estimates were not particularly high, it was within the range reported in the literature for rearing performance (Fogarty *et* al., 1985; Haughey *et al.*, 1985; Piper *et al.*, 1982; Shelton and Menzies, 1970). Selection against rearing failure at 2 or 3 years, will thus result in gains, at least in the current flock.

Results from this investigation suggest a positive relationship of pelvic dimensions to rearing performances of ewes. This relationship would presumably have been found to be stronger if rearing failure could have been narrowed down to lambs that died as a result of stressful or prolonged births, as implied by results in sheep (Fogarty and Thompson, 1974; McSporran and Fielden, 1979; Quinlivan, 1971) and cattle (Haughey, 1991; Johnson *et al.*, 1988; Meijering, 1984). Recent findings, where length of parturition was found to be repeatable, with a marked breed difference between Dormer and SA Mutton Merino ewes (Cloete, 1992), also seem to support this contention. The fact that the relationship of rearing ability to pelvic dimensions was not sufficiently strong for accurate predictions, implies that other factors also contribute to lamb deaths. According to the review by Alexander (1984), these include aberrant maternal or fetal behaviour, low resistance to cold, mismothering, inadequate nutrition during late pregnancy, predation, disease, high concentrations of lambing ewes as well as teat and udder abnormalities.

Results from one of the flocks suggested that selection will improve rearing performance, at least in the current flock. This conclusion is in accordance with an emerging school of thought contending that selection for reproductive efficiency should also include a measure of rearing performance (Fogarty, 1984; Haughey, 1991; Lindsay *et al.*, 1990). Selective breeding for rearing ability has been found not only to reduce levels of dystocia and birth stress in Romney sheep (Knight *et al.*, 1988), but also to result in strains with behavioural characteristics conducive to lamb survival (Knight *et al.*, 1988; Lindsay *et al.*, 1990; Putu, 1990). The success of breeding programmes for enhanced lamb survival (Donnelly, 1982; Haughey, 1983) and ewe multiple rearing ability (Atkins, 1980; Cloete and Durand, 1994), should be seen against this background.

There thus appears to be very real prospects of improving ewe rearing-performance by selection. A comparatively simple method, such as the "wet and dry" technique (Fourie and Cloete, 1993) may be used for this purpose. The implementation of such a programme is seen to result in the establishment of "easy care" pasture-fed sheep, adapted to a low-cost environment (Haughey, 1991). These principles also appear to apply to flocks with higher than average prolificacy (Quinlivan, 1981). The adoption of these principles in the local sheep industry, is likely to improve productivity without markedly influencing input costs, resulting in meaningful economic gains for producers.

Acknowledgements

Sincere gratitude is expressed to Dr K G Haughey for stimulating interest in this topic, and for instruction in the technique of radiographic pelvimetry. The assistance of those responsible for the care, management and recording of the experimental flocks is also gratefully acknowledged. P Adams, S Adams, F Franck, P J A Lombard, F Martin, A Scholtz and J M ten Hoope are also thanked for their valuable assistance. This investigation was supported by a grant from the SA Wool Board.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay, D. R., Pearce, D. T., (Eds.), Reproduction in Sheep. Australian Academy of Science in Conjunction with Australian Wool Corporation, Canberra, Australia, pp. 199 - 209

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of Australian Society of Animal Production* 13: 174 - 176.

Cloete, S.W.P., 1992. Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and SA Mutton Merino ewes. *South African Journal of Animal Science* 22: 214 - 221.

Cloete, S.W.P., Durand, A., 1994. A note on the reproduction of Merino sheep subjected to divergent selection for maternal values for lambs weaned per ewe joined. *South African Journal of Animal Scien*ce 24: 26 - 29.

Cloete, S.W.P., Haughey, K.G., 1988. Preliminary note on mature pelvic dimensions and rearing efficiency in Merino ewes. *South African Journal of Animal Science* 18: 171 - 174.

Cloete, S.W.P., Haughey, K.G., 1990. Radiographic pelvimetry for the estimation of pelvic dimensions in live Merino, Dormer and SA Mutton Merino ewes. *Journal of the South African Veterinary Association* 61: 55 - 58.

Donnelly, F.B., 1982. A practical attempt to breed for better lamb survival. *Proceedings of Australian Society of Animal Production* 14: 30 - 34.

Fogarty, N.M., 1984. Breeding for reproductive performance. In: Lindsay, D. R., Pearce, D. T., (Eds.), Reproduction in Sheep, Australian Academy of Science in Conjunction with Australian Wool Corporation, Canberra, Australia, pp 226 - 233.

Fogarty, N.M, Dickerson, G.E., Young, L.D., 1985. Lamb production and its components in pure breeds and composite lines. III. Genetic parameters. *Journal of Animal Science* 60: 40 - 57.

Fogarty, N.M., Thompson, J.M., 1974. Relationship between pelvic dimensions, other body measurements and dystocia in Dorset Horn ewes. *Australian Veterinary Journal* 50: 502 - 506.

Fourie, A.J., Cloete, S.W.P., 1993. Reproductive performance of commercial Merino, Dohne Merino and SA Mutton Merino flocks in the southern Cape. *South African Journal of Animal Science* 23: 104 - 110.

Harvey, W.R., 1990. User's guide for LSMLMW and MIXMDL. PC – 2 version MIMEOGRAPH.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361 - 363.

Haughey, K.G., 1989. Studies on causes of perinatal lamb mortality in the western Cape and pelvic dimensions of ewes relative to their lifetime rearing performance. Report on activities during a visiting research fellowship 1987 – 1988, Department of Agriculture and Water Supply, Private Bag, Elsenburg.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Haughey, K.G., George, J.M., McGuirk, B.J., 1985. The repeatability of rearing performance of Merino and Dorper Horn ewes and its relationship with mature pelvic size. *Australian Journal of Experimental Agriculture* 25: 541 - 549.

Haughey, K.G., Gray, C.H., 1982. A radiographic technique for pelvimetry of unanaesthestised ewes and a comparison of three methods of estimating the area of the pelvic inlet. *Australian Veterinary Journal* 58: 51 - 59.

Heydenrych, H.J., Du Plessis, J.J., Cloete, S.W.P., 1984. Increasing the wool production of Merino sheep in the South Western Districts of South Africa by direct and indirect selection. Proceedings of the second World Congress on Sheep and Beef Cattle Breeding 16 - 19 April, Pretoria. South African Studbook and Livestock Improvement Association, Bloemfontein, South Africa pp. 399 - 412.

Johnson, S.K., Deutscher, G.H., Parkhurst, A.J., 1988. Relationships of pelvic structure, body measurements, pelvic area and calving difficulty. *Journal of Animal Science* 66: 1081 - 1088.

Kilgour, R.J., Haughey, K.G., 1993. Pelvic size in Merino ewes selected for lambrearing ability is greater than that of unselected Merino ewes. *Livestock Production Science* 31: 237 - 242.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H.-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259 - 271.

Lindsay, D.R., Nowak, R., Putu, I.G., McNeill, D., 1990. Behavioural interactions between the ewe and her young at parturition: a vital step for the lamb. In: Oldham, C. M., Martin, G. B., Purvis, I. W., (Eds.), Reproductive Physiology of Merino Sheep School of Agriculture, University of Western Australia, pp. 191 - 205.

McSporran, K.D., Fielden, E.D., 1979. Studies on dystocia in sheep. II. Pelvic measurements of ewes with histories of dystocia and eutocia. *New Zealand Veterinary Journal* 27: 75 - 78.

Meijering, A., 1984. Dystocia and stillbirths in cattle – a review of causes, relations and implications. *Livestock Production Science* 11: 143 - 177.

Morrison, D.B., Humes, P.E., Keith, N.K., Godke, R.A., 1985. Discriminant analysis for predicting dystocia in beef cattle. I. Comparison with regression analysis. *Journal of Animal Science* 60: 608 - 616.

Piper, L.R., Hanrahan, J.R., Evans, R., Bindon B.M., 1982. Genetic variation in individual and maternal components of lamb survival of Merinos. *Proceedings of Australian Society of Animal Production* 14: 29 - 32.

Putu, I.G., 1990. Maternal behaviour in Merino ewes during the first two days after parturition and survival of lambs. Ph.D. thesis. University of Western Australia.

Quinlivan, T.D., 1971. Dystocia in sheep: preliminary observations on within- and between-breed differences in various skeletal measurements. *New Zealand Veterinary Journal* 19: 73 - 77.

Quinlivan, T.D., 1981. Co-operative ram breeding. Proceedings No. 58 Refresher course in sheep. Post-Graduate Committee in Veterinary Science. University of Sydney: 280.

Shelton, M., Menzies, J.W., 1970. Repeatability and heritability of components of reproductive efficiency in fine-wool sheep. *Journal of Animal Science* 30: 1 - 5.

Turner, H.N., Young, S.S.Y., 1969. Quantitative genetics in sheep breeding. Ithaca New York, USA.

Van der Merwe, C.A., 1976. Genetiese en nie-genetiese faktore wat die produksie en reproduksie van die Elsenburg Dormerskaapkudde beïnvloed. Ph.D.-proefskrif, Universiteit van Stellenbosch.

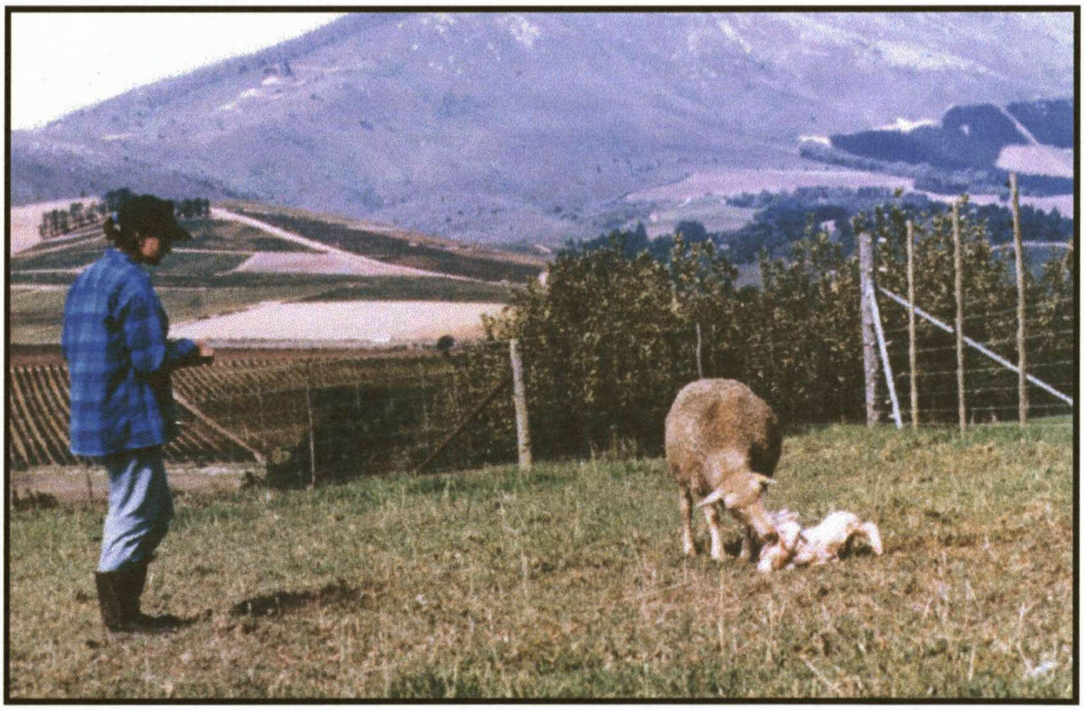
Van Wyk, J.B., 1992. The genetic evaluation of the Elsenburg Dormer stud. Ph.D. dissertation, University of the Orange Free State.

Vosloo, L.P., 1967. Faktore wat die produksie en reproduksie van die Elsenburg Duitse Merinovleisskaapkudde beïnvloed. Ph.D. - proefskrif, Universiteit van Stellenbosch.

PART 2

The dynamics of behaviour in lambing flocks

Chapters 4 to 7



CHAPTER 4

OBSERVATIONS ON LITTER SIZE, PARTURITION AND MATERNAL BEHAVIOUR IN RELATION TO LAMB MORTALITY IN FECUND DORMER AND SOUTH AFRICAN MUTTON MERINO EWES

S.W.P.Cloete

Elsenburg Agricultural Centre,
Private Bag Elsenburg 7607,
Republic of South Africa

Published in:
South African Journal of Animal Science (1992) 22: 214 - 221

Reproduced with permission of:
South African Journal of Animal Science

Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and South African Mutton Merino ewes

S.W.P. Cloete
Elsenburg Agricultural Centre, Private Bag, Elsenburg, 7607 Republic of South Africa

Received 17 January 1992; revised 25 August 1992; accepted 21 October 1992

Abstract: Dormer (n = 166) and SA Mutton Merino (n = 147) ewes were observed continuously during lambing in the autumn lambing seasons of 1989 - 1991. Although SA Mutton Merino ewes had larger ($P \leq 0.01$) litters at birth than Dormers (2.08 *vs.* 1.75), higher ($P \leq 0.05$) levels of mortality at birth (0.101 *vs.* 0.031) and from 3 days to weaning (0.180 *vs.* 0.110) resulted in this difference being eliminated at weaning (1.35 *vs.* 1.37). SA Mutton Merino ewes generally took longer to give birth ($P \leq$ 0.01; 92 *vs.* 67 min) and were more likely to be assisted at birth ($P \leq 0.01$; 0.231 *vs.* 0.102) than Dormers. Post-mortem results suggested that birth stress was more prevalent ($P = 0.053$) amongst 61 perinatal deaths in SA Mutton Merino lambs than in 30 Dormers (0.575 *vs.* 0.333). Mortalities within *ca.* 1 week of birth amongst assisted lambs (pooled across breeds) were generally higher than in their unassisted contemporaries, significantly ($P \leq 0.05$) so in singles (0.444 *vs.* 0.044) and triplets (0.604 *vs.* 0.156). Length of parturition was found to be repeatable ($t = 0.36 \pm 0.07$). Permanent and temporary separation of ewes from ≥ 1 lamb were independent of breed, but were lower ($P \leq 0.05$) amongst ewes caring for singles (0.011) than in ewes caring for twins (0.197) or triplets (0.323). Permanent separation was caused by interference and desertion in respectively 0.500 and 0.239 of affected ewes, while lambs followed a non-interfering ewe in 0.174 of cases. Separation was attributed to udder malfunction in 0.043 of the ewes. The incidence of permanent separation caused by interference by other ewes was higher ($P \leq 0.05$) in Dormer ewes than in SA Mutton Merinos (0.654 *vs.* 0.300). Ewes moving from their birth sites ≤ 120 min after birth were more likely ($P \leq 0.01$) to be permanently separated from ≥ 1 lamb than ewes which remained longer (0.400 *vs.* 0.134). This observation was mainly caused by ewes classified as deserting their lamb(s). These ewes left their birth sites sooner (P ≤ 0.01) than those that were not separated from any lambs (156 *vs.* 351 min). Separation of ewes from ≥ 1 lamb was related to the density of lambed ewes ($r = 0.56$) increasing by 2.01% ($SE_b = 0.35$) for 1 lambed ewe / ha. Udder malfunction was recorded in 18 ewes, and was accompanied by high levels of lamb mortality (0.643). Selection against rearing failure should be investigated for the improvement of rearing ability and lamb survival in these flocks, before further attempts are made to increase fecundity. Management should facilitate for ewes remaining on their birth sites for a long time after birth, and avoid stocking densities > 11 pregnant ewes / ha at lambing.

Keywords: Birth problems, lamb mortality, length of parturition, separation, udder malfunction.

Introduction

Lamb mortality, which is an important source of reproductive failure in sheep production (Johnson *et al.*, 1980; Dalton *et al.*, 1980), was recently reviewed (Alexander, 1984; Haughey, 1991). In most flocks, problems at parturition and the starvation-mismothering-exposure (SME) complex are the most important causes of lamb mortality with variable contributions from a host of minor causes, including infections, nutrient deficiencies and predation. Since both major causes involve the ability of ewes to give birth to, and care for their offspring successfully, increasing attention is being focused upon maternal behaviour (Alexander, 1988). Lamb mortality is high in prolific breeds and flocks (Maund *et al.*, 1980; Fogarty and Hall, 1987), with increased levels of prenatal deaths, as well as deaths due to 'prolonged' births (Hinch *et al.*, 1986).

Separation of ewes from ≥ 1 lamb increases with litter size (Alexander *et al.*, 1983b; Alexander *et al.*, 1990), due to interference and lamb stealing by parturient ewes (Winfield, 1970; Alexander *et al.*, 1983a), as well as poor maternal care (Stevens *et al.*, 1982; Alexander *et al.*, 1983a).

In order to identify ways of improving the efficiency of South African mutton sheep, this study employed intensive observations on ease of birth, post parturient maternal behaviour and separation of ewes from ≥ 1 viable lamb(s) in relation to lamb mortality. Fecund Dormer and SA Mutton Merino ewes were used under conditions regarded as representative of the stud industry in the Western Cape.

Material and Methods

Animals and location

The experimental animals were drawn from the registered Elsenburg Dormer and SA Mutton Merino flocks, described by Van der Merwe (1976) and Vosloo (1967) respectively. These flocks are maintained on the Elsenburg Experimental Farm near Stellenbosch, longitude 18°50 'E and latitude 33°51 'S. The climate is generally mild with maximum average summer temperatures *ca.* 29°C and minimum winter temperatures *ca.* 7°C. The average annual precipitation of 605.8 mm falls mainly in winter. During the observation period, maximum temperatures exceeded 30°C only on very few days and minimum temperatures were generally higher than 10°C. A total precipitation of 19.5 - 32.7 mm over 2 - 4 days was recorded for the respective years. Mean hourly wind speeds averaged 5.9 - 6.5 km / h, rarely exceeding 10 km / h in any of the years.

Experimental procedure

The experiment was conducted on an area of *ca.* 5 ha, divided into 10 paddocks of *ca.* 0.5 ha each, containing irrigated pasture mainly of kikuyu (*Pennisetum clandestinum).* After being drafted in the observed groups on udder development, ewes were side-branded with stock-marker paint for identification. During the observational period, which lasted for *ca.* 14 days, 1 - 2 new mobs of ewes were drafted into the experiment every 4 - 7 days, to replace lambed ewes. Observations were taken in March / April 1989, and in April 1990 and 1991. Periparturient behaviour was recorded for 166 Dormer and 147 SA Mutton Merino ewes, giving birth to 290 and 306 lambs respectively.

Observations were collected by 1 - 2 observers who walked the paddocks continuously. The ewes adapted to human presence within a short period of time and could be approached very closely (< 5 m) without undue disturbance. Information was relayed by radio to a central recorder overlooking the area, to enable him / her to direct the field observer(s). Five paddocks were used during daylight hours, while five were floodlit for use at night. Every morning at 07:00, unlambed ewes were drifted out of the previous night paddock into the next day paddock. At 18:30, unlambed ewes were drifted into the following night paddock. Care was taken not to disturb recently lambed ewes or their lambs during drifting. Ewes were left on their lambing paddocks for 2.5 - 3 days. Lambs were weaned at *ca.* 100 days of age, mainly off dryland lucerne pastures.

Data recorded

Recordings included the first definite sign of parturition (straining or the presentation of membranes in > 90% of cases) and length of parturition from the first definite sign to the birth of the last lamb. After being groomed by their mothers for at least 15 min, new-born lambs were tagged, sexed and identified according to the order of birth within a litter. The birth site was marked. Lambs were weighed and side-branded with their mother's number immediately after drifting. Observations were frequent until the lamb(s) had suckled. Subsequently the behaviour of ewes and lambs was recorded every 30 min, for *ca.* 24 h. Intermittent observations continued for 3 days.

Ewes were assisted 3.5 - 4.5 h after the first definite sign of parturition or as soon as convenient thereafter. Five ewes with abnormal presentations were assisted 30 min after it became clear that a normal birth was unlikely. The incidence of separation of ewes from ≥ 1 lambs was recorded, and an attempt was made to identify causes. Separation was ascribed to interference, desertion (lambs left on birth site for whatever reason), poor milk supply, or a lamb following another non-interfering ewe. Ewes were regarded as being temporarily separated from ≥ 1 lamb after 2 h without contact. Permanent separation was defined as 5.5 - 6 h without contact and regarded as unlikely to be resolved without human intervention. Lambs not permanently fostered by other ewes, were returned to their mothers at this stage. Lambs not accepted were removed from the trial and regarded as dead. Fourteen lambs, shared equally between two ewes, were regarded as separated from their mothers due to interference. Ewes moving > 15 m from their birth sites for ≥ 2 h were considered to have left the site permanently. Distances were estimated by reference to a grid system in the paddocks.

Ninety-one lambs which died during the perinatal period (before, during or within 7 days of birth) were collected and delivered to the Regional Veterinary Laboratory once daily, or after storage in a cool room (4°C) over weekends and public holidays. Using procedures described by Haughey (1989), lambs were classified as having died in the antenatal period (characterized by autolysis, subcutaneous oedema or mummification), in the parturient or postparturient period due to birth stress (characterized by oedema of the presenting portion, meconium staining, epicardial petechiae, haemorrhages and congestion of the brain and spinal chord), in the postparturient period with evidence of starvation / mismothering / exposure (SME, characterized by depleted fat reserves, inadequate milk ingesta) or due to other causes (lethal congenital malformations, infections acquired after birth, unknown causes).

Statistical analysis

Reproduction data were analysed by standard least squares procedures (Harvey, 1977; 1982). The fixed model employed for this purpose included the effects of breed (Dormer or SA Mutton Merino), year (1989 - 1991) and age at lambing (2 years, 3 - 6 years and ≥ 7 years – referred to as maiden, mature and old ewes respectively). The same procedure was used to analyse litter mass at birth and rearing as well as length of parturition (transformed to logarithms_{10} to account for a skew distribution), but the fixed effect of litter size (single, twin or triplet) was added to the model. Actual length of parturition was analysed in ewes assisted at birth, since length of parturition almost exclusively determined the need to render assistance. For the analysis on the time that ewes remained on their birth sites (also transformed to logarithms_{10}), the number of viable lambs cared for just after birth was used instead of litter size. Two-factor interactions were generally unimportant, and omitted from the discussions. Repeatability (t) of some parameters was estimated with 128 records of 59 ewes that were observed twice or more ($k = 2.18$). A general mixed model, containing the random effect of ewes within contemporary groups (breed and birth year) and the fixed effect of age, was fitted to the data (Harvey, 1977). Repeatability was calculated from between and within ewe variance components from these analyses (Turner and Young, 1969). Data were pooled and expressed as proportions where applicable, and compared by non-parametric Chi^2 methods. In the case of lamb mortality data, this was done after least-squares appraisal (Harvey, 1982) to ascertain no significant two-factor interactions between main effects.

Results

Ewe litter size and lamb mortality

Number of lambs born / ewe was 19% higher ($P \leq 0.01$) in SA Mutton Merinos than in Dormers (Table 1). Higher ($P \leq 0.05$) levels of mortality at birth and from 3 days to weaning amongst SA Mutton Merino lambs resulted in no breed difference in lambs weaned / ewe, but Dormers tended to have a higher mass of lamb weaned / ewe (38.2 ±1.7 *vs.* 34.4 ± 1.8 kg; $P = 0.055$). The number of lambs born / ewe was highest ($P \leq 0.01$) in 1989. Ewes which lambed in 1991 weaned more lambs / ewe than those which lambed in 1990 ($P \leq 0.01$), due to lower levels of preweaning mortality. Number of lambs weaned / ewe was also higher ($P \leq 0.05$) in 1989 than in 1990. Ewe age did not affect reproduction significantly, but overall lamb mortality levels were higher ($P \leq 0.05$) amongst progeny of old ewes compared to young ewes. Ram lambs sustained higher ($P \leq 0.05$) levels of mortality at birth than ewes, with a similar tendency ($Chi^2 = 2.499$; $P = 0.11$) in total lamb mortalities. Triplets generally had higher ($P \leq 0.05$) age specific and overall mortalities than either singles or twins. Total lamb mortalities were roughly equally divided between the periods: birth to 3 days and 3 days to weaning.

Table 1. Least squares means (± *SE*) for the effects of breed, year and age on the reproductive performance of Dormer and SA Mutton Merino ewes continuously observed during lambing in 1989 - 1991 as well as the effects of breed, year, sex, dam age and birth type on the mortality of lambs, assessed by Chi^2 procedures

Reproduction	**Number of ewes**	**Number of lambs / ewe available**			
		At birth	**Born alive**	**Alive at 3 days**	**Alive at weaning**
Overall mean	313	1.92 ± 0.05	1.79 ± 0.05	1.68 ± 0.05	1.36 ± 0.06
Breed		**	NS	NS	NS
Dormer	166	$1.75^1 \pm 0.06$	1.72 ± 0.07	1.51 ± 0.07	1.37 ± 0.07
SA Mutton Merino	147	$2.08^2 \pm 0.06$	1.86 ± 0.07	1.75 ± 0.07	1.35 ± 0.07
Year		**	**	**	**
1989	98	$2.24^2 \pm 0.09$	$2.08^2 \pm 0.10$	$1.85^b \pm 0.10$	$1.41^b \pm 0.10$
1990	105	$1.67^1 \pm 0.07$	$1.55^1 \pm 0.08$	$1.45^a \pm 0.08$	$1.14^a \pm 0.08$
1991	110	$1.85^1 \pm 0.09$	$1.74^1 \pm 0.10$	$1.73^b \pm 0.10$	$1.53^b \pm 0.10$
Age		NS	NS	NS	NS
Maiden	60	1.80 ± 0.09	1.71 ± 0.10	1.63 ± 0.10	1.37 ± 0.10
Mature	216	1.95 ± 0.04	1.75 ± 0.04	1.67 ± 0.05	1.40 ± 0.05
Old	37	2.01 ± 0.10	1.91 ± 0.12	1.74 ± 0.12	1.31 ± 0.12

Lamb mortality	**Number of lambs**	**Lamb mortality / lamb born**			
		At birth	**Birth – 3 days**	**3 days – weaning**	**Total**
Overall mean	596	0.067	0.064	0.146	0.277
Breed		**	NS	*	**
Dormer	290	0.031^1	0.062	0.110^a	0.203^1
SA Mutton Merino	306	0.101^2	0.065	0.180^b	0.345^2
Year		NS	**	**	**
1989	214	0.065	0.136^2	0.192^b	0.393^2
1990	180	0.078	0.039^1	0.172^b	0.289^2
1991	202	0.059	0.009^1	0.074^a	0.144^1
Sex		*	NS	NS	NS
Ram	312	0.090^a	0.051	0.163	0.304
Ewe	284	0.042^b	0.077	0.127	0.246
Dam age		NS	NS	*	*
Maiden	103	0.049	0.068	0.097	0.214^a
Mature	416	0.077	0.053	0.142	$0.272^{a,b}$
Old	77	0.039	0.117	0.234	0.390^b
Birth type		**	**	**	**
Single	77	$0.065^{1,2}$	0.026^a	0.052^1	0.143^1
Twin	375	0.032^1	0.043^a	0.123^1	0.197^1
Triplet	144	0.160^2	0.139^b	0.257^2	0.556^2

NS Not significant ($P > 0.05$) * significance ($P \leq 0.05$); ** significance ($P \leq 0.01$)

^{a,b} Denote significance ($P \leq 0.05$)

^{1,2} Denote significance ($P \leq 0.01$)

Mass of lamb born and length of parturition

SA Mutton Merinos gave birth to heavier ($P \leq 0.01$) litters than Dormers (Table 2). Mass of lamb born / ewe was also affected ($P \leq 0.01$) by year and age of ewe. Litter size at birth markedly influenced ($P \leq 0.01$) mass of lamb born/ewe available. Dormers experienced shorter ($P \leq 0.01$, $\log_{10}$ transformed) births than SA Mutton Merinos (55.2 *vs.* 94.4 min; means ± *SE*s – 1.74 ± 0.05 and 1.98 ± 0.05 respectively). A higher ($P \leq 0.05$) proportion of 101 twin-bearing Dormers had births of < 2 h than of 87 SA Mutton Merinos (0.693 *vs.* 0.515; $Chi^2 = 5.366$; $df = 1$). No significant breed differences were obtained in single or triplet bearing ewes when classified in this way. A higher ($P \leq 0.05$) proportion of 53 single bearing Dormers did, however, give birth within an hour than of 24 SA Mutton Merinos (0.698 *vs.* 0.375; $Chi^2 =$ 5.89; $df = 1$).

Table 2. Least squares means for the effects of breed, year, age and number of lambs born on mass of lamb born and length of parturition ($\log_{10}$ transformed) in Dormer and SA Mutton Merino ewes continuously observed during lambing in 1989 - 1991

	Mass of lamb born (kg)	**Length of parturition (min)**	
		Mean ± *SE*	**Antilog**
Overall mean	7.70 ± 0.10	1.893 ± 0.046	78.2
Breed	**	**	
Dormer	$7.52^1 \pm 0.12$	$1.824^1 \pm 0.052$	66.7
SA Mutton Merino	$7.88^2 \pm 0.12$	$1.962^2 \pm 0.054$	91.6
Year	**	NS	
1989	$7.68^{a,b} \pm 0.17$	1.913 ± 0.076	81.8
1990	$7.37^a \pm 0.13$	1.852 ± 0.059	71.1
1991	$8.05^b \pm 0.17$	1.915 ± 0.077	82.2
Age	*	NS	
Maiden	$7.30^a \pm 0.21$	1.945 ± 0.097	88.1
Mature	$7.88^b \pm 0.08$	1.919 ± 0.034	82.9
Old	$7.92^b \pm 0.20$	1.816 ± 0.091	65.5
Number of lambs born	**	**	
1	$4.92^1 \pm 0.18$	$1.658^a \pm 0.079$	45.5
2	$7.96^2 \pm 0.10$	$1.861^b \pm 0.043$	72.6
3	$10.23^3 \pm 0.24$	$2.161^c \pm 0.106$	144.9

NS Not significant ($P > 0.05$)

* Significant ($P \leq 0.05$)

** Significant ($P \leq 0.01$)

^{a,b,c} Denote significance ($P \leq 0.05$)

^{1,2,3} Denote significance ($P \leq 0.01$)

Least squares adjustment for the larger litters being borne by SA Mutton Merinos reduced the difference in length of parturition between breeds, but it remained significant ($P \leq 0.01$, Table 2). The linear effect of mass of lamb born / ewe as a covariant in the model reduced the observed breed effect substantially ($P = 0.068$), but failed to remove it conclusively. Individual class regressions (± *SE*) for the logarithm$_{10}$ of length of parturition on litter mass at birth were different ($P = 0.04$) for Dormers and SA Mutton Merinos (1.40 *vs.* 1.22 min/kg; regressions ± *SE*s: 0.147 ± 0.037 and 0.088 ± 0.034). Triplet litters took longer to be born than twins which, in turn, had longer parturitions than singles ($P \leq 0.05$), but year and ewe age did not significantly affect length of parturition.

Assistance at birth and survival of assisted lambs

Assistance at birth was independent of year ($Chi^2 = 2.01$; $df = 2$) and ewe age ($Chi^2 = 2.62$; $df = 2$). Ewes bearing singles ($n = 77$) and twins ($n = 188$) were less likely to be assisted than 48 triplet bearing ewes (0.117 and 0.138 *vs.* 0.333; $Chi^2 = 12.25$; $df = 2$, $P \leq 0.01$). The incidence of assistance at birth was higher ($P \leq 0.01$) in SA Mutton Merino ewes than in Dormers (0.231 *vs.* 0.102; $Chi^2 = 8.57$; $df = 1$). In singles and twins, levels of assistance were at least two times higher in SA Mutton Merino ewes than in Dormers, but the difference only tended to be significant ($P = 0.06$) in twins (0.195 *vs.* 0.089; $Chi^2 = 3.58$; $df = 1$). One in every three triplet bearing ewes was assisted in both breeds (12/36 and 4/12 respectively).

Lamb mortality to *ca.* 1 week was investigated in relation to assistance at birth. Tendencies were similar for Dormer and SA Mutton Merino lambs, and the data were pooled across breeds. Single lambs ($n = 9$), given birth to by assisted ewes, had a lower ($P \leq 0.01$) probability of survival than 68 contemporaries born without assistance (0.444 *vs.* 0.044; $Chi^2 = 10.95$; $df = 1$). A similar tendency was observed in twins, but the difference failed to reach significance (assisted – 7/52 = 0.135 *vs.* not assisted – 21/324 = 0.065; $Chi^2 = 2.24$; $df = 1$). Triplet lambs ($n = 48$) rendered assistance at birth had a markedly lower ($P \leq 0.01$) probability of survival to 1 week than 96 contemporaries born naturally (0.604 *vs.* 0.156; $Chi^2 = 28.18$; $df = 1$).

Repeatability

The between-ewe variance component for length of parturition was significant ($P \leq 0.01$), and repeatability (± *SE*) was estimated at 0.36 ± 0.07. Including number of lambs born as main effect or litter mass at birth as covariant had little effect on this estimate. Between-ewe variance components for ewes losing ≥ 1 lamb during the perinatal period and mass of lamb weaned ≥ 1 lamb during the perinatal period and mass of lamb weaned/ewe were also significant ($P \leq 0.05$; $t = 0.29 \pm 0.08$ in both cases).

Levels and causes of separation of ewes from ≥ 1 of their lambs.

Of 304 ewes caring for ≥ 1 viable lamb shortly after birth, 46 (0.151) were separated permanently from at least one lamb. A further 23 ewes were temporarily separated from at least one lamb. Permanent and temporary separation of ewes from ≥ 1 lamb showed no dependence on year or breed. Permanent separation was lower ($P \leq 0.05$) in 95 ewes caring for singles than in respectively 178 and 31 ewes caring for twins or triplets (0.011 *vs.* 0.197 and 0.323; $Chi^2 = 24.59$; $df = 2$). Temporary separation followed the same trend (singles – 0.011; twins – 0.144; triplets – 0.235; $Chi^2 = 12.17$; $df = 2$).

Interference by other parturient ewes was the main cause of permanent separation, involving 23 (0.50) of all ewes being permanently separated from ≥ 1 lamb(s). Permanent separation as a result of desertion was recorded in 11 ewes (0.239). Lambs followed other non-interfering ewes in eight cases (0.174). Udder problems occurred in two SA Mutton Merino ewes (0.043). Although not significantly different, it was interesting to note that 14 lambs, being shared equally by two ewes during observations, had a low mortality to weaning (0.071) compared to 510 other lambs where no complicating factors (interference, desertion or udder malfunction) were involved (0.251). Interference was a more important cause of permanent separation of 26 Dormer ewes from ≥ 1 lambs than of 20 SA Mutton Merino ewes (0.654 *vs.* 0.300; $Chi^2 = 4.34$; $df = 1$; $P \leq 0.05$). No significant breed effects were found for other causes of separation.

Movement of ewes from the birth site

Dormers remained longer ($P \leq 0.05$; $\log_{10}$ transformed) on their birth sites than SA Mutton Merinos (257 *vs*. 338 min; means ± *SE*s – 2.41 ± 0.03 and 2.53 ± 0.04 respectively). The time that ewes remained on their birth sites was unaffected by lambing year, ewe age or number of lambs cared for. Ewes separated permanently from ≥ 1 lamb moved sooner ($P \leq 0.05$) from their birth sites than ewes not separated from any progeny (250 *vs*. 325 min; $\log_{10}$ transformed means ± *SE*s – 2.40 ± 0.04 and 2.51 ± 0.02 respectively). Similar results were obtained for temporary separation (248 *vs*. 338 min respectively; means ± *SE*s – 2.40 ± and 2.53 ± 0.02).

Ewes which remained on their birth sites for ≤ 120 min ($n = 20$), were more likely ($P \leq 0.01$) to be separated from ≥ 1 lamb than 284 ewes remaining for > 120 min (0.400 *vs*. 0.134; $Chi^2 = 8.34$; $df = 1$; Figure 1). The incidence of temporary separation was higher ($Chi^2 = 7.316$; $df = 1$, $P \leq 0.01$) in 67 ewes that remained on their sites for ≤ 240 min (0.149), than in 125 ewes that remained for > 360 min (0.032). The relationship of permanent separation with time on the birth site was due solely to ewes leaving lambs. This category ($n = 11$) was the only group that remained shorter ($P \leq 0.05$) on their birth sites than ewes not separated from any lambs ($n = 260$; 156 *vs*. 351 min; $\log_{10}$ transformed means ± *SE*s – 2.19 ± 0.08 and 2.55 ± 0.02 respectively).

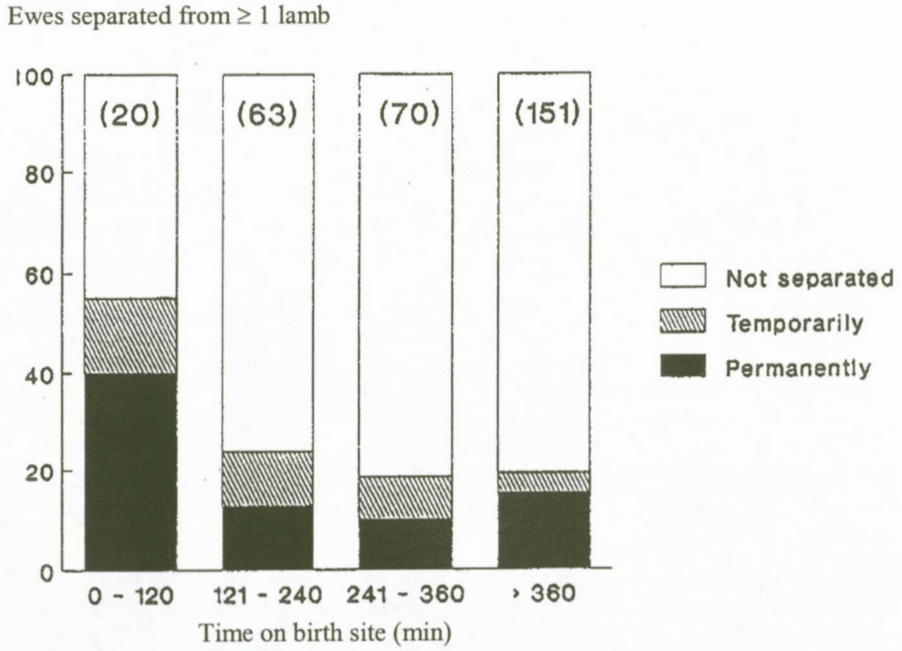


Figure 1. Separation of ewes from at least one lamb in relation to the time that ewes remained within 15 m from their birth sites. The number of ewes in each class is given in parentheses.

The density of lambed ewes

The incidence of permanent separation was related to the number of lambed ewes within paddocks (Figure 2), and increased by 2.01% ($SE_b = 0.35$) ewes separated from $\geq$ 1 lamb for every additional ewe that lambed. Regressions for the respective lambing years (1989 - 1991) ranged between 1.7 and 2.3% ewes separated from $\geq$ 1 lamb / lambed ewe, and were not significantly different ($P > 0.35$).

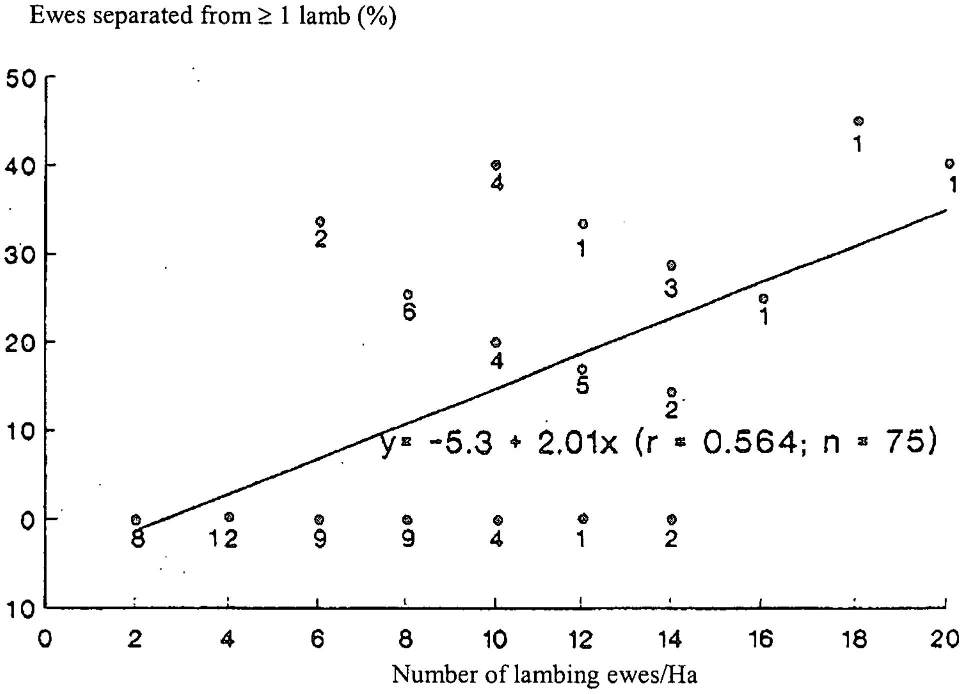


Figure 2. The percentage of ewes permanently separated from at least one lamb in relation to the number of lambed ewes caring for at least one viable lamb per hectare. Each marker represents the number of observations printed underneath.

Causes of perinatal mortality

Antenatal deaths constituted a proportion of *ca.* 0.11 of 30 Dormer and 61 SA Mutton Merino lambs autopsied during the course of the study (Figure 3). Birth stress was more prevalent amongst SA Mutton Merino lambs than in Dormers ($Chi^2 = 3.74$; $P = 0.053$; $df = 1$). Symptoms of SME were diagnosed in 21 lambs with no breed difference. Dormer lambs were more likely to succumb to other causes than SA Mutton Merinos ($Chi^2 = 4.57$; $P \leq 0.05$; $df = 1$).

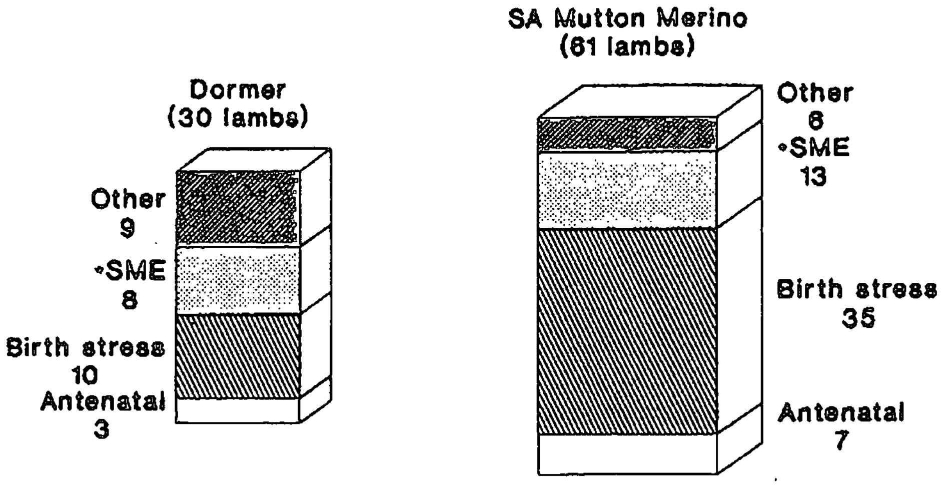


Figure 3. Causes of perinatal lamb mortality in Dormer and SA Mutton Merino lambs, as determined by autopsy of 91 lambs.

Udder problems

Of the 304 ewes caring for ≥ 1 viable lamb, 18 (0.056) were found to have udder abnormalities. Of these ewes, half had only one functional teat due to shearing injury, while milk production was severely reduced by scar tissue from previous mastitis in the remainder. Mortality amongst lambs from these ewes was high (21/33 = 0.643). No cases of severe, acute mastitis occurred during the investigation.

Discussion and Conclusions

Ewe litter size and lamb mortality

The higher multiple birth rate and levels of lamb mortality of SA Mutton Merino ewes and lambs compared to Dormers is in good agreement with previous results (Brand *et al.*, 1985). Lamb mortality figures for singles and twins were similar, with substantially higher mortality levels for triplets. Corresponding results were reported previously in studies involving fecund breeds or strains (Maund *et al.*, 1985; Brand *et al.*, 1985; Scales *et al.*, 1986). The comparatively high level of lamb mortality from 3 days to weaning is another cause of concern. The causes of these deaths were not determined, but a previous study suggested that mismothering syndromes played a role, while deaths due to acute haemonchosis were also reported (Haughey, 1989).

Length of parturition and birth problems

SA Mutton Merino ewes required more assistance at birth, underwent a longer parturition and displayed a higher proportion of birth stressed lambs than Dormers, thus supporting previous work in these breeds (Brand *et al.,* 1985) and in others (Smith, 1977; Dalton *et al.,* 1980; Woolliams *et al.,* 1983; Alexander *et al.,* 1990). A larger pelvic size was related to selection for increased lamb survival in the Romney breed and lower levels of dystocia in the Marshall Romney strain (Knight *et al.,* 1988) and in other studies (Quinlivan, 1971; Fogarty and Thompson, 1974; McSporran and Fielden, 1979; Haughey *et al.,* 1985; Cloete and Haughey, 1988). The increase in parturition time and deaths with increasing litter size supports previous work (Owens, *et al.,* 1985). This study and previous work (Hinch *et al.,* 1986; Haughey, 1991) suggest that the increased total foetal mass of larger litters theoretically imposes greater uterine work load during parturition, increasing its duration. Litter mass at birth was more important as a determinant of length of parturition in Dormer ewes than in SA Mutton Merinos, suggesting that length of parturition in SA Mutton Merino ewes may be partially dependent on other factors. Birth difficulty was clearly related to neonatal deaths in the present study, as was also reported by Arnold and Morgan (1975) and Scales *et al.,* (1986).

The finding that length of parturition was repeatable also warrants further attention. Selection may thus alter this parameter, at least in the current flock. Judged by the breed difference in length of parturition, it seems reasonable to assume that this trait has a genetic basis. Breed and strain differences in birth problems and dystocia in the literature may well be related to length of parturition. The occurrence of between-ewe variation for the losing of ≥ 1 lamb in the perinatal period may also be related to repeatability estimates for ewe rearing ability in the literature (Piper *et al.,* 1982; Haughey *et al.,* 1985), although the present estimate of 0.29 is somewhat higher. The estimate of 0.29 for mass of lamb weaned/ewe was also higher than most estimates, ranging from 0.06 - 0.24 (Clarke and Hohenboken, 1983; Fogarty *et al.,* 1985; Bunge *et al.,* 1990). These parameters were, however, expressed on a per ewe lambed basis, while literature estimates were on a per ewe joined basis.

Selective breeding, as advocated by several authors (Fogarty, 1984; Lindsay *et al.*, 1990; Haughey, 1991), may be important in the control of lamb mortalities. In flocks of low and medium fecundity, lamb survival was demonstrated to respond to selective breeding (Donnelly, 1982; Haughey, 1983; Knight *et al.*, 1988; Cloete, 1990), while selection for the ability to rear multiples also were successful (Atkins, 1980). It is uncertain whether lamb losses will be affected by the same mechanisms in fecund Dormer and SA Mutton Merino ewes. It is also uncertain whether selection will influence lamb survival at ages older than 3 days, when roughly half of the lamb deaths in the present study was recorded. Investigations into multiple rearing ability should nonetheless preclude further attempts to enhance the fecundity of particularly the SA Mutton Merino breed.

Prevalence and causes of separation of ewes from ≥ 1 lamb

The incidence of permanent separation amongst ewes caring for multiples was markedly less than in studies involving finewool Merino ewes (Stevens *et al.*, 1982; Alexander *et al.*, 1983a), but was in the same order in studies involving Merinos (Alexander *et al.*, 1983b; Putu *et al.*, 1988a). In other studies, levels of separation amongst ewes belonging to a number of breeds and caring for multiples were less than 10% (Alexander *et al.*, 1983a; 1990). No breed effect was observed in the present study, but the prevalence of separation due to interference was higher amongst Dormer ewes than SA Mutton Merinos. Alexander *et al.* (1990) found a tendency towards higher levels of permanent separation from ≥ 1 lamb in Border Leicester ewes than in Glen Vales. Putu (1990) attributed behavioural characteristics conducive to lamb survival in Trangie Fertility Merinos to selection for increased rearing ability in this strain.

Ewes that were separated from ≥ 1 lamb remained for a shorter time on their birth sites than ewes not separated, as was also reported by Alexander *et al.*, (1983b). This observation was mainly due to ewes leaving lambs on the birth site. Separation of ewes from ≥ 1 twin lamb was also related to the time that fine-wool Merino ewes remained on their birth sites in a study involving high levels of permanent separation and rapid movement from birth sites (Alexander *et al.*, 1983a). The time that ewes remained on their birth sites was influenced by shelter (Alexander *et al.*, 1983a) and the availability of pasture (Putu *et al.,* 1988a). The disturbance of recently lambed ewes from their birth sites by humans or supplementary feeding aggravated the incidence of separation of ewes from their lambs (Putu *et al.,* 1988b). Supplementation by the broadcasting of lupines less frequently (Morcombe *et al.,* 1988) may cause less disturbance to lambing ewes without altering live mass change.

An increase of 1 lambed ewe / ha resulted in an increase of *ca.* 2% in the incidence of ewes permanently separated from ≥ 1 lamb. Winfield (1970) and Alexander *et al.,* (1983b) reported increased levels of interference and separation as the number of lambed ewes/ha increased, resulting in inaccuracies in litter size records of ewes, as well as in pedigree information. A stocking density of 2.6 lambed ewes / ha theoretically resulted in no separations. Following reasoning of Alexander *et al.,* (1983b), it was calculated that a stocking rate of 11 pregnant ewes / ha would minimize recording errors and separations under the conditions of the present trail. Alexander *et al.* (1983b) correspondingly recommended a stocking rate of 18 pregnant ewes / ha.

Causes of perinatal mortality

Although the proportion of *ca.* 0.11 antenatal deaths in the present study is high compared to the generally accepted value of 2% (Haughey, 1991), it is recognized that antenatal death constitutes a more important cause of lamb mortalities in fecund flocks (Hinch *et al.*, 1986). Birth stress was an important cause of perinatal death, particularly in SA Mutton Merino lambs. Starvation/mismothering/exposure were probably underestimated as causes of perinatal death, as some lambs were returned to their mothers when permanent separation was unlikely to be resolved without human intervention, and since lambs taken from the experiment and regarded as dead were not autopsied. There was furthermore strong evidence that mismothering played a major role in deaths from 3 days to weaning (Haughey, 1989). Dormer lambs were more susceptible to other causes of lamb mortality than SA Mutton Merinos. The practical implication of this finding does, however, need further clarification before it can be turned into a practical advantage.

Udder problems

The incidence of udder problems in the present study was on the lower end of the range reported by Jordan *et al.*, (1984). Survival of lambs with affected mothers was correspondingly low. When comparing the performance of ewes with two functional teats with that of ewes with only one functional teat, Jordan *et al.*, (1984) found that milk production was reduced by 15 - 42%, and lambs reared / 100 ewes by 6 - 42. Low levels of nutrition aggravated the effects of udder malfunction (Jordan and Mayer, 1989). Udder health should thus also receive attention in the flocks concerned.

Acknowledgements

The author thanks the following persons for assistance rendered during the course of the investigation: P. Adams, S. Adams, T.S. Brand, F. Franck, J.E. Fourie, P. Lombard, Farida Martin, Ansie Scholtz, J.M. ten Hoope, J.B. van der Vyver and B.J. van Rooyen. I also thank Dr. G. Alexander (CSIRO Division of Animal Production, P.O. Box 239, Blacktown, NSW 2148 Australia) and his team for the privilege to work under their guidance, albeit for a short period of time, as well as Drs. A. van Halderen and D.J. Schneider (Veterinary Regional Laboratory, Stellenbosch), who performed the post-mortem examinations.

References

Alexander, G., 1984. Constraints to lamb survival. In: Reproduction in sheep. Eds. Lindsay, D.R. and Pearce, D.T., Australian Academy of Science in conjunction with Australian Wool Corporation, Canberra, Australia, p. 199.

Alexander, G., 1988. What makes a good mother? Components and comparative aspects of maternal behaviour in ungulates. *Proceedings of the Australian Society of Animal Production* 17: 25.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27.

Alexander, G., Stevens, D., Kilgour, R., De Langen, H., Mottershead, B.E., Lynch, J.J., 1983a. Separation of ewes from twin lambs: Incidence in several sheep breeds. *Applied Animal Ethology* 10: 301.

Alexander, G., Stevens, D., Mottershead, B.E., 1983b. Problems in the accurate recording of lambing data. *Australian Journal of Experimental Agriculture and Animal Husbandry* 23: 361.

Arnold, G.W., Morgan, P.D., 1975. Behaviour of the ewe and lamb at lambing and its relationship to lambing mortality. *Applied Animal Ethology* 2: 25.

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of the Australian Society of Animal Production* 13: 174.

Brand, A.A., Cloete, S.W.P., De Villiers, T.T., 1985. Faktore wat lamvrektes in die Elsenburg Dormer- en S.A. Vleismerino-kuddes beïnvloed. Suid-Afrikaanse Tydskrif vir Veekunde 15: 155.

Bunge, R., Thomas, D.L., Stookey, J.M., 1990. Factors affecting productivity of Rambioullet ewes mated to ram lambs. *Journal of Animal Science* 68: 2253.

Clarke, S.E., Hohenboken, W.D., 1983. Estimation of repeatability, heritability and breed differences for lamb production. *Journal of Animal Science* 56: 309.

Cloete, S.W.P., 1990. Observations on two-tooth fleece and body traits and reproduction up to three years in Merino ewes descended from dams differing in number of lambs weaned per joining. *Proceedings of the World Merino Conference* Vol. 2: 2- 4 May 1990, Pretoria. Paper 4, p. 1.

Cloete, S.W.P., Haughey, K.G., 1988. Preliminary note on mature pelvic dimensions and rearing efficiency in Merino ewes. *South African Journal of Animal Science* 18: 171.

Dalton, D.C., Knight, T.W., Johnson, D.L., 1980. Lamb survival in sheep breeds on New Zealand hill country. *New Zealand Journal of Agricultural Research* 23: 167.

Donnelly, F.B., 1982. A practical attempt to breed for better lamb survival. *Proceedings of the Australian Society of Animal Production* 14: 30.

Fogarty, N.M., 1984. Breeding for reproductive performance. In: Reproduction in sheep. Eds. Lindsay, D.R. and Pearce, D.T., Australian Academy of Science in conjunction with Australian Wool Corporation, Canberra, Australia, p. 226.

Fogarty, N.M., Dickerson, G.E., Young, L.D., 1985. Lamb production and its components in pure breeds and composite lines. III. Genetic parameters. *Journal of Animal Science* 60: 40.

Fogarty, N.M., Hall, D.G., 1987. Lifetime reproduction and wool production of Trangie Fertility Merino x Dorset and Booroola Merino x Dorset ewes. In: Merino improvement programs in Australia. Ed. McGuirk, B.J., Australian Wool Corporation, Melbourne, Australia, p. 283.

Fogarty, N.M., Thompson, J.M., 1974. Relationship between pelvic dimensions, other body measurements and dystocia in Dorset Horn ewes. *Australian Veterinary Journal* 50: 502.

Harvey, W.R., 1977. User's guide for LSML76 – a mixed model least squares and maximum likelihood computer program. Ohio State University, Colombus.

Harvey, W.R., 1982. Least-squares analysis of discrete data. *Journal of Animal Science* 54: 1067.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361.

Haughey, K.G., 1989. Studies on causes of perinatal lamb mortality in the Western Cape and pelvic dimensions of ewes relative to their lifetime rearing performance. Report on activities during a visiting research fellowship 1987-1988, Department of Agriculture and Water Supply, Private Bag, Elsenburg.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78.

Haughey, K.G., George, J.M., McGuirk, B.J., 1985. The repeatability of rearing performance of Merino and Dorset Horn ewes and its relationship with mature pelvic size. *Australian Journal of Experimental Agriculture* 25: 541.

Hinch, G.N., Davis, G.H., Crosbie, S.F., Kelly, R.W., Trotter, R.W., 1986. Causes of lamb mortality in two highly prolific Booroola Crossbred flocks and a Romney flock. *Livestock Production Science* 12: 47.

Johnston, W.S., Maclachlan, G.K., Murray, I.S., 1980. A survey of sheep losses and their causes on commercial farms in the north of Scotland. *Veterinary Record* 106: 238.

Jordan, D.J., Dempsey, N., Stephenson, R.G., Wilson, K., 1984. The effect of udder damage on milk yield, lamb growth and survival. In: Lindsay, D.R., Pearce, D.T., (Eds.). Reproduction in sheep. Australian Academy of Science in conjunction with the Australian Wool Corporation, Canberra, Australia, p. 220.

Jordan, D.J., Mayer, D.G., 1989. Effects of udder damage and nutritional plane on milk yield, lamb survival and lamb growth of Merinos. *Australian Journal of Experimental Agriculture* 29: 315.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259.

Lindsay, P.R., Nowak, R., Putu, I.G., McNeill, D., 1990. Behavioural interactions between the ewe and her young at parturition: A vital step for the lamb. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.). Reproductive Physiology of Merino sheep. School of Agriculture, University of Western Australia, p. 191.

Maund, B.A., Duffel, S.J., Winkler, C.E., 1980. Lamb mortality in relation to prolificacy. *Experimental Husbandry* 36: 99.

McSporran, K.D., Fielden, E.D., 1979. Studies on dystocia in sheep. II. Pelvic measurements of ewes with histories of dystocia and eutocia. *New Zealand Veterinary Journal* 27: 75.

Morcombe, P.W., Ralph, I.G., Ferguson, J., 1988. Frequency of feeding lupin grain supplements to lambing ewes grazing wheat stubble. *Proceedings of the Australian Society of Animal Production* 17: 262.

Owens, J.L., Bindon, B.M., Edey, T.M., Piper, L.R., 1985. Behaviour at parturition and lamb survival of Booroola Merino sheep. *Livestock Production Science* 13: 359.

Piper, L.R., Hanrahan, J.R., Evans, R., Bindon, B.M., 1982. Genetic variation in individual and maternal components of lamb survival of Merinos. *Proceedings of the Australian Society of Animal Production* 14: 29.

Putu, I.G., 1990. Maternal behaviour in Merino ewes during the first two days after parturition and survival of lambs. Ph.D. thesis, University of Western Australia.

Putu, I.G., Poindron, P., Lindsay, D.R., 1988A. A high level of nutrition during late pregnancy improves subsequent maternal behaviour of Merino ewes. *Proceedings of the Australian Society of Animal Production* 17: 294.

Putu, I.G., Poindron, P., Lindsay, D.R., 1988b. Early disturbance of Merino ewes from the birth site increases lamb separations and mortality. *Proceedings of the Australian Society of Animal Production* 17: 298.

Quinlivan, T.D., 1971. Dystocia in sheep: preliminary observations on within- and between-breed differences in various skeletal measurements. *New Zealand Veterinary Journal* 19: 73.

Scales, G.H., Burton, R.N., Moss, R.A., 1986. Lamb mortality, birth weight and nutrition in late pregnancy. *New Zealand Journal of Agricultural Research* 29: 75.

Smith, G.M., 1977. Factors affecting birth weight, dystocia and preweaning survival in sheep. *Journal of Animal Science* 44: 745.

Stevens, D., Alexander, G., Lynch, J.J., 1982. Lamb mortality due to inadequate care of twins by Merino ewes. *Applied Animal Ethology* 8: 243.

Turner, Helen Newton, Young, S.S.Y., 1969. Quantitative genetics in sheep breeding. Ithaca, New York, USA.

Van der Merwe, C.A., 1976. Genetiese en nie-genetiese faktore wat die produksie en reproduksie van die Elsenburg Dormerskaapkudde beïnvloed. Ph.D. – proefskrif, Universiteit van Stellenbosch.

Vosloo, L.P., 1967. Faktore wat die produksie en reproduksie van die Elsenburg Duitse Merinovleisskaapkudde beïnvloed. Ph.D. –proefskrif, Universiteit van Stellenbosch.

Winfield, C.G., 1970. The effect of stocking intensity at lambing on lamb survival and ewe and lamb behaviour. *Proceedings of the Australian Society of Animal Production* 8: 291.

Woolliams, Carol, Wiener, G., MacLeod, N.S.M., 1983. The effects of breed, breeding system and other factors on lamb mortality. 2. Factors influencing the incidence of delayed birth, dystocia, congenital deaths and miscellaneous causes of early death. *Journal of Agricultural Science, Cambridge* 100: 553.

CHAPTER 5

OBSERVATIONS ON NEONATAL PROGRESS OF DORMER AND SOUTH AFRICAN MUTTON MERINO LAMBS

S.W.P.Cloete

Elsenburg Agricultural Centre,
Private Bag, Elsenburg 7607,
Republic of South Africa

Published in:
South African Journal of Animal Science (1993) 23: 38 - 42

Reproduced with permission of:
South African Journal of Animal Sciences

Observations on neonatal progress of Dormer and South African Mutton Merino lambs

S.W.P. Cloete
Elsenburg Agricultural Centre, Private Bag, Elsenburg, 7607 Republic of South Africa

Received 10 February 1992; accepted 13 November 1992

Abstract: Data of Dormer (*n* = 290) and SA Mutton Merino (*n* = 306) lambs, born by ewes which were observed continuously during lambing in 1989 - 1991, formed the basis of this investigation. Progeny of SA Mutton Merino ewes were heavier at birth ($P \leq 0.05$) than progeny of Dormers in 1989 and 1990, but no difference was observed in 1991. Lambs given birth to by maiden ewes (2 years) were slower ($P \leq 0.01$) to stand than progeny of adult (3 - 6 years) and old (≥ 7 years) ewes. A significant interaction between dam age and birth type was observed with regard to progress from standing to first suckling. Single lambs born to maiden ewes responded slower ($P \leq 0.05$) than multiples. Amongs the progeny of mature ewes, singles progressed faster ($P \leq 0.05$) than multiples, and a similar tendency was observed in progeny of old ewes. Time-lapses from birth to standing and from standing to apparently suckling declined ($P \leq 0.01$) with an increase in birth mass. Halfsib analysis of variance heritability estimates were 0.46 ± 0.16 for the interval from birth to standing and 0.22 ± 0.12 for the interval from standing to suckling. Lambs which died subsequently were slower ($P \leq 0.01$) to stand, and tended ($P = 0.07$) to progress more slowly from standing to suckling than their contemporaries which survived. It is doubtful whether these results will find application in practice, since such observations are very labour-intensive. From a scientific viewpoint it is important to take cognisance of the possibility of genetic variation in neonatal progress, suggesting that selection may have a role to play in the reduction of lamb mortality. Live-mass gain to *ca.* 3 days of age was found to be a reliable indicator of subsequent lamb mortality in twin and triplet lambs. An increase of 1 kg was associated with decreases of 22% in twin mortality and 43% in triplet mortality.

Keywords: Birth mass, neonatal lamb progress, survival.

Introduction

Hofmeyr and Boyazoglu (1965) estimated the overall lamb mortality in the Western Cape to be 16%. In a more recent investigation, Haughey (1989) estimated perinatal lamb mortality in the Western and Southern Cape to be 15.1% (8 to 45%). Fourie and Cloete (1990) similarly reported that 12% of 12 374 commercial Merino ewes which lambed in the Bredasdorp district in 1988 - 89 failed to rear any lamb to marking at *ca.* 6 weeks of age. It thus seems that lamb mortality still remains at unacceptably high levels, despite considerable effort in the care and management of lambing flocks in this area.

When levels of lamb mortality exceed *ca.* 15%, it is usually possible to identify one or more major causes of death, whereas it is often not as well defined in flocks with lower mortality levels (Alexander, 1984). Aberrant behaviour by ewes and lambs is a factor implicated in lamb mortality (Alexander, 1984; 1988). Behavioural traits with survival value in lambs include standing soon after birth, suckling soon after standing, close following of the mother, and absence of separation from the mother (Alexander, 1988). Some of these traits may be determined genetically, as suggested by the fact that crossbred lambs were less likely to be separated from their Merino dams than purebreds (Stevens *et al.*, 1984). Crossbred lambs were similarly better at recognizing their dams than purebred Merino lambs (Nowak *et al.*, 1987).

Against this background, birth mass and behavioural traits with possible survival value were investigated in the offspring of fecund Dormer and SA Mutton Merino ewes which were observed continuously during lambing.

Material and Methods

The 596 lambs (306 SA Mutton Merino and 290 Dormer lambs) born during the investigation described by Cloete (1992) formed the basis of this report. The previous paper (Cloete, 1992) can be consulted for details regarding the experimental site, flocks observed and procedure.

Data recorded

Complete information regarding parentage (identity of sire and dam), birth year, breed, sex, age of dam, and birth type was available for all lambs. Birth mass was recorded within 12 h of birth. Lamb progress, reflected by the time-lapse between birth and first standing, first seeking teats, reaching the udder and apparently suckling was also investigated. Maternal co-operation during attempts to suckle was scored by the allocation of points for desirable behaviour (standing still, back slightly arched, nuzzling the lamb into correct position) and the absence of undesirable behaviour (backing, circling, butting). Points thus ranged from a maximum of 6 for a combination of all the desirable behaviour patterns, to 1 when a ewe rejected her lamb(s) with aggression. By the end of the observation period (at an age of *ca.* 3 days) lambs were weighed again before being combined in larger groups with other lambed ewes and their lambs.

Statistical analysis

The data were unbalanced, and standard least squares procedures were used in most analyses (Harvey, 1977; 1982). A general fixed model was fitted, including the effects of breed (SA Mutton Merino or Dormer), birth year (1989 - 1991), sex (ram or ewe), age of dam (2 years, 3 - 6 years or ≥ 7 years, designated as maiden, mature or old respectively) and birth type (single, twin, triplet). In subsequent analyses, birth mass or maternal co-operation score was included as covariate, to adjust neonatal progress data for differences in these traits. The distribution of data recorded as time intervals (lamb progress) was skew, and these data were analysed after a standard $\log_{10}$ transformation to normalize the distribution. The effects of the respective main effects were tabulated for ease of presentation. Significant two-factor interactions were discussed in the text where they occurred.

Data of 514 lambs sired by 42 rams contributing > 3 progeny to the data set (k = 10.4), for which information regarding time intervals between birth and standing, birth and apparently suckling as well as standing and apparently suckling were available, were used to obtain heritability estimates for these traits by standard halfsib analysis of variance procedures (Harvey, 1977). The general mixed model applied contained the random effect of sires within contemporary groups (consisting of breed and birth year) and the other fixed effects mentioned earlier, with or without the inclusion of birth mass as covariate. Heritability estimates and standard errors were calculated from the between-sire and error variance components, using formulaes given by Harvey (1977) and Swiger *et al.* (1964).

Results

Birth mass

Birth mass results were complicated by a significant ($P \leq 0.01$) interaction between breed and year of birth. In 1989 and 1990, SA Mutton Merino lambs were heavier ($P \leq 0.05$) than Dormers (1989 – 4.3 ± 0.1 *vs*. 4.0 ± 0.1 kg; 1990 – 4.1 ± 0.1 *vs*. 3.7 ± 0.1 kg), while no difference was observed between the breeds in 1991 (4.3 ± 0.1 *vs*. 4.3 ± 0.1 kg). Overall, SA Mutton Merino and ram lambs were heavier ($P \leq 0.01$) than Dormers and ewes respectively (Table 1). Lambs born to mature and old dams were heavier ($P \leq 0.01$) than lambs borne by maidens. Birth type was closely related to birth mass with 1 kg separating singles from twins ($P \leq 0.01$) and a further 0.7 kg separating twins from triplets ($P \leq 0.01$).

Table 1 The effects of breed, year, sex, dam age and birth type on birth mass and time to stand and to suckle in Dormer and SA Mutton Merino lambs observed continuously during 1989 - 1991

Effect	Number of lambs	Birth mass (kg)	Number of lambs	Time to stand (min)		Standing to suckling (min)	
				Mean ± *SE*	Antilog	Mean ± *SE*	Antilog
Overall mean	596	4.1 ± 0.05	516	1.30 ± 0.03	19.9	1.40 ± 0.04	25.1
Breed		**		NS		NS	
Dormer	290	$4.0^1 \pm 0.1$	260	1.31 ± 0.04	20.4	1.42 ± 0.05	26.3
SA Mutton Merino	306	$4.2^2 \pm 0.1$	256	1.30 ± 0.04	19.9	1.38 ± 0.05	24.0
Year		**		NS		NS	
1989	214	$4.2^2 \pm 0.1$	173	1.39 ± 0.06	24.5	1.31 ± 0.08	20.4
1990	180	$3.9^1 \pm 0.1$	161	1.30 ± 0.04	19.9	1.41 ± 0.05	25.7
1991	202	$4.3^2 \pm 0.1$	182	1.22 ± 0.06	16.6	1.47 ± 0.08	29.5
Sex		**		NS		NS	
Ram	312	$4.2^1 \pm 0.1$	256	1.32 ± 0.04	20.9	1.41 ± 0.05	25.7
Ewe	284	$4.0^2 \pm 0.1$	260	1.29 ± 0.04	19.5	1.39 ± 0.05	24.5
Dam age		**		**		**	
2 years	103	$3.9^1 \pm 0.1$	92	$1.46^2 \pm 0.05$	28.8	$1.53^2 \pm 0.07$	33.9
3 - 6 years	416	$4.2^2 \pm 0.1$	360	$1.27^1 \pm 0.03$	18.6	$1.26^1 \pm 0.04$	18.2
7+ years	77	$4.3^2 \pm 0.1$	64	$1.18^1 \pm 0.07$	15.1	$1.40^{1,2} \pm 0.09$	25.1
Birth type		**		NS		NS	
Single	77	$5.0^3 \pm 0.1$	71	1.21 ± 0.07	16.2	1.38 ± 0.10	24.0
Twin	375	$4.0^2 \pm 0.1$	340	1.33 ± 0.03	21.4	1.42 ± 0.03	26.3
Triplet	144	$3.3^1 \pm 0.1$	105	1.36 ± 0.06	22.9	1.40 ± 0.08	25.1

NS = Not significant ($P > 0.05$); ** significant ($P \leq 0.01$).

^{1,2} Denote significance ($P \leq 0.01$).

Neonatal lamb progress

The interval between birth and first standing was correlated with the time-lapse between birth and teat seeking ($r = 0.87$), birth and reaching the udder ($r = 0.69$) and birth and apparently suckling ($r = 0.54$), due to the period from birth to standing it had in common. The time-lapses from birth to standing and from standing to apparently suckling, were however, uncorrelated ($r = -0.01$). These measures of lamb progress are presented in Table 1. The interval from birth to standing was largely unaffected by the main effects included in the analysis, except for quicker ($P \leq 0.01$) progress in lambs born to mature and old ewes in comparison with progeny of maidens. Multiple lambs correspondingly tended ($P \leq 0.23$) to be slower to stand than singles.

The interval between standing and apparently suckling was largely independent of the known sources of variation, with the exception of dam age (Table 1). There was, however, also a significant ($P \leq 0.05$) interaction between dam age and birth type. Single lambs given birth to by maiden ewes were found to be slower ($P \leq 0.05$) to progress from standing to apparently suckling than twins and triplets (54.9 *vs*. 27.5 and 25.7 min respectively; $\log_{10}$ transformed means ± *SE*s – 1.74 ± 0.13 *vs*. 1.44 ± 0.06 and 1.41 ± 0.16). Amongst the progeny of mature ewes, singles progressed ($P \leq 0.05$) faster than multiples (14.5 *vs*. 21.3 and 20.6 min respectively; $\log_{10}$ transformed means ± *SE*s – 1.16 ± 0.07 *vs*. 1.33 ± 0.03 and 1.31 ± 0.07). A similar tendency was observed in lambs borne by old ewes (16.9 *vs*. 30.9 and 30.2 min respectively; $\log_{10}$ transformed means 1.23 ± 0.22 *vs*. 1.49 ± 0.08 and 1.48 ± 0.14).

The interval between birth and first standing declined ($P \leq 0.01$) with an increase in birth mass (b ± *SE* = -0.145 ± 0.039; antilog = 1.4 min/kg birth mass). Individual class regressions for Dormer and SA Mutton Merino lambs tended ($P = 0.06$) to differ (-0.194 ± 0.048 *vs*. –0.096 ± 0.046 for the respective breeds). The interval between standing and apparently suckling also declined ($P \leq 0.01$) as birth mass increased (b ± *SE* = -0.139 ± 0.053; antilog = 1.38 min/kg birth mass). The inclusion of birth mass as covariate reduced the effect of dam age on neonatal lamb progress, but it remained significant ($P \leq 0.05$). As would have been expected, higher scores for maternal co-operation with attempts to suckle were associated ($P \leq 0.01$) with shorter intervals between standing and apparently suckling (b ± *SE* = -0.082 ± 0.023; antilog = 1.21 min/unit increase in maternal co-operation score).

It was furthermore attempted to relate early postnatal progress of lambs to subsequent lamb mortality. Lambs which died prior to weaning ($n = 101$) were slower ($P \leq 0.01$) to stand than their contemporaries which survived to weaning ($n = 415$; 27.2 *vs*.19.4; $\log_{10}$ transformed means ± *SE*s – 1.435 ± 0.041 *vs*. 1.287 ± 0.023 respectively). Similar differences were found with regard to the intervals between birth and first seeking teats, reaching the udder and apparently suckling. Lambs which died prior to weaning correspondingly tended ($P = 0.07$) to progress slower from standing to apparently suckling than their contemporaries which survived to weaning (32.3 *vs*. 25.5 min, $\log_{10}$ transformed means ± *SE*s 1.510 ± 0.056 *vs*. 1.406 ± 0.031 respectively).

Between-sire variance components were significant ($P \leq 0.05$) for birth mass and the various measures of lamb progress in the postnatal period. Heritability estimates (±

*SE*s) were 0.194 ± 0.117 for birth mass, 0.458 ± 0.156 for the time interval between birth and standing, and 0.218 ± 0.121 for the interval between standing and apparently suckling. The inclusion of birth mass as covariate resulted in little change in the heritability estimates for the latter two traits, which were 0.561 ± 0.170 and 0.225 ± 0.123 respectively. The variance between sires was therefore not associated with birth mass differences.

Live mass at the end of the observation period and gain to ca. 3 days

Live mass at *ca.* 3 days of age was recorded for 518 lambs which survived to the end of the observation period. Except for the absence of significant ($P \geq 0.05$) breed and year effects, live mass at *ca.* 3 days was influenced similarly as birth mass by sex, dam age and birth type (Table 2).

Table 2 The effects of breed, year, sex, dam age and birth type on lamb mass at the end of the observation period (*ca.* 3 days), and gain from birth to the end of the observation period in Dormer and SA Mutton Merino lambs

Effect	**Number of lambs**	**Live mass at *ca.* 3 days (kg)**	**Gain: birth to *ca.* 3 days (kg)**
Overall mean	518	5.0 ± 0.1	0.81 ± 0.04
Breed		NS	NS
Dormer	263	4.9 ± 0.1	0.85 ± 0.06
SA Mutton Merino	255	5.0 ± 0.1	0.77 ± 0.05
Year		NS	**
1989	171	5.0 ± 0.1	0.78^{1} ± 0.08
1990	159	4.9 ± 0.1	1.05^{2} ± 0.06
1991	188	5.0 ± 0.1	0.60^{1} ± 0.08
Sex		**	NS
Ram	268	5.1^{2} ± 0.1	0.83 ± 0.05
Ewe	250	4.8^{1} ± 0.1	0.79 ± 0.05
Dam age		**	NS
2 years	91	4.7^{1} ± 0.1	0.76 ± 0.08
3 – 6 years	362	5.1^{2} ± 0.1	0.84 ± 0.04
7+ years	65	5.2^{2} ± 0.1	0.83 ± 0.09
Birth type		**	**
Single	70	6.2^{3} ± 0.2	1.08^{3} ± 0.10
Twin	347	4.8^{2} ± 0.1	0.82^{2} ± 0.03
Triplet	101	4.0^{1} ± 0.1	0.53^{1} ± 0.08

NS = Not significant ($P > 0.05$); ** significant ($P \leq 0.01$).

$^{1-3}$ Denote significance ($P \leq 0.01$).

Gain to the end of the observation period (at ca. 3 days) was largely dependent of breed, sex and dam age (Table 2). The significant effects of birth year and birth type were complicated further by a significant ($P \leq 0.05$) interaction between these factors. In 1989, gain of single lambs (0.91 ± 0.20 kg; $n = 9$) was similar to that of twins (0.83 ± 0.06 kg; $n = 99$), with triplets gaining only slightly less (0.58 ± 0.09 kg; $n = 63$). In 1990, gain of triplets and twins was similar (0.94 ± 0.12 kg *vs*. 0.87 ± 0.06 kg; $n = 25$ and 94 respectively). In 1991, triplets gained markedly slower ($P \leq 0.05$) than twins or singles (0.13 ± 0.15 kg, $n = 13$ *vs*. 0.67 ± 0.06 kg, $n = 154$ and 0.98 ± 0.13 kg, $n = 21$ respectively). These effects could be related to sampling, as the number of singles in 1989 and triplets in 1991 were relatively few.

The gain to *ca*. 3 days of four single lambs that died between the end of the observation period and weaning was similar to that of 66 survivors (1.04 ± 0.10 *vs*. 0.83 ± 0.26 kg). In larger litters, the gain of lambs which subsequently died was lower ($P \leq 0.05$) than that of survivors in twins (0.894 ± 0.034 *vs*. 0.496 ± 0.069 kg; $n = 301$ and 46 respectively) and in triplets (0.721 ± 0.082 *vs*. 0.308 ± 0.097 kg; $n = 64$ and 37 respectively). On the basis of these results, lamb deaths in the post-observation period were regressed on gain to *ca*. 3 days. The overall regression coefficient suggested that lamb deaths declined by 0.23 ($SE_b = 0.04$) lambs died/lambs born for an increase of 1 kg in gain to *ca*. 3 days. Individual class regressions for breeds and birth years were similar, but it differed for the respective birth type classes. In singles, post-observational deaths were largely independent of gain to *ca*. 3 days ($b \pm SE = -0.03 \pm 0.04$), while lamb deaths and gain to *ca*. 3 days were related in twins ($b \pm SE = -0.22 \pm 0.04$) and triplets ($b \pm SE = -0.43 \pm 0.08$). The lack of a significant regression in the case of singles could probably be ascribed to the low level of deaths amongst singles in the post-observation period.

Discussion and Conclusions

Birth mass

Van der Merwe (1976) and Brand *et al.* (1985) reported that Dormer lambs weighed less ($P \leq 0.01$) at birth than SA Mutton Merinos. The interaction of breed and birth year, and the lack of a significant difference between the two breeds in 1991 should perhaps be seen as coincidental against this background. According to De Villiers and Cloete (1984), one of the intentions with the formation of the Dormer breed was to provide a sire breed suitable for terminal crossbreeding with Merino ewes. The comparatively small size of Dormer lambs at birth was seen as an advantage in this regard (Van der Merwe, 1976). The effects of sex and dam age on birth mass accorded with results in the literature (Hight and Jury, 1970; Dalton *et al.,* 1980; Scales *et al.*, 1986). Birth type effects corresponded to those reported by Maund *et al.* (1980), Hinch *et al.* (1985), Owens *et al.* (1985), and Scales *et al.* (1986).

Neonatal lamb progress

In this study we found that progeny of maiden ewes were slower to stand than those lambs born to adult and old ewes. Owens *et al.* (1985) reported that the first-born of multiple lambs of maidens took longer before they attempted to stand than first-born lambs of adult ewes. No effect of ewe age was observed in the investigation of Arnold and Morgan (1975).

Alexander *et al.* (1990) similarly found no parity effect in their study, but reported that lamb progress was affected by birth type. In this study we found that single lambs, born to mature ewes, progressed faster from standing to suckling and a similar tendency was observed in the progeny of old ewes, but in lambs borne by maiden ewes, singles were at a disadvantage compared to multiples. It seems reasonable to assume that progress in higher-order births should be slower than in singles (Owens *et al.,* 1985; Alexander *et al.,* 1990), although the effect may largely be related to birth mass differences (Slee and Springbett, 1986).

In the present study, heavier lambs were quicker to stand and to progress from standing to suckling as was reported by Owens *et al.* (1985) and Slee and Springbett (1986). The inclusion of birth mass as a covariate did not eliminate the effect of dam age, although it was somewhat reduced.

It is acknowledged that the present set of data was too small for a comprehensive genetic analysis. The heritability of lamb progress from standing to apparently suckling was furthermore smaller than twice its standard error, and thus not significant in conventional terms. The significant between-sire variance for lamb progress after birth does, however, warrant further attention. Although no significant breed variation occurred in the present investigation, Slee and Springbett (1986) and Alexander *et al.* (1990) reported significant differences between breeds. These differences suggest that these traits are, to an extent, determined genetically. The independence of the estimated heritability values from birth mass must also be seen against the observation that birth mass significantly influenced early lamb progress within, but not necessarily across, breeds (Slee and Springbett, 1986). It was furthermore clear that postnatal lamb progress was at least phenotypically related to subsequent lamb survival, as lambs which died later were slower to stand, and tended to be slower to progress from standing to suckling than their contemporaries which survived. Owens *et al.* (1985) correspondingly reported that an increase in time to standing and commencement in seeking the udder was associated with a concomitant decrease in survival. At this stage it was not even attempted to estimate a genetic correlation between subsequent lamb mortality and early postnatal progress, as it is generally known that between-sire variance for lamb survival is low (Smith, 1977; Cundiff *et al.*, 1982; Gama *et al.*, 1991) and the results are highly unpredictable. The practical application of these results in the industry is also doubtful, since it is evidently not practical to use it on a large scale in commercial flocks as a selection criterion. From a scientific viewpoint it is important to take cognisance of the possibility that neonatal lamb progress is heritable, which suggests that at least one component related to lamb mortality is controlled genetically. These results support the contention of Fogarty (1984) and Lindsay *et al.* (1990) that a measure of lamb survival should be included in selection programmes for increased fecundity. Neonatal progress may also be studied as a correlated response in selection programmes aimed at the improvement of ewe rearing ability and lamb survival (Atkins, 1980; Donnelly, 1982; Haughey, 1983) in order to understand the complex interrelationships between lamb survival and other traits.

Live-mass gain to ca. 3 days

Live-mass gain to *ca.* 3 days of age was found to be quite a reliable indicator of subsequent lamb mortality in twin and triplet lambs, as lambs which subsequently died gained less up to *ca.* 3 days than survivors. An increase of 1 kg in live-mass gain to *ca.* 3 days was associated with respective decreases of 22 and 43% in twin and triplet mortality. It is reasonable to assume that gain to *ca.* 3 days is mainly dependent on the maternal environment and milk supply. The present results thus support the conclusion of Haughey (1989) that a major part of deaths after 1 week of age was associated with symptoms of mismothering. The weighing of lambs at *ca.* 3 days may be of value for the identification of multiple lambs for handrearing in very intensive systems aimed at maximum output of lamb per ewe available, but needs to be refined further in order to fulfill this purpose. The possibility that lamb mortality may actually be increased in large flocks by human interference during such a practice must also be considered.

Acknowledgements

The author thanks the following persons for assistance rendered during the course of the investigation: P. Adams, S. Adams, T.S. Brand, F. Franck, J.E. Fourie, P. Lombard, Farida Martin, Ansie Scholtz, J.M. ten Hoope, J.B. van der Vyver and B.J. van Rooyen. I also thank Dr G. Alexander (CSIRO Division of Animal Production, P.O. Box 239, Blacktown, NSW 2148 Australia) and his team for the privilege to work under their guidance, albeit for a short period of time.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay, D.R., Pearce, D.T. (Eds.), Reproduction in sheep. Australian Academy of Science in Conjunction with Australian Wool Corporation, Canberra, Australia, 1984, pp. 199 - 209.

Alexander, G., 1988. What makes a good mother? Components and comparative aspects of maternal behaviour in ungulates. *Proceedings of the Australian Society of Animal Production* 17: 25 - 41.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27 - 38.

Arnold, G.W., Morgan, P.D., 1975. Behaviour of the ewe and lamb at lambing and its relationship to lambing mortality. *Applied Animal Ethology* 2: 25 - 46.

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of the Australian Society of Animal Production* 13: 174 - 176.

Brand, A.A., Cloete, S.W.P., De Villiers, T.T., 1985. Faktore wat lamvrektes in die Elsenburg Dormer- en SA Vleismerino-kuddes beïnvloed. *Suid–Afrikaanse Tydskrif vir Veekunde* 15: 155 - 161.

Cloete, S.W.P., 1992. Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and SA Mutton Merino ewes. *South African Journal of Animal Science* 22: 214 - 221.

Cundiff, L.V., Gregory, K.E., Koch, R.M., 1982. Selection for increased survival from birth to weaning. *Proceedings of the 2nd World Congress on Genetic Applied Livestock Production.* 1982, p. 310.

Dalton, D.C., Knight, T.W., Johnson, D.L., 1980. Lamb survival in sheep breeds on New Zealand hill country. *New Zealand Journal of Agricultural Research* 23: 167 - 173.

De Villiers, T.T., Cloete, S.W.P., 1984. The Dormer sheep breed. *Proceedings of the 2nd World Congress on Sheep and Beef Cattle Breeding,* 16 - 19 April 1984, Pretoria. South African Stud Book and Livestock Improvement Organisation, Bloemfontein 1984, p. 695.

Donnelly, F.B., 1982. A practical attempt to breed for better lamb survival. *Proceedings of the Australian Society for Animal Production* 14: 30 - 32.

Fogarty, N.M., 1984. Breeding for reproductive performance. In: Lindsay, D.R., Pearce, D.T. (Eds.), Reproduction in sheep. Australian Academy of Science in Conjunction with Australian Wool Corporation, Canberra, Australia, pp. 266 - 233.

Fourie, A.J., Cloete, S.W.P., 1990. Reproductive efficiency of breeding ewes in commercial Merino flocks in the Bredasdorp district. *Proceedings of the World Merino Conference* Vol. 2: 2 - 4 May 1009, Pretoria, Paper 5, p. 1.

Gama, L.T., Dickerson, G.E., Young, L.D., Leymaster, K.A., 1991. Genetic and phenotypic variation in sources of preweaning lamb mortality. *Journal of Animal Science* 69: 2744.

Harvey, W.R., 1977. User's guide for LSML76 – a mixed model least squares and maximum likelihood computer program. Ohio State University, Colombus.

Harvey, W.R., 1982. Least-squares analysis of discrete data. *Journal of Animal Science* 54: 1067.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361 - 363.

Haughey, K.G., 1989. Studies on causes of perinatal lamb mortality in the Western Cape and pelvic dimensions of ewes relative to their lifetime rearing performance. Report on activities during a visiting research fellowship 1987 - 1988, Department of Agriculture and Water Supply, Private Bag, Elsenburg.

Hight, G.K., Jury, K.E., 1970. Hill country sheep production. II. Lamb mortality and birth weights in Romney and Border Leicester x Romney flocks. *New Zealand Journal of Agricultural Research* 13: 735.

Hinch, G.N., Kelly, R.W., Davis, G.H., Owens, J.L., Crosbie, S.F., 1985. Factors affecting lamb birth weights from high fecundity Booroola ewes. *Livestock Production Science* 8: 53.

Hofmeyr, H.J., Boyazoglu, J.G., 1965. Verslag oor die opname by Merino-boere. Ongepubliseerde rapport, Departement Landbou-tegniese Dienste, Pretoria.

Lindsay, P.R., Nowak, R., Putu, I.G., McNeill, D., 1990. Behavioural interactions between the ewe and her young at parturition: A vital step for the lamb. In: Oldham, C.M., Martin, G.B. and Purvis, I.W. (Eds.), Reproductive physiology of Merino sheep, School of Agriculture, University of Western Australia, pp. 191 – 205.

Maund, B.A., Duffe, S.J., Winkler, C.E., 1980. Lamb mortality in relation to prolificacy. *Experimental Husbandry* 36: 99.

Nowak, R., Poindron, P., Le Neidre, P., Putu, I.G., 1987. Ability of 12-hour-old Merino and crossbred lambs to recognise their mothers. *Applied Animal Behaviour Science* 17: 263.

Owens, J.L., Bindon, B.M., Edey, T.M., Piper, L.R., 1985. Behaviour at parturition and lamb survival of Booroola Merino sheep. *Livestock Production Science* 13: 359 - 372.

Scales, G.N., Burton, R.N., Moss, R.A., 1986. Lamb mortality, birth weight, and nutrition in late pregnancy. *New Zealand Journal of Agricultural Research* 29: 75 - 82.

Slee, J., Springbett, Anthea, 1986. Early post-natal behaviour in lambs of ten breeds. *Applied Animal Behaviour Science* 15: 229 - 340.

Smith, G.M., 1977. Factors affecting birth weight, dystocia and preweaning survival in sheep. *Journal of Animal Science* 44: 745 - 753.

Stevens, D., Alexander, G., Mottershead, B., Lynch, J.J., 1984. Role of the lamb in postpartum separation of ewes from twin lambs. *Proceedings of the Australian Society of Animal Production* 15: 751.

Swiger, L.A., Harvey, W.R., Everson, D.O., Gregory, K.E., 1964. The variance of intra-class correlation involving groups with one observation. *Biometrics* 20: 818.

Van der Merwe, C.A., 1976. Genetiese en nie-genetiese faktore wat die produksie en reproduksie van die Elsenburg Dormerskaapkudde beïnvloed. Ph.D.-proefskrif, Universiteit van Stellenbosch.

CHAPTER 6

EASE OF BIRTH RELATION TO PELVIC DIMENSIONS, LITTER WEIGHT AND CONFORMATION OF SHEEP

S.W.P.Cloete[a], A.J.Scholtz[a], J.M.Ten Hoope[a], P.J.A.Lombard[a] and M.C.Francken[b]

[a] Elsenburg Agricultural Development Institute,
Private Bag X1, Elsenburg 7607, South Africa
[b] Regional Veterinary Laboratory,
Private bag X5020, Stellenbosch 7600, South Africa

Published in:
Small Ruminant Research (1998) 31: 51 - 60

Reproduced with permission of:
Small Ruminant Research

Ease of birth relation to pelvic dimensions, litter weight and conformation of sheep

S.W.P. Cloete, Anna J.Scholtz, J.M. Ten Hoope, P.J.A. Lombard
Elsenburg Agricultural Development Institute, Private Bag X1, Elsenburg, 7607, South Africa

M.C. Franken
Regional Veterinary Laboratory, Private Bag X5020, Stellenbosch 7600, South Africa

Accepted 21 February 1997

Abstract: Assistance at birth and probable cause for assistance were recorded for 335 SA Mutton Merino and 273 Dormer ewes during 1992 - 1995. Length of parturitions and litter weight were analysed for single and twin births only. Pelvic dimensions were obtained by radiographic pelvimetry. Subjective conformation was scored by an experienced classer. SA Mutton Merino ewes had shorter ($P \leq 0.01$) transverse diameters and longer ($P \leq 0.01$) conjugate diameters than Dormers. The area of the pelvic inlet did not differ between breeds. SA Mutton Merino ewes had higher ($P \leq 0.01$) scores for hind legs (side as well as hind view) than Dormers. They were also more likely to have a difficult birth than Dormers, as was reflected by higher ($P \leq 0.05$) levels of assistance at birth in single- and twin-bearing ewes, and longer ($P \leq 0.01$) parturitions. The causes for assisted birth differed between the two breeds. Dormer ewes were more ($P \leq 0.01$) likely to fail to deliver a lamb(s) as a result of uterine inertia, while posterior presentations and feto-pelvic disproportion were more ($P \leq 0.05$) prevalent in SA Mutton Merino. Ease of birth clearly influenced survival of birth, as reflected by a higher ($P \leq 0.01$) peri-parturient survival rate in lambs born naturally compared to those requiring assistance at birth (0.966 *vs.* 0.828; $Chi^2 = 48.8$). Length of parturition was also found to be longer ($P \leq 0.01$) in litters containing one or more lambs showing signs of birth stress at autopsy compared to litters where all lambs survived birth. A multiple stepwise regression for the prediction of length of parturition in SA Mutton Merino contained significant ($P \leq 0.01$) effects (in the order of inclusion) of conjugate diameter, litter weight, rump score and area of the pelvic inlet. The cumulative R^2 for the model at each step was 0.055, 0.106, 0.120, 0.134, respectively. Length of parturition depended ($P \leq 0.01$) on litter weight only for Dormer ewes ($R^2 = 0.131$), with no significant contributions from pelvic dimensions or conformation scores. It was concluded that these equations were of limited value in the prediction of ease of birth.

Keywords: Parturition; Birth difficulty; Pelvic dimensions; Litter weight; Ewe conformation; Survival

Introduction

Lamb mortality constitutes a major source of reproduction losses in sheep flocks worldwide (Alexander, 1984). Losses during the perinatal period (shortly before, during or within 7 days of birth) may contribute up to 80% of such losses (Haughey, 1991). Up to 60% of perinatal deaths could be attributed to stressful birth in the study of Haughey (1989).

Birth difficulty is widely regarded as being economically important in sheep (Haughey, 1991; Majeed and Taha, 1995) and cattle (Hagger and Hofer, 1990; Kriese *et al.*, 1994). Levels of birth difficulty were reported to differ between sheep breeds (Alexander *et al.*, 1990; Cloete, 1992) and between lines within breeds (Knight *et al.*, 1988). Little, however, is known of the specific mechanisms involved in these breed differences, although the relationship between pelvic dimensions and rearing performance was found to differ between lines (Haughey *et al.*, 1985) and breeds (Cloete, 1994). In beef cattle, it has been shown that dystocia cases could be predicted fairly accurately using information on pelvic dimensions and the weight of the foetus (Morrison *et al.*, 1985; Johnson *et al.*, 1988). Conformation traits have also been assessed in relation to dystocia in cattle (Dadati *et al.*, 1985; Johnson *et al.*, 1988). No corresponding information could be obtained for sheep.

Birth difficulty in South African (SA) Mutton Merino and Dormer sheep was studied against this background. The investigation included information regarding pelvic dimensions, litter size and weight, as well as conformation in relation to length of parturition.

Material and Methods

Experimental animals and location

The investigation was carried out on the Elsenburg SA Mutton Merino (Vosloo, 1967) and Elsenburg Dormer (Van Wyk, 1992) registered sheep studs, comprising about 150 breeding ewes each. The Dormer is a synthetic breed, developed from a cross between the German Merino and Dorset Horn in the mid-1940s (Van Wyk, 1992). The Dormer breed originated from the Elsenburg stud, which is still maintained as a closed flock.

During the course of the experiment, the self-replacing flocks were mated in single sire groups to seven rams within breeds during October - November, to lamb in March - April. Mating and lambing took place on irrigated kikuyu (*Pennisetum clandestinum)* pastures, subdivided into units of approximately 0.5 ha each. The breeding flock were maintained on dry-land lucerne (*Medicago sativa*) or oat (*Avena sativa)* pastures during winter and spring, and on irrigated kikuyu paddocks of 1.5 – 2.0 ha during the dry summer months. Both flocks lambed in full fleece, being crutched ≤ 4 weeks before lambing. Although the breeds were maintained in separate flocks prior to and after lambing, they utilised similar pastures.

Data recorded

Details of the parturition process were recorded at lambing by trained observers. These observations were carried out on 10 irrigated kikuyu paddocks (approximately 0.5 ha each) of which five were floodlit for use at night (Cloete, 1992). Length of parturition (the period from the first sign of impending birth up to the last lamb) was recorded for 355 SA Mutton Merino and 273 Dormer parturitions during the period 1992 - 1995. Ewes that failed to deliver a lamb by 4 h after parturition started (64 SA Mutton Merinos and 25 Dormers) were assisted. After careful vaginal examination, the malpresentation of the fetus(es) was corrected, and the lamb(s) were delivered by manual traction. The probable cause of birth difficulty and presentation of the fetus(es) were recorded at this stage. Attempts were made to classify birth difficulty as being of fetal or maternal origin, adapting criteria set out by Majeed and Taha (1995) for this purpose. Lamb and litter weight were recorded within 24 h of birth. The lambs which died during and within 7 days of birth were autopsied, using the procedures and classification described by Cloete *et al.* (1993). Lambs that survived birth for at least 8 h were regarded as having survived the peri-parturient period.

Pelvic dimensions of 180 SA Mutton Merino and 182 Dormer 2.5 years or older ewes were recorded by radiographic pelvimetry performed between August and November, after shearing. The radiographic technique (method C) described by Haughey and Gray (1982) was used. Pelvic dimensions estimated were the transverse diameters (the maximum distance between the ilia of the pelvis), conjugate diameter (the distance between the sacral promontory and the pecten of the pubis) and the area of the pelvic inlet (the product of the transverse and conjugate diameter). The maximum angle (A) between the sacrum and conjugate diameter was also estimated, as depicted in Fig. 1. This angle could be estimated reliably, judged from a correlation of 0.916 between replicate estimates made on separate lateral radiographs obtained from the same animal ($n = 30$).

Conformation traits were assessed subjectively, using a 50-point linear scoring system as described by Olivier *et al.* (1987). Three traits were scored by an experienced classer. These included the slope of the rump (1 – very steep slope; 25 - intermediate slope; 50 - square rump with virtually no slope), side view of the hind legs (1 – stance very sickle-hocked; 25 – stance normal; 50 – stance very straight-hocked or upright) and hind view of the hind legs (1 – cow hocked; 25 – straight hocked; 50 – very bow-legged).

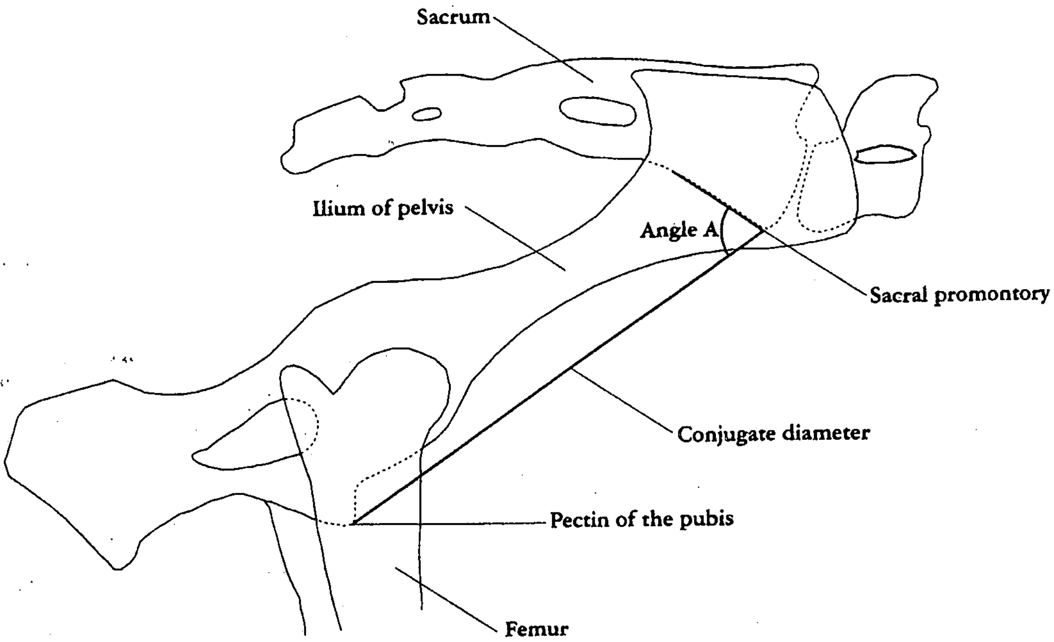


Fig.1. Schematic representation of the lateral view of the pelvis, depicting the maximum angle of the sacrum with the conjugate diameter as angle *A*.

Statistical methods

Proportions were compared using *Chi*^{2} - procedures, or Fisher's exact test, depending on the number and distribution of observations (Siegel, 1956). Mean litter size at birth was compared for the two breeds by using the method described by Brown (1988). Length of parturition and litter weight were analysed by fixed model least squares procedures (Harvey, 1990). Length of parturition was analysed after a standard $\log_{10}$ transformation, stabilizing its variance. The fixed model included the effects of breed (SA Mutton Merino and Dormer), year (1992 - 1995), age (2 - 6 years) and litter size (single or twin). Triplet parturitions were excluded as they were relatively few (39 for SA Mutton Merinos and seven for Dormers). Interactions between main effects were not significant, but the breed and litter size interaction was retained to account for litter size differences between breeds.

A dataset comprising 178 ewes that were observed two or more times at lambing was used to estimate the repeatability of length of parturition and litter weight. Phenotypic correlations of length of parturition with litter size, litter weight, transverse diameter, conjugate diameter, area of the pelvic inlet, pelvic angle, rump score, hind leg score (side as well as hind view) and live weight at radiography were calculated. Length of parturition was also regressed on these variables using stepwise regression techniques. Separate analyses were conducted for each breed, as there was strong evidence of breed differences in the relationships of length of parturition with the respective independent variables.

Results

Levels and causes of assistance at birth

The average litter size of SA Mutton Merino ewes at birth (1.87) was higher (Chi^2 = 35.9; $P \leq 0.01$) than that of Dormers (1.59). Single- and twin-bearing SA Mutton Merino ewes were more ($P \leq 0.05$) likely to require assistance at birth than Dormers (Table 1). No breed difference was recorded for triplet births. Overall, levels of assistance in SA Mutton Merino ewes were about twice that in Dormer ewes ($P <$ 0.01).

Table 1. Assistance at parturition to SA Merino and Dormer ewes during 1992 - 1995

Litter size	**Breed**		***Chi***^{2}
	SA Mutton Merino	**Dormer**	
Single			
Number of ewes	84	119	
Proportion assisted	0.155	0.059	4.08*
Twin			
Number of ewes	212	147	
Proportion assisted	0.198	0.109	4.47*
Triplets			
Number of ewes	39	7	
Proportion assisted	0.231	0.286	0.0 ^{NS}
Overall			
Number of ewes	335	273	
Proportion assisted	0.191	0.092	11.13**

NS, *, ** = $P > 0.05$, $P \leq 0.05$, $P \leq 0.01$, respectively.

Numbers within litter size classes precluded comparisons of causes recorded for rendering of assistance of singles, twins and triplets, separately. No breed differences were found with regard to assistance required as a result of the malpresentation of the head of the fetus, or as a result of lambs entangled in the birth canal. There was a suggestion that posterior presentations were more prevalent in SA Mutton Merinos than in Dormers ($P < 0.05$). In totality, lambs were presented in the anterior, longitudinal position in 84.9% of ewes requiring assistance associated with causes of fetal origin.

Marked-breed differences were recorded for birth difficulty of maternal origin (Table 2). Dormers were much more likely ($P < 0.01$) to be classified to have uterine inertia than SA Mutton Merinos.

Table 2. Causes recorded for rendering of assistance at birth to SA Mutton Merino and Dormer ewes

Origin and description	**Breed**		**Fisher's exact probability**
	SA Mutton Merino	**Dormer**	
Total number of assisted births	64	25	
Causes of fetal origin:			
Number of observations	36	17	
Proportion of total	0.563	0.680	
Description:			
Malpresentation of head	0.083 (3)[a]	0.0 (0)[a]	0.610
Malpresentation of limbs	0.611 (22)	0.765 (13)	0.613
Posterior presentations	0.222 (8)	0.0 (0)	0.044
Lambs entangled in birth canal	0.083 (3)	0.235 (4)	0.404
Causes of maternal origin:			
Number of observations	28	8	
Proportion of total	0.438	0.320	
Description:			
Uterine inertia	0.321 (9)[a]	0.875 (7)[a]	0.012
Failure of cervix to dilate	0.107 (3)	0.125 (1)	1.000
Feto-pelvic disproportion	0.571 (16)	0.0 (0)	0.005

[a] Number of ewes shown in parentheses

Fetuses of these ewes were presented normal, with no indication of feto-pelvic disproportion. Lambs were easily delivered by manual traction. The proportion of ewes where the cervix failed to dilate completely or partially was similar for both breeds. This condition was limited to ewes bearing multiples. The presenting fetus was invariably positioned with its rump or shoulder against the cervix, suggesting that the failure of the cervix to dilate may be due to mechanical reasons. Feto-pelvic disproportion was cited as reason for assistance in more than 50% of SA Mutton

Merino births where birth difficulty of maternal origin was recorded. This condition was absent in Dormers, the breed difference being significant ($P < 0.01$).

Peri-parturient survival of lambs

Peri-parturient survival was similar ($P > 0.15$) for SA Mutton Merino and Dormer lambs when classified according to cause of birth difficulty (Table 3) for the categories where breed comparisons were possible.

Table 3. Survival of birth in SA Mutton Merino and Dormer lambs classified according to cause recorded for assistance of mother

Description	**Breed**		**Fisher's exact probability**
	SA Mutton Merino	**Dormer**	
Total number of lambs requiring assistance	124	45	
Causes of fetal origin:			
Number of lambs born	73	31	
Description:			
Malpresentation of head or limbs	0.936 (47)[a]	0.864 (22)[a]	0.375
Posterior presentations	0.789 (19)	- (0)	-
Lambs entangled in birth canal	0.571 (7)	0.889 (9)	0.262
Causes of maternal origin:			
Number of lambs born	51	14	
Description:			
Uterine inertia	1.000 (17)[a]	0.917 (12)[a]	0.414
Failure of cervix to dilate	0.286 (7)	0.000 (2)	1.000
Feto-pelvic disproportion	0.741 (27)	- (0)	-

[a] Number of lambs born is shown in parentheses

Lambs of the respective breeds were pooled, to get an indication of differences in survival of birth between the respective birth-difficulty classes. Peri-parturient survival was not affected ($P > 0.15$) by classification in cases where birth difficulty of fetal origin was diagnosed. Peri-parturient survival of all the lambs involved was, however, lower than in 891 contemporaries born naturally (0.865 *vs.* 0.966; $Chi^2 = 20.1$; $P < 0.01$). Survival of birth was high in lambs assisted because of uterine inertia (Table 3). Lambs born to ewes where the cervix failed to dilate properly, or where feto-pelvic disproportions were recorded, had lower ($P < 0.05$) peri-parturient survival rates compared to lambs borne by ewes with uterine inertia. The difference between the latter two groups was also significant ($P < 0.05$). Peri-parturient survival was impaired ($P < 0.01$) relative to unassisted contemporaries in lambs where feto-pelvic disproportion was recorded (0.741 *vs*. 0.966; $Chi^2 = 28.9$; $P < 0.01$) and in lambs born to ewes where the cervix failed to dilate properly (0.222 *vs*. 0.966; $Chi^2 = 107.0$; $P < 0.01$).

Peri-parturient survival was marginally higher in 434 Dormer lambs born in the study than in 626 SA Mutton Merino contemporaries (0.963 *vs*. 0.933; $Chi^2 = 3.29$; $P = 0.07$).

Length of parturition, litter weight and stressful births

The parturitions of single and twin-bearing SA Mutton Merino ewes were 28.5 min longer (53%; $P < 0.01$) compared to their Dormer contemporaries (Table 4). The difference in litter weight at birth amounted to 9.4% ($P < 0.01$). The inclusion of litter weight as a linear covariable in the model resulted in a marginal reduction in the breed difference for length of parturition, but it remained significant (Log_{10} transformed means: SA Mutton Merino 1.916 ± 0.026; Dormer 1.784 ± 0.028; respective antilogs 82.3 *vs*. 60.8 min; $P < 0.01$). Length of parturition was independent of year of birth and ewe age (Table 4). Litter weight was higher ($P < 0.05$) in 1995 than in 1993 and 1994. It increased ($P < 0.05$) with increasing ewe age, to stabilize at 4 - 6 years. Both length of parturition and litter weight were increased ($P < 0.01$) in twin births relative to singles.

The between year repeatability of the length of parturition was 0.28 ± 0.07 (degrees of freedom were 176 for ewes within breeds; 228 for remainder with a *k*-value of 2.11). The corresponding estimate to litter weight was 0.22 ± 0.07. The inclusion of triplets in the dataset on litter weight as a covariable only resulted in marginal changes in the repeatability estimate for length of parturition.

Length of parturition in 29 litters containing one or more birth stressed lambs was nearly two times longer ($P < 0.05$) than in 502 litters where all lambs survived the perinatal period (Log_{10} transformed means being 2.01 ± 0.07 *vs*. 1.80 ± 0.02 min, respectively). Length of parturition in 31 litters where another cause of perinatal death was diagnosed, was similar to litters where all lambs survived (Log_{10} transformed means being 1.78 ± 0.07 *vs.* 1.80 ± 0.02 min, respectively).

Table 4. Means (± *SE*) for length of parturition and litter weight at birth according to breed, birth year, ewe age and number of lambs born

Effect	Number of observations	Log_{10} of length of parturition	Antilog (min)	Litter weight (kg)
Overall mean	562	1.81 ± 0.019	66.2	6.35 ± 0.046
Breed				
Dormer	266	$1.728^{2} \pm 0.025$	53.5	$6.06^{2} \pm 0.062$
SA Mutton Merino	296	$1.914^{1} \pm 0.026$	82.0	$6.63^{1} \pm 0.065$
Year		NS		*
1992	86	1.856 ± 0.044	71.8	$6.33^{b,a} \pm 0.11$
1993	156	1.805 ± 0.032	63.8	$6.26^{b} \pm 0.08$
1994	146	1.772 ± 0.032	59.2	$6.23^{b} \pm 0.08$
1995	174	1.849 ± 0.030	70.6	$6.55^{a} \pm 0.08$
Age		NS		**
2 years	138	1.839 ± 0.033	69.0	$5.65^{c} \pm 0.08$
3 years	134	1.754 ± 0.034	56.8	$6.26^{b} \pm 0.09$
4 years	121	1.833 ± 0.037	68.1	$6.64^{a} \pm 0.09$
5 years	90	1.832 ± 0.042	67.9	$6.64^{a} \pm 0.11$
6 years	79	1.847 ± 0.044	70.3	$6.54^{a} \pm 0.11$
Number of lambs born		**		**
Single	203	$1.715^{2} \pm 0.029$	51.9	$4.87^{2} \pm 0.07$
Twin	359	$1.926^{1} \pm 0.021$	84.3	$7.82^{1} \pm 0.05$

*, ** = $P \leq 0.05$, $P \leq 0.01$

^{a,b} Denote significance ($P < 0.01$) in columns.

^{c,d,e} Denote significance ($P < 0.05$) in columns.

NS Not significant ($P > 0.05$)

Pelvic dimensions and conformation scores

Dormer ewes had a 1.8% longer ($P < 0.05$) transverse diameter and a 3% shorter ($P < 0.05$) conjugate diameter than the corresponding dimensions in SA Mutton Merinos (Table 5). The area of the pelvic inlet consequently did not differ between the two breeds, but the angle of the sacrum with the conjugate diameter was larger ($P < 0.01$) in Dormer relative to SA Mutton Merino ewes.

The breeds did not differ for mean rump score, the SA Mutton Merino ewes were more ($P < 0.01$) sickle-hocked and bow-legged than the Dormers (Table 5). The mean live weight of ewes at radiography did not differ between breeds.

Table 5. Means (± *SE*) for pelvic dimensions and subjective conformation scores of Dormer and SA Mutton Merino ewes

Trait	**Breed**		**Significance of breed difference**
	SA Mutton Merino	**Dormer**	
Number of observations	180	182	
Pelvic dimensions			
Transverse diameter (cm)	9.78 ± 0.03	9.96 ± 0.03	**
Conjugate diameter (cm)	11.96 ± 0.05	11.60 ± 0.05	**
Pelvic area (cm^2)	116.6 ± 0.5	115.7 ± 0.5	NS
Pelvic angle (degrees)	67.5 ± 0.4	71.5 ± 0.4	**
Subjective scores			
Rump	26.1 ± 0.2	25.9 ± 0.2	NS
Back legs (side view)	25.3 ± 0.1	25.9 ± 0.1	**
Back legs (hind view)	25.5 ± 0.1	24.5 ± 0.1	**
Live weight at radiography	67.1 ± 0.6	68.3 ± 0.6	NS

NS, **$P > 0.05$, $P \leq 0.01$.

Relations with length of parturition

Pelvic dimensions of SA Mutton Merino ewes were associated with length of parturition (Table 6), but no such relationship existed in Dormers. Larger and heavier litters resulted in longer parturitions in both breeds, the relationship being more pronounced in Dormers. Subjective scores for rump suggested that SA Mutton Merino ewes with sloping rumps would generally have shorter parturitions than square-rumped contemporaries. The corresponding correlation in Dormer ewes was not significant. Apart from significant correlations with litter size and litter weight, length of parturition was largely independent of other known sources of variation in Dormer ewes. Even significant correlations in both breeds were generally low, accounting for only 3,2 - 13.2% of the variation in length of parturition. There was, however, a clear suggestion that the mechanisms involved in length of parturition differed in the two breeds.

The stepwise regression model for length of parturition of SA Mutton Merino ewes included the significant ($P < 0.01$) effects of conjugate diameter, litter weight, subjective score for rump and area of the pelvic inlet in order of selection. Cumulative R^2 values after each step were 0.055, 0.106, 0.120 and 0.134, respectively. Inclusion of litter weight eliminated litter size effects, and inclusion of conjugate diameter accounted for a large proportion of the effect of area of the pelvic inlet. A large portion of the variation in length of parturition was not accounted for, as reflected by a cumulative R^2 value of 0.134 for the final fitted model. Regression for Dormer ewes only included litter weight in the final model, with an R^2 value of 0.131. Inclusion of this variable completely eliminated the influence of litter size, as was also found for SA Mutton Merinos. Both regressions were, thus, of limited predictability, particularly if only traits measurable on the dam prior to parturition were considered.

Table 6. Correlations of maternal and fetal characteristics with length of parturition ($\log_{10}$ transformed) of 277 SA Mutton Merino and 232 Dormer parturitions.

Trait	**Breed**	
	SA Mutton Merino	**Dormer**
Pelvic dimensions		
Transverse diameter (cm)	-0.03	0.02
Conjugate diameter (cm)	-0.24**	0.01
Pelvic area (cm^2)	-0.21**	0.02
Pelvic angle (degrees)	0.09	0.03
Litter characteristics		
Litter size	0.19**	0.30**
Litter weight (kg)	0.23**	0.36**
Conformation traits		
Rump	0.18**	0.12
Back legs (side view)	-0.06	-0.08
Back legs (hind view)	-0.04	0.08
Live weight at radiography	-0.03	0.11

** $P \leq 0.01$

Discussion

Survival of birth (peri-parturient survival) was clearly associated with ease of birth. These findings are in good agreement with previous reports in the literature (Arnold and Morgan, 1975; Scales *et al.*, 1986; Haughey, 1991; Cloete, 1992; Cloete *et al.*, 1993). The percentage of lambs not surviving the birth process in this study (3.7% in Dormers and 6.7% in SA Mutton Merinos) contributed about 50% to the overall perinatal lamb death, making it an economic source of reproductive failure taken cognisance of Haughey (1989).

Assistance at birth could be attributed to fetal factors in 56 - 68% of the cases in SA Mutton Merino and Dormer ewes. Majeed and Taha (1995) correspondingly reported that 54% of dystocia cases in Awassi ewes were of fetal origin. Their study reported more cases where the cervix failed to dilute sufficiently (ringwomb) and fewer cases of uterine inertia than the present study. This difference is understandable, given the background that problem cases were brought to them, probably after assisted delivery by manual correction of malpresentation and traction by owner were found to be unsuccessful. The percentage of posterior presentations was lower than anterior presentations, as was also reported by Grommer *et al.* (1985) and Majeed and Taha (1995).

Birth difficulty was clearly more likely to be encountered in single- and twin-bearing SA Mutton Merino ewes than Dormers. There was, however, no breed difference in levels of assistance to triplet-bearing ewes. This result is in close agreement with a previous study (Cloete, 1992), but more likely to be associated with a lack of observation than biological differences between triplet-bearing ewes of the two breeds and twin- and single-bearing contemporaries.

It thus, seems reasonable that Dormer ewes experienced easier parturition than SA Mutton Merinos, as was reported previously (Cloete, 1992). This result accorded with literature reports regarding breed differences in birth stress and dystocia cases (Smith, 1977; Dalton *et al.*, 1980; Wooliams *et al.*, 1983; Grommer *et al.*, 1985; Alexander *et al.*, 1990). Selection within breeds was also reported to have an influence on ease of birth or peri-parturient lamb mortality percentages (Haughey, 1983; Knight *et al.*, 1988), supporting the contention that these traits are partially under genetic control. The fact that length of parturition was repeatable in the study also contributes to this line of reasoning, although the repeatability estimate was marginally lower than the previous one on an earlier, smaller dataset in the same breed (Cloete, 1992). No other supporting evidence was found in the sheep literature, but a small and real tendency to repeat prior calving performance was also reported for dairy cattle (Thompson and Rege, 1984). Repeatability estimates for calving difficulty score in the latter study was 0.10 - 0.16 depending on the parities involved.

The etiology of birth difficulty, leading to assistance at birth, was markedly dissimilar between breeds. It was previously reported that flock rearing performance of Dormer ewes was unrelated to pelvic size (Cloete, 1994). Flock performance of three other flocks in a latter study, including the Elsenburg SA Mutton Merino flock, could be related to one or more pelvic dimensions. It stands to reason, and it has been shown previously that dystocia, still-birth and mal-presentation were associated with small maternal pelvic size (Fogarty and Thompson, 1974; McSporran and Fielden, 1979). Rearing performance was also found to be associated with pelvic dimensions, and particularly conjugate diameter, on a flock basis (Haughey *et al.*, 1985; Cloete, 1994). Flocks selected for improved lamb rearing performance were further found to have larger pelvic inlets than unselected control population (Knight *et al.*, 1988; Kilgour and Haughey, 1993). Present results, and those obtained previously (Haughey *et al.*, 1985; Cloete, 1994), however, suggest that this relationship could not be generalised to include all breeds and flocks.

Litter weight was contained in the final equations for the prediction of length of parturition in both breeds. Since it is only known after lambing, it cannot be included in a model attempting to predict length of parturition on prior knowledge. It could be argued that litter size, determined by ultrasonography (Fowler and Wilkins, 1984) could be used as a substitute, without a marked reduction in accuracy. The accuracy of predictions is, however, too low to be of practical significance in sheep husbandry ($R^2 \approx 0.13$). It is important, however, to recognize the marked difference between two breeds. In cattle, where the situation is not complicated by multiple births, it has been shown that pelvic size and calf weight are traits of major importance for the prediction of dystocia (Morrison *et al.*, 1985; Johnson *et al.*, 1988; Basarab *et al.*, 1993). These results stand to reason, and the significant contributions of litter weight and pelvic dimensions to the prediction equation in SA Mutton Merinos could, thus, be expected. Independency of length of parturition from pelvic size in Dormers does not conform to the conceptual model, and requires further investigation. The only other significant factor was subjective score for rump in SA Merinos. No comparable results were obtained from the sheep literature, but Philipson (1976) and Dadati *et al.* (1985) reported that a sloping rump was associated with calving ease in dairy cattle. Johnson *et al.* (1988) measured the slope of the rump in Hereford Heifers objectively, but neither this, nor subjective estimation were correlated with the calving difficulty score. The angle between the sacrum and conjugate diameter was similarly not associated with length of parturition in the present study.

The marked difference in the etiology of birth difficulty in two related breeds highlights the necessity for a comprehensive study on dystocia and ease of lambing in sheep. Dystocia and still-births have been subjected to genetic analyses in beef and dairy cattle, as reviewed by Meijering (1984) and reported more recently by Hagger and Hofer (1990). Corresponding studies on sheep are rare, although overall lamb mortality from birth to weaning has been subjected to genetic analyses, using linear and/or nonlinear methods (Yapi *et al.*, 1992; Brash *et al.*, 1994a, b; Konstantinov *et al.*, 1994). Heritability in these studies was mostly equal to or below 0.10. Analysts generally concluded that fast progress to selection for lamb survival is unlikely. Selection studies on lamb survival, however, obtained surprisingly large realised responses (Donnelly, 1982; Haughey, 1983; Knight *et al.*, 1988). Peri-parturient survival (Haughey, 1983) and ease of birth (Knight *et al.*, 1988) were among the factors probably leading to improved lamb survival in these studies.

Conclusions

Ease of parturition could not be predicted with reasonable accuracy when the variables recorded in this study were used. Clear differences in the mechanisms involved in the birth process emerged between the two related breeds (the Dormer is a synthetic with the SA Mutton Merino as one parent). Involvement of genetic factors in the differences should be elucidated in further investigations, to assist in the formulation of sound selection goals for dual purpose and mutton sheep.

Acknowledgements

The authors wish to thank Messrs J.E. Fourie, P. Adams, S. Adams, B.J. van Rooyen, P.W. de Bruyn and Miss F. Martin for assistance with observation, radiographic pelvimetry of ewes, maintenance of the breeding flock and recording of data. We would also like to thank Mr. A. Engelbrecht for the preparation of the figure. The study was supported by a grant from the SA Wool Board, enabling the purchase of radiographic equipment.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay, D.R., Pearce, D.T. (Eds.), Reproduction in sheep. Australian Academy of Science in Conjuction with Australian Wool Corporation, Canberra, Australia, pp. 199 - 209.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27 - 38.

Arnold, G.W., Morgan, P.D., 1975. Behaviour of the ewe and lamb at lambing and its relationship to lambing mortality. *Applied Animal Ethology* 2: 25 - 46.

Basarab, J.A., Rutter, L.M., Day, P.A., 1993. The efficiency of predicting dystocia in yearling beef heifers: II. Using discriminant analysis. *Journal of Animal Science* 71: 1372 - 1380.

Brash, L.D., Fogarty, N.M., Gilmour, A.R., 1994a. Reproductive performance and genetic parameters for Australian Dorset sheep. *Australian Journal of Agricultural Research* 45: 427 - 441.

Brash, L.D., Fogarty, N.M., Gilmour, A.R., 1994b. Genetic parameters for Australian maternal and dual-purpose meatsheep breeds. II. Live weight, wool and reproduction in Corriedale sheep. *Australian Journal of Agricultural Research* 45: 469 - 480.

Brown, G.H., 1998. The statistical comparison of reproduction rates for group of sheep. *Australian Journal of Agricultural Research* 39: 899 - 905.

Cloete, S.W.P., 1992. Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and SA Mutton Merino ewes. *South African Journal of Animal Science* 22: 214 - 221.

Cloete, S.W.P., 1994. Rearing performance of Merino, SA Mutton Merino and Dormer ewes in relation to live mass, reproduction and pelvic dimensions. *Journal of the South African Veterinary Association* 65: 10 – 17.

Cloete, S.W.P., Van Halderen, A., Schneider, D.J., 1993. Causes of perinatal lamb mortality amongst Dormer and SA Mutton Merino lambs. *Journal of the South African Veterinary Association* 64: 121 - 125.

Dadati, E., Kennedy, B.W., Burnside, E.B., 1985. Relationships between conformation and reproduction in Holstein cows: Type and calving performance. *Journal of Dairy Science* 68: 2639 – 2645.

Dalton, D.C., Knight, T.W., Johnson, D.L., 1980. Lamb survival in sheep breeds on New Zealand hill country. *New Zealand Journal of Agricultural Research* 23: 167 - 173.

Donnelly, F.B., 1982. A practical attempt to breed for better lamb survival. *Proceedings of Australian Society of Animal Production* 14: 30 - 32.

Fogarty, N.M., Thompson, J.M., 1974. Relationship between pelvic dimensions, other body measurements and dystocia in Dorset Horn ewes. *Australian Veterinary Journal* 50: 502 - 506.

Fowler, D.G., Wilkins, J.F., 1984. Diagnosis of pregnancy and number of fetuses in sheep by real-time ultrasonic imaging. I. Effects of number of fetuses, stage of gestation, operator and breed of ewe on accuracy of diagnosis. *Livestock Production Science* 11: 437 - 450.

Grommer, F.J., Elving, L., Van Eldike, P., 1985. Parturition difficulties in sheep. *Animal Reproduction Science* 9: 365 - 374.

Hagger, C., Hofer, A., 1990. Genetic analysis of calving traits in the Swiss Black and White, Braunvieh and Simmental breeds by REML and MAPP procedures. *Livestock Production Science* 24: 93 - 107.

Harvey, W.R., 1990. User's guide for LSMLMW and MIXMDL. PCL – version, MIMEOGRAPH.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361 - 363.

Haughey, K.G., 1989. Studies on causes of perinatal lamb mortality in the western Cape and pelvic dimensions of ewes relative to their lifetime rearing performance. Report on activities during a visiting research fellowship 1987 – 1988, Department of Agriculture and Water Supply, Private Bag, Elsenburg.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Haughey, K.G., George, J.M., McGuirk, B.J., 1985. The repeatability of rearing performance of Merino and Dorset Horn ewes and its relationship with mature pelvic size. *Australian Journal of Experimental Agriculture* 25: 541 - 549.

Haughey, K.G., Gray, C.H., 1982. A radiographic technique for pelvimetry of unanaesthestised ewes and a comparison of three methods of estimating the area of the pelvic inlet. *Australian Veterinary Journal* 58: 51 - 59.

Johnson, S.K., Deutcher, G.H., Parkhurst, A., 1988. Relationship of pelvic structure, body measurements, pelvic area and calving difficulty. *Journal of Animal Science* 66: 1081 - 1088.

Kilgour, R.J., Haughey, K.G., 1993. Pelvic size in Merino ewes selected for lambrearing ability is greater than that of unselected Merino ewes. *Animal Reproduction Sciences* 31: 237 - 242.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259 - 271.

Konstantinov, K.V., Erasmus, G.J., Van Wyk, J.B., 1994. Evaluation of Dormer sires for litter size and lamb mortality using a threshold mode. *South African Journal of Animal Science* 24: 119 - 121.

Kriese, L.A., Van Vleck, L.D., Gregory, K.E., Bolman, K.G., Cundiff, L.V., Koch, R.M., 1994. Estimates of genetic parameters for 320 - day pelvic measurements of males and females and calving ease of 2-year-old females. *Journal of Animal Science* 72: 1954 - 1963.

Majeed, A.F., Taha, M.B., 1995. Obstetrical disorders and their treatment in Iraqi Awassi ewes. *Small Ruminant Research* 17: 65 - 69.

McSporran, K.D., Fielden, E.D., 1979. Studies on dystocia in sheep. II. Pelvic measurements of ewes with histories of dystocia and eutocia. *New Zealand Veterinary Journal* 27: 75 - 78.

Meijering, A., 1984. Dystocia and stillbirths in cattle – a review of causes, relations and implications. *Livestock Production Science* 11: 143 - 177.

Morrison, D.B., Humes, P.E., Ketih, N.K., Godke, R.A., 1985. Discriminant analysis for predicting dystocia in beef cattle. I. Comparison with regression analysis. *Journal of Animal Science* 60: 608 - 616.

Olivier, J.J., Delport, G.J., Erasmus, G.J., Eksteen, T.J., 1987. Linear-type scoring in Merino sheep. *Karoo Agric* 3(9): 1 - 4.

Philipson, J., 1976. Studies on calving difficulty, still-birth and associated factors in Swedish cattle breeds. IV. Relationships between calving performance, precalving body measurements and size of pelvic opening of Friesland Heifers. *Acta Agriculturae Scandinavica* 26: 221 - 229.

Scales, G.H., Burton, R.N., Moss, R.A., 1986. Lamb mortality, birth weight and nutrition in late pregnancy. *New Zealand Journal of Agricultural Research* 29: 75 - 82.

Siegel, S., 1956. Non Parametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Smith, G.M., 1977. Factors affecting birth weight, dystocia and preweaning survival in sheep. *Journal of Animal Science* 44: 745 - 753.

Thompson, J.R., Rege, J.E.O., 1984. Influences of dam on calving difficulty and early calf mortality. *Journal of Dairy Science* 67: 847 - 853.

Van Wyk, J.B., 1992. The Genetic Evaluation of the Elsenburg Dormer stud. Ph.D. dissertation, University of the Orange Free State, South Africa.

Vosloo, L.P., 1967. Faktore wat die produksie en reproduksie van die Elsenburg Duitse Merinovleisskaapkudde beïnvloed (in Afrikaans). Ph.D. dissertation, University of Stellenbosch, South Africa.

Woolliams, Carol, Weiner, G., MacLeod, N.S.M., 1983. The effect of breed, breeding system and other factors on lamb mortality. 2. Factors influencing the incidence of delayed birth, dystocia, congenital deaths and miscellaneous causes of early death. *Journal of Agricultural Science, Cambridge* 100: 553 – 562.

Yapi, V.V., Boylan, W.J., Robinson, R.A., 1992. Heritability and repeatability estimates and correlations of lamb mortality with birth weight and litter size. *World Review of Animal Production* 27: 55 - 60.

CHAPTER 7

GENETIC AND ENVIRONMENTAL EFFECTS ON LAMBING AND NEONATAL BEHAVIOUR OF DORMER AND SA MUTTON MERINO LAMBS

S.W.P.Cloete[a], A.J.Scholtz[a], A.R.Gilmour[b] and J.J.Olivier[c]

[a]Animal Production Division, Elsenburg Agricultural Development Centre,
Private bag X1, Elsenburg 7607,
South Africa
[b]New South Wales Agriculture, Orange Agricultural Institute,
Forest Road, Orange 2800,
New South Wales, Australia
[c]Agricultural Research Council: Animal Improvement Institute
Private Bag X529, Middelburg 5900,
South Africa

Published in:
Livestock Production Science (2002) 78: 183 - 193.

Genetic and environmental effects on lambing and neonatal behaviour of Dormer and SA Mutton Merino lambs

S.W.P. Cloete[a], Anna J. Scholtz[a], A.R. Gilmour[b], J.J. Olivier[c]

[a]Animal Production Division, Elsenburg ADC, Private Bag X1, Elsenburg 7607, South Africa

[b]NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia.

[c]ARC:Animal Improvement Institute, Private Bag X529, Middelburg, 5900, South Africa

Abstract: Data were accumulated for birth weight, lambing and neonatal behaviour of Dormer and SA Mutton Merino lambs from 1989 - 1998. Numbers of records amounted to 1167 - 1298 for SA Mutton Merinos and 1036 - 1118 for Dormers, depending on the trait analysed. Behaviour traits were expressed as time intervals in minutes. Length of parturition was defined as the period between the first definite sign of impending parturition in the ewe to the birth of a specific lamb. In multiples, the birth of the preceding littermate was regarded as the beginning of parturition for preceding litter mates. Other observations on lambs included the intervals from birth to standing for > 10 second and from standing to apparently suckling. Single lambs were heavier than twins in both breeds, which were heavier than triplets ($P < 0.05$). Subsequent multiple lambs had shorter parturitions than singles and first-born multiples ($P < 0.05$). Triplets were slower ($P < 0.05$) to progress from standing to suckling than singles. Ram lambs were heavier, with longer parturitions than ewes. Lamb birth weight was curvi-linearly related to dam age, while length of parturition tended to decrease with an increasing dam age in SA Mutton Merino lambs. Lambs borne by 2 - year old maidens and 7 - year old ewes generally tended to take longer to progress from standing to suckling. Direct heritability estimates ($h^2 \pm SE.$) in SA Mutton Merinos were 0.11 ± 0.05, 0.03 ± 0.04, 0.10 ± 0.05 and 0.08 ± 0.05 respectively for birth weight, length of parturition, and intervals from birth to standing and standing to suckling respectively. Corresponding estimates for Dormers were 0.22 ± 0.06, 0.04 ± 0.05, 0.12 ± 0.05 and 0.12 ± 0.06 respectively. The inclusion of the maternal genetic variance ratio (m^2) resulted in an improvement in the log likelihood ratio for length of parturition in SA Mutton Merino and Dormer lambs, yielding estimates of respectively 0.15 ± 0.04 and 0.14 ± 0.04. Maternal permanent environment variance ratios (c^2) were 0.18 ± 0.03 for birth weight and 0.17 ± 0.04 for the interval from standing to suckling in SA Mutton Merino lambs. A corresponding c^2 estimate of 0.15 ± 0.06 was computed for birth weight in Dormer lambs. On a phenotypic level, length of parturition was positively related to birth weight in both breeds. Corresponding maternal permanent environmental correlations between the traits amounted to 0.44 ± 0.14 in SA Mutton Merinos and 0.47 ± 0.16 in Dormers. Phenotypic correlations of birth weight with neonatal lamb progress were negative in both breeds, but the only significant maternal permanent environmental correlation was an estimate of -0.75 ± 0.23 between birth weight and the interval from birth to standing. Direct genetic correlations between traits rarely exceeded their standard errors. Lambs that succumbed during parturition and prior to weaning generally had higher ($P < 0.05$) direct and maternal breeding values for length of parturition. Corresponding results were found when derived breeding values for neonatal progress were related to post-parturient deaths, particularly in Dormer lambs. These results are discussed with reference to sheep production.

Keywords: Heritability, Mortality, Neonatal progress, Parturition, Standing, Suckling

Introduction

Lamb mortality is regarded as a major constraint to efficient sheep production (Alexander, 1988; Haughey, 1991). A "core" level of lamb losses remains, even in cases where managerial inputs are optimised (Alexander, 1984). Even very intensive management failed to reduce lamb mortality in South African (SA) Meat Merino and

Dormer lambs to levels of below 15 % (Brand *et al.*, 1985). The cost of intensification prohibits the improvement of lamb survival by, for instance, providing permanent supervision and confining ewes and lambs to indoor pens during the perinatal period. Selective breeding was advocated as a possible means of improving lamb survival and ewe rearing ability under paddock conditions (Lindsay *et al.*, 1990; Haughey 1991). It was hypothesised that behavioural adaptations may contribute to selection responses in lamb survival (Alexander, 1988). Published estimates for genetic (co)variances of peri-parturient behaviour in sheep were reported to be scarce in the literature (Hohenboken, 1986). When the most recent review by Hinch (1997) is considered, it is evident that little progress has been made since. Among reasons provided by Faure (1994) for this state of affairs, are that behaviour is difficult to measure, and that it is often perceived as being determined by the environment. Studies therefore tend to be based on small sample sizes, and genetic parameter estimates are thus often associated with large standard errors (Hinch, 1997). Breed and line differences in some traits are therefore often regarded as indicative of genetic variation (Hinch, 1997).

Against this background, we report results pertaining to environmental factors effects associated with peri-parturient behaviour of sheep, as well as genetic (co)variances among traits. The study extends preliminary findings presented earlier (Cloete *et al.*, 1998a), using a larger data set. The present study also reports selected covariances between traits, which were not estimated previously.

Material and methods

The fully pedigreed Dormer and SA Mutton Merino studs maintained at the Elsenburg Experimental Farm near Stellenbosch supplied material for the study. The locality, experimental animals and procedures are well described (Cloete, 1992; Cloete *et al.*, 1998a, b), and only brief descriptions are provided in this paper. Readers requiring a more extensive description are referred to the papers cited. Lambs born in the two studs over a period of 10 years from 1989 to 1998 were observed with their dams during the peri-parturient period, using the facilities described by Cloete (1992). Ten kikuyu (*Pennisetum clandestinum*) paddocks, of which 5 were floodlit for use at night, were used during the study. Animals were watched continuously during peak-lambing. One to two trained observers collected the data within shifts, by walking the paddocks continuously. Data that were recorded included the length of parturition of individual lambs, defined as the period (in minutes) between the first definite sign of impending parturition in the ewe to the birth of a specific lamb. In multiples, the birth of the preceding litter mate was regarded as the beginning of parturition for subsequent litter mates. Ewes that experienced difficult births and had not delivered 3.5 hours after parturition started were assisted (Cloete *et al.*, 1998a). A small number of ewes were assisted if they had not delivered by 2 hours after presentation or 30 minutes after the obvious malpresentation of body parts (see Cloete and Scholtz, 1998). Since assistance was based on time intervals, the interval prior to assistance was accepted as an indication of the true length of parturition. Other observations on the lambs included the period from birth to first standing for > 10 seconds, and from standing to apparently suckling. After being groomed by their dams for a period of > 15 minutes, lambs were identified with stock marker spray according to the identity of their dams and order of birth. Birth weight was recorded to the nearest 0.1 kg within 24 hours of the birth of individual lambs.

Other recordings included pedigree information (identity of the sire and dam), breed (Dormer or SA Mutton Merino), lambing year (1989 to 1998), sex (male or female), dam age (2 to 7+ years), as well as birth type (single, twin or triplet) or order of birth (single, first multiple or subsequent multiple). The latter trait exerted a marked influence on length of parturition, and was only fitted in analyses involving this trait. One SA Mutton Merino quadruplet was regarded as a triplet for the purpose of study. Previous work has shown that the two related breeds differed for birth weight and the behavioural parameters that were studied (Cloete, 1992, Cloete *et al.*, 1998a, b). It was therefore decided to analyse data for the breeds separately. The basic methods for these analyses were similar for the two breeds. The ASREML program (Gilmour *et al.*, 1999) was used for the estimation of the fixed effects, and also subsequently to derive variance components for birth weight and the behavioural traits in univariate analyses. The first analysis involved fitting various combinations of fixed effects and interactions between them to obtain an operational model. Effects found to be significant ($P < 0.05$) in these preliminary analyses were included in subsequent analyses. Random terms were then added to the operational model, resulting in the following models for analyses (in matrix notation):

$$y = Xb + Z_1a + e \tag{1}$$

$$y = Xb + Z_1a + Z_2c + e \tag{2}$$

$$y = Xb + Z_1a + Z_3m + e \tag{3}$$

[Covariance (a,m)=0]

$$y = Xb + Z_1\mathrm{a} + Z_3m + Z_2c + e \tag{4}$$

[Covariance (a,m)=0]

$$y = Xb + Z_1\mathrm{a} + Z_3m + e \tag{5}$$

[Covariance $(a,m)=A\sigma_{am}$]

$$y = Xb + Z_1\mathrm{a} + Z_3m + Z_2c + e \tag{6}$$

[Covariance $(a,m)= A\sigma_{am}$]

With y being a vector of observations for live weight traits or survival; b, a, m and c vectors of fixed effects, direct genetic variances, maternal genetic variances and maternal permanent environmental variances respectively; X, Z_1, Z_2, and Z_3, the corresponding incidence matrices relating the respective effects to y; e the vector of residuals; A the numerator relationship matrix, and σ_{am} the covariance between direct genetic and maternal effects.

It was assumed that:

$V(a) = A\sigma^2_a$; $V(m) = \mathrm{A}\sigma^2_{\mathrm{m}}$; $\mathrm{V}(c) = \mathrm{A}\sigma^2_c$; $V(e) = I\sigma^2_e$,

With I being an identity matrix; σ^2_a, σ^2_{m}, σ^2_{c} and σ^2_e direct genetic variance, maternal genetic variance (as a trait of the lamb) and the maternal permanent environmental variance and environmental (residual) variance respectively.

Log likelihood tests were conducted to determine the most suitable model for each trait in univariate analyses. The random effects models that fitted the data for each trait best were identified, using the log likelihood ratios obtained from the respective analyses (Snyman *et al.*, 1996). Subsequently, 2-trait animal models were fitted within breeds. These analyses allowed the calculation of all relevant direct and maternal correlations between traits, together with their appropriate standard errors. For traits influenced by either direct maternal genetic variances (m^2) or maternal permanent environmental variances (c^2), it was decided to pool the latter two effects in the analyses. The derived maternal correlations thus comprised of both m^2 and c^2 effects.

Results

In both breeds, singles were heavier ($P < 0.05$) than twins at birth (Tables 1 and 2). Twins, in turn, had heavier ($P < 0.05$) birth weights than triplets. Length of parturition was affected by order of birth. Singles and first-born multiples (twins as well as triplets) did not differ as far as length of parturition was concerned. Subsequent multiples, however, were born after shorter ($P < 0.05$) parturitions in both breeds. Birth type did not influence the interval from birth to standing in either breed. No significant ($P < 0.05$) differences were observed as far as the interval from standing to suckling was concerned. The effect of birth type upon the interval from standing to suckling was complicated by a significant interaction with sex in both breeds. These interactions are presented in Table 3. Ram and ewe triplet lambs of both breeds consistently took longer ($P < 0.05$) to progress from standing to suckling than single contemporaries. Results for twin lambs were, however, inconsistent between sexes. Twin SA Mutton Merino ewe lambs and Dormer ram lambs resembled singles in this respect. Twin SA Mutton Merino ram lambs and twin Dormer ewe lambs, on the other hand, behaved like triplets.

Table 1. Least squares means (± *SE*) depicting the fixed effects of birth type, sex and dam age on birth weight, length of parturition and early neonatal progress in SA Mutton Merino lambs. Behavioural traits were measured in minutes and logarithm$_{10}$ transformed prior to analysis. Antilogs are given in parentheses.

Fixed effect	Birth weight (kg)	Logarithm$_{10}$ transformed behaviour traits (antilog)		
		Parturition	Birth – standing	Standing – suckling
Overall mean	4.2 ± 0.1	1.64 ± 0.05 (44)	1.32 ± 0.03 (21)	1.38 ± 0.04 (24)
Birth type or order#	**	**	NS	NS
1	5.1 ± 0.1	1.84 ± 0.06 (69)	1.30 ± 0.03 (20)	1.28 ± 0.05 (19)
2	4.1 ± 0.1	1.77 ± 0.05 (59)	1.30 ± 0.03 (20)	1.39 ± 0.04 (25)
3	3.3 ± 0.1	1.33 ± 0.05 (21)	1.36 ± 0.03 (23)	1.48 ± 0.05 (30)
Sex	**	**	NS	NS
Ram	4.3 ± 0.1	1.71 ± 0.05 (51)	1.32 ± 0.03 (21)	1.36 ± 0.04 (23)
Ewe	4.0 ± 0.1	1.59 ± 0.05 (39)	1.32 ± 0.03 (21)	1.40 ± 0.04 (25)
Dam age	**	*	NS	*
2 years	3.8 ± 0.1	1.69 ± 0.06 (49)	1.34 ± 0.03 (22)	1.46 ± 0.05 (29)
3 years	4.2 ± 0.1	1.67 ± 0.06 (47)	1.30 ± 0.03 (20)	1.34 ± 0.04 (22)
4 years	4.3 ± 0.1	1.74 ± 0.06 (55)	1.30 ± 0.03 (20)	1.38 ± 0.04 (24)
5 years	4.4 ± 0.1	1.64 ± 0.06 (44)	1.33 ± 0.03 (21)	1.39 ± 0.05 (25)
6 years	4.2 ± 0.1	1.60 ± 0.06 (40)	1.34 ± 0.04 (22)	1.35 ± 0.05 (22)
7 years	4.1 ± 0.1	1.55 ± 0.06 (35)	1.31 ± 0.04 (20)	1.42 ± 0.05 (26)
Birth year	**	**	**	*

NS Not significant ($P > 0.05$)

* Significant ($P < 0.05$)

** Significant ($P < 0.01$)

\# Single, first multiple and subsequent multiple for length of parturition, single, twin and triplet for other traits.

Table 2. Least squares means (± *SE*) depicting the fixed effects of birth type, sex and dam age on birth weight, length of parturition and early neonatal progress in Dormer lambs. Behavioural traits were measured in minutes and logarithm$_{10}$ transformed prior to analysis. Antilogs are given in parentheses.

Fixed effect	Birth weight (kg)	Logarithm$_{10}$ transformed behaviour traits (antilog)		
		Parturition	Birth – standing	Standing – suckling
Overall mean	3.8 ± 0.1	1.50 ± 0.05 (32)	1.36 ± 0.05 (23)	1.51 ± 0.05 (32)
Birth type or order#	**	**	NS	NS
1	4.6 ± 0.1	1.58 ± 0.06 (38)	1.32 ± 0.05 (21)	1.41 ± 0.05 (26)
2	3.8 ± 0.1	1.53 ± 0.06 (34)	1.36 ± 0.05 (23)	1.51 ± 0.04 (32)
3	3.1 ± 0.1	1.38 ± 0.05 (24)	1.41 ± 0.07 (26)	1.60 ± 0.08 (40)
Sex	**	*	NS	NS
Ram	4.0 ± 0.1	1.53 ± 0.05 (34)	1.37 ± 0.05 (23)	1.54 ± 0.05 (35)
Ewe	3.7 ± 0.1	1.46 ± 0.05 (29)	1.36 ± 0.05 (23)	1.48 ± 0.05 (30)
Dam age	**	NS	**	NS
2 years	3.4 ± 0.1	1.54 ± 0.06 (35)	1.46 ± 0.06 (29)	1.59 ± 0.06 (39)
3 years	3.7 ± 0.1	1.46 ± 0.06 (29)	1.43 ± 0.06 (27)	1.50 ± 0.05 (32)
4 years	3.8 ± 0.1	1.50 ± 0.06 (32)	1.37 ± 0.06 (23)	1.48 ± 0.05 (30)
5 years	4.0 ± 0.1	1.49 ± 0.06 (31)	1.40 ± 0.06 (25)	1.42 ± 0.05 (26)
6 years	4.0 ± 0.1	1.47 ± 0.06 (30)	1.27 ± 0.06 (19)	1.47 ± 0.06 (30)
7 years	4.1 ± 0.1	1.52 ± 0.07 (33)	1.25 ± 0.07 (18)	1.59 ± 0.07 (39)
Birth year	**	**	**	**

NS Not significant ($P > 0.05$)

* Significant ($P < 0.05$)

** Significant ($P < 0.01$)

\# Single, first multiple and subsequent multiple for length of parturition, single, twin and triplet for other traits

Ram lambs were heavier ($P < 0.01$) and had longer ($P < 0.05$) parturitions than ewes in both breeds (Tables 1 and 2). Birth weight in both breeds increased ($P < 0.01$) curvilinearly with an increase in dam age (Tables 1 and 2). Maximum birth weights were obtained at a dam age of 5 years in SA Mutton Merinos, and at 6 years in Dormers. Length of parturition generally declined ($P < 0.05$) with an increasing dam age in SA Mutton Merino lambs (Table 1). A corresponding trend was obtained as far as the interval from birth to standing in Dormers was concerned (Table 2). Lambs cared for by primiparous maidens and old (7+ years) ewes generally took longer to progress from birth to suckling than lambs from three to six year old ewes (Tables 1 and 2).

Table 3. Least squares means (± *SE*) for the interaction of birth type with sex regarding the interval between standing and suckling in SA Mutton Merino and Dormer lambs. The trait was measured in minutes and logarithm$_{10}$ transformed prior to analysis. Antilogs are given in parentheses.

Breed and birth type	**Sex**	
	Ram	**Ewe**
SA Mutton Merino	*	*
Single	1.25 ± 0.05 (18)	1.31 ± 0.06 (20)
Twin	1.42 ± 0.04 (26)	1.36 ± 0.04 (23)
Triplet	1.43 ± 0.04 (27)	1.53 ± 0.05 (34)
Dormer	*	*
Single	1.48 ± 0.06 (30)	1.35 ± 0.06 (22)
Twin	1.49 ± 0.05 (31)	1.53 ± 0.05 (33)
Triplet	1.64 ± 0.10 (44)	1.55 ± 0.10 (35)

* Significant ($P < 0.05$)

For birth weight, log likelihood ratios indicated a model that included the direct additive variance (h^2) and maternal permanent environmental effect (c^2) in SA Mutton Merinos, while the model also included the maternal genetic variance (m^2) in Dormers. Direct genetic and m^2 effects were included in analyses on length of parturition in both breeds. The inclusion of h^2 resulted in an improvement in the log likelihood ratio for neonatal progress in both breeds. Only the interval from standing to suckling in SA Mutton Merino lambs was subject to a significant c^2 effect.

When expressed relative to the overall phenotypic variance for birth weight, estimates of h^2 were 0.11 for SA Mutton Merino lambs and 0.21 for Dormers lambs (Table 4). The m^2 estimate was significant only in Dormers, amounting to 0.16. Respective c^2 estimates for Dormer and SA Mutton Merinos were 0.18 and 0.15. In the case of length of parturition, h^2 was below 0.05 in both breeds. This trait was, however, subject to significant m^2 effects, computed variance ratios amounting to 0.14 in Dormers and 0.15 in SA Mutton Merinos. Estimates of h^2 for the interval from birth to standing were 0.10 in SA Mutton Merinos and 0.22 in Dormers. Estimates of h^2 for the interval from standing to apparently suckling were 0.08 in SA Mutton Merinos and 0.12 in Dormers. This trait was also affected by c^2 in SA Mutton Merino lambs. The computed variance ratio amounted to 0.17, when expressed relative to the overall phenotypic variance.

Table 4. Variance components and estimates of the direct genetic (h^2), maternal genetic (m^2) and maternal permanent environmental (PE – c^2) variance ratios (± *SE*) for birth weight and the respective behavioural traits in SA Mutton Merino and Dormer lambs

Breed and description of variances or ratios	Birth weight	Length of parturition	Birth – standing	Standing – suckling
SA Mutton Merino				
Variances:				
Environmental	0.3044	0.1667	0.0804	0.1253
Direct additive	0.0476	0.0070	0.0087	0.0130
Maternal additive	-	0.0309	-	-
Maternal PE	0.0772	-	-	0.0293
Total phenotype	0.4291	0.2046	0.0891	0.1676
Ratios:				
h^2	0.11 ± 0.06	0.03 ± 0.04	0.10 ± 0.05	0.08 ± 0.05
m^2	-	0.15 ± 0.04	-	-
c^2	0.18 ± 0.03	-	-	0.17 ± 0.04
Dormer				
Variances:				
Environmental	0.1940	0.1803	0.1137	0.1733
Direct additive	0.0832	0.0095	0.0329	0.0234
Maternal additive	0.0662	0.0308	-	-
Maternal PE	0.0599	-	-	-
Total phenotype	0.4034	0.2206	0.1466	0.1968
Ratios:				
h^2	0.21 ± 0.07	0.04 ± 0.05	0.22 ± 0.06	0.12 ± 0.05
m^2	0.16 ± 0.07	0.14 ± 0.04	-	-
c^2	0.15 ± 0.06	-	-	-

(-) Inclusion of variance component did not result in an improved ($P < 0.05$) log likelihood ratio

Genetic correlations between traits were variable, inconsistent between breeds and seldom larger than the corresponding standard errors. The maternal genetic correlation (± *SE*) between birth weight and length of parturition was positive and different from zero (exceeded twice its standard error) in Dormers (0.71 ± 0.13). The corresponding ewe permanent environmental correlation in SA Mutton Merinos amounted to 0.35 ± 0.16. Maternal correlations involving other traits did not differ from zero. Phenotypic correlations between traits were fairly consistent between breeds. Birth weight was positively correlated with length of parturition in both breeds (SA Mutton Merino: 0.14 ± 0.03; Dormer: 0.19 ± 0.03), suggesting that length of parturition may be increased in heavier lambs. Correlations of birth weight with early neonatal progress were negative (ranging from -0.10 ± 0.03 to -0.17 ± 0.03), suggesting that smaller lambs at birth would tend to make slower progress.

In the absence of genetic correlations between the behavioural traits recorded and lamb mortality, mean direct (and maternal in the case of length of parturition) breeding values were compared for lambs that died or survived at a specific stage (Table 5). Direct breeding values for length of parturition were lower ($P < 0.05$) in lambs that survived parturition than in those dying in the peri-parturient period in both breeds. A similar difference was found in maternal breeding values. Similar conclusions were made as far as the differences between lambs that died prior to weaning or those that survived to weaning were considered (Table 5). Direct breeding values for the neonatal progress of Dormer lambs that died in the post-parturient period were higher ($P < 0.05$) than in contemporaries that survived. A similar difference was observed as far as overall rates of lamb mortality (including parturient deaths) were considered. Similar tendencies were observed in the breeding values of SA Mutton Merino lambs. The only significant ($P < 0.05$) difference was, however, for the interval from standing to suckling, involving lambs that succumbed in the post-parturient period compared to those that survived this period.

Discussion

Although a breed comparison was not the objective of the present study it should be noted that overall least squares means for birth weight were 4.2 for SA Mutton Merino lambs and 3.8 for Dormers. Corresponding backtransformed means were 44 and 32 minutes for length of parturition, 21 and 23 minutes for the interval from birth to standing as well as 24 and 30 minute for the interval from standing to apparently suckling. Previous results suggested that SA Mutton Merino lambs were heavier at birth (Brand *et al.*, 1985; Cloete 1993; Cloete *et al.*, 1998a) with longer parturitions (Cloete, 1992; Cloete *et al.*, 1998a, b). Neonatal progress was similarly reported to be slower in Dormer

Table 5. Means (± *SE*) for direct or maternal breeding values (where applicable) for behavioural traits in lambs when classified according to stage of mortality. Breeding values are on a logarithm$_{10}$ scale.

Breed and stage of mortality	**Length of parturition (direct)**	**Length of parturition (maternal)**	**Birth – standing**	**Standing – suckling**
SA Mutton Merino				
Parturient				
Dead at birth	0.018[a] ± 0.002	0.036[a] ± 0.007	0.001 ± 0.007	0.008 ± 0.005
Survived birth	0.005[b] ± 0.001	0.010[b] ± 0.002	0.001 ± 0.002	0.013 ± 0.002
Post-parturient				
Dead after birth	0.007 ± 0.002	0.011 ± 0.004	0.005 ± 0.005	0.019[a] ± 0.003
Alive at weaning	0.006 ± 0.001	0.013 ± 0.002	-0.001 ± 0.002	0.011[b] ± 0.002
Overall				
Died	0.011[a] ± 0.001	0.018[a] ± 0.004	0.004 ± 0.004	0.016 ± 0.003
Alive at weaning	0.005[b] ± 0.001	0.010[b] ± 0.002	-0.001 ± 0.003	0.011 ± 0.002
Dormer				
Parturient				
Dead at birth	0.013[a] ± 0.004	0.025[a] ± 0.012	0.009 ± 0.012	0.016 ± 0.009
Survived birth	0.006[b] ± 0.001	-0.001[b] ± 0.002	-0.001 ± 0.002	0.008 ± 0.002
Post-parturient				
Dead after birth	0.008 ± 0.002	0.004 ± 0.005	0.019[a] ± 0.006	0.021[a] ± 0.004
Alive at weaning	0.006 ± 0.001	-0.002 ± 0.002	-0.003[b] ± 0.003	0.005[b] ± 0.002
Overall				
Died	0.009[a] ± 0.002	0.008[a] ± 0.004	0.017[a] ± 0.005	0.020[a] ± 0.004
Alive at weaning	0.005[b] ± 0.001	-0.002[b] ± 0.002	-0.004[b] ± 0.003	0.005[b] ± 0.002

[a,b] Denote significant ($P < 0.05$) differences between the averaged breeding values of lambs that have died and those that have survived

lambs than in SA Mutton Merinos (Cloete *et al.*, 1998a). Corresponding breed or line differences in ease of parturition (Knight *et al.*, 1988; Alexander *et al.*, 1990b; *Fahmy et al.*, 1997; Cloete and Scholtz, 1998) or early post-natal progress (Slee and Springbett, 1986; Cloete and Scholtz, 1998; Kuchel and Lindsay, 1999) were found in the literature.

The effects of the various fixed effects upon birth weight were similar to that expected from the literature (Tables 1 and 2). These patterns are well established and discussion would be superfluous. Subsequent lambs in multiple litters had shorter parturition than either singles or their first-born littermates. Similar results in the literature (Arnold and Morgan, 1975; Cloete *et al*, 1998a) were related to dilation of the cervix, facilitating the delivery of subsequent lambs (Arnold and Morgan, 1975). Haughey (1991) also reported marked differences in length of parturition between first-born and second-born twins. Owens *et al.* (1985) reported that second-born twins were quicker to appear at the vulva than first-born littermates. Similar tendencies were found for triplets and quadruplets, but significance could not be demonstrated. No difference in the length of parturition for first-born and second-born twins was, however, reported in goats (Ramirez *et al.*, 1995).

Ram lambs had longer ($P < 0.05$) parturitions than ewes in both breeds. This confirms previous results, based on part of the same data set, as reported by Cloete *et al.* (1998a). Alexander *et al.* (1993) correspondingly reported that male Merino lambs had longer parturitions than female contemporaries. Length of parturition decreased ($P < 0.05$) with an increase in dam age in SA Mutton Merino lambs (Table 1). No such effect was observed in Dormer lambs (Table 2). Alexander *et al.* (1993) found no effect of parity on length of parturition in progeny of ewes of > 2 years of age. They did, however, report that length of parturition was longer in progeny of 2 - year old maiden ewes than in lambs given birth to by older ewes.

The interval of birth to standing was generally independent of birth type (Tables 1 and 2). The interval from standing to suckling was complicated by an interaction between sex and birth type in both breeds. The interaction was not consistent between breeds, and it is thus impossible to draw robust conclusions from it. The only robust conclusion that could be made was that triplets of both sexes took longer ($P < 0.05$) to progress from standing to apparently suckling than singles. Booroola Merino triplets and quadruplets were found to take longer to stand and apparently suckle than twins and singles in the study of Owens *et al.* (1985). In goitre-affected Merino lambs, Alexander *et al.* (1990a) found that twins generally progressed slower during the neonatal period than singles. Slee and Springbett (1986) reported that progress to standing was independent of birth type in lambs from a number of breeds. Birth type did, however, exert an influence on the time lambs took to reach the udder. Absolute differences in neonatal progress between singles and twins of Romanov, Finsheep and Suffolk lambs were comparatively large in the study of Fahmy *et al.* (1997). No significant differences were found, possibly owing to relatively few observations. A previous study at this institution, involving part of the data used in this study, also did not find an influence of birth type on the neonatal progress of SA Mutton Merino and Dormer lambs (Cloete, 1993).

Early neonatal progress of lambs was independent of sex (Table 1 and 2). Slee and Springbett (1986) as well as Alexander *et al.* (1993) similarly found no effect of sex on the interval from birth to standing. In the latter study, ram lambs were found to progress slower ($P < 0.05$) from standing to apparently suckling than ewe contemporaries. In the study of Cloete and Scholtz (1998), medium wool Merino ewe lambs were found to progress faster ($P < 0.05$) than ram contemporaries to standing. No sex difference was found in the latter study with regard to the period from standing to apparently suckling. The only influence of dam age on the neonatal progress of lambs was a generally linear decline of the interval from birth to standing in Dormer lambs as dam age increased. In the literature, it was commonly found that lambs of maiden ewes took a longer time to progress from standing to suckling than lambs cared for by mature ewes (Cloete, 1993; Cloete and Scholtz, 1998). Primiparous maiden ewes were more likely to engage in activities to discourage suckling (*e.g.* circling or backing) than experienced mothers (Alexander *et al.*, 1993; Cloete and Scholtz, 1998).

Genetic parameters for birth weight in Dormers were in very good agreement with corresponding estimates recently summarised from the literature by Cloete *et al.* (2001). Estimates for the SA Mutton Merinos, where no direct maternal effect were found, agreed with results presented by Conington *et al.* (1995). They reported a h^2 estimate of 0.08 and a c^2 estimate of 0.41 for hill sheep in Britain. Corresponding estimates for SA Mutton Merinos were 0.11 and 0.18 in the present study.

Estimates of h^2 were small and not significant for length of parturition in both breeds (Table 4). Estimates of m^2 were much higher, indicating that the inheritance of ease of parturition is likely to be maternal. The existence of some genetic variation for this trait agreed with results in the literature, where differences between breeds (Alexander *et al.*, 1990b; Fahmy *et al.*, 1997; Cloete *et al.*, 1998a) or lines (Cloete and Scholtz, 1998) were reported. It has also previously been shown that parturient deaths were associated with distocia and prolonged parturitions (Arnold and Morgan, 1975; Haughey, 1991; *Cloete et al.*, 1993). Differences in the occurrence of parturient deaths between lines selectively bred for ewe rearing ability (Haughey, 1983; Knight *et al.*, 1988) also has to be seen from this perspective.

Intervals from birth to standing and from standing to suckling exhibited some genetic variation. Estimates of h^2 were low to moderate and ranged from 8 to 22% of the overall phenotypic variance (Table 4). Differences between breeds were correspondingly reported for early neonatal progress in lambs (Slee and Springbett, 1986; Alexander *et al.*, 1990; Cloete *et al.*, 1998a), supporting the contention that it is partially under genetic control. Other studies, however, reported no breed differences for early neonatal behaviour (Fahmy *et al.*, 1997). Maternal effects (m^2) were generally not significant for these traits. In the case of SA Mutton Merinos, a c^2 estimate of 0.17 ± 0.04 was derived for the interval from standing to first apparently suckling. This result suggests that the environment created by the dam to facilitate suckling is important. Super-ovulated superfine wool embryos were transplanted into either superfine wool or medium wool ewes in an embryo transfer study (Kuchel and Lindsay, 1999). It is of interest to note that superfine wool lambs cared for by medium wool ewes showed faster neonatal progress than their contemporaries cared for by superfine wool ewes. Lambmarking percentages were correspondingly affected, and were markedly lower in the superfine wool lambs cared for by superfine wool dams (Kuchel and Lindsay, 1999). In another study, Cloete and Scholtz (1998) found that the interval from standing to apparently suckling was shorter in a Merino line that was selected for multiple rearing ability than in a parallel line that was divergently selected against multiple rearing ability. The line difference was partially accounted for by the inclusion of maternal co-operation with the first suckling attempts of the neonate in the model of analysis. Both studies indicate that the maternal environment to facilitate suckling, as provided by the dam, plays a role in the neonatal progress of lambs.

Estimates of the genetic components of lamb survival indicate limited genetic variation (Hall *et al.*, 1995; Lopez-Villalobos and Garrick, 1999; Morris *et al.*, 2000; Cloete *et al.*, 2001). Maternal permanent environmental variances were found to contribute mostly to the repeatability of ewe rearing performance (Morris *et al.*, 2000). Despite limited genetic variation in lamb survival, several studies reported responses in rearing ability after rigorous selection for a number of generations (Haughey, 1983; Cloete and Scholtz, 1998). From the foregoing discussion, it is evident that some behavioural traits conducive to lamb survival (see Alexander, 1988 for review) showed significant genetic variation. These results provide an explanation for the observed selection progress in lamb survival.

On a phenotypic level, an increase in birth weight was generally associated with longer parturitions and shorter intervals from birth to standing or from standing to apparently suckling in both breeds. Litter weight was previously shown to be associated with length of parturition in ewes (Fahmy *et al.*, 1997). In the study of Owens *et al.* (1985), an increase in lamb birth weight was also associated with neonatal lamb vigour in Booroola lambs, although only regression coefficients were given. No previous reports were found where it was attempted to partition these covariances in direct and maternal components. Maternal correlations between birth weight and length of parturition were positive in lambs of both breeds. In a previous study it was shown that length of parturition (expressed as a trait of the ewe) was associated with litter weight when assessed in Dormer and SA Mutton Merino ewes (Cloete *et al.*, 1998b). Genetic and maternal correlations among the respective behavioural traits were generally low, and seldom exceeded their standard errors.

So far, there has been evidence that ewe and lamb behaviour were phenotypically related to lamb survival or rearing ability (Owens *et al.*, 1985; Cloete, 1993; Cloete *et al.*, 1993), but this relationship could not be established on a genetic basis. The breeding values for behavioural traits of lambs that survived birth, or that survived through to weaning were thus compared to those that died during the corresponding period (Table 5). These results suggested that survivors generally had lower ($P < 0.05$) direct and maternal breeding values for length of parturition than contemporaries that died. Very few results in this regard were found in the literature. In one study, the length and difficulty of the birth process were genetically correlated with the survival of singles (Alexander and Stevens, 1992; as cited by Lynch, 1997). In this respect, it should also be noted that selection for ewe rearing ability resulted in lower levels of parturient deaths (Haughey, 1983; Knight *et al.*, 1988), and shorter parturitions (Cloete and Scholtz, 1998) in selected lines. The relationship between direct breeding values and neonatal lamb progress was not as evident in SA Mutton Merino lambs, but clear differences were found in Dormers. Selective breeding for ewe rearing ability was similarly noted to result in a reduction in neonatal lamb mortality (Haughey, 1983, Cloete and Scholtz, 1998), and faster neonatal lamb progress as far as the interval from standing to suckling was concerned (Cloete and Scholtz, 1998).

Conclusions

A large portion of the evidence for genetic variation in behaviour of sheep is based on breed comparisons (Hinch, 1997). In this study, it was not only possible to estimate variance ratios for lambing and neonatal behaviour in sheep, but also to partition variances in direct and maternal components. In this sense, the study contributes to a better understanding of the underlying principles involved in ovine lamb mortality. Lamb mortality was related to breeding values for the behavioural traits in lambs (Table 5), suggesting a genetic association between these traits. The main outcomes of the study thus accorded with the contention made by Alexander (1988) that behavioural patterns during the peri-parturient period were likely to have a genetic basis, although no estimates of genetic variances were available at that stage. The latter author also contended that selection for behaviour conducive to lamb survival could result in improvements in the latter trait, and *vice versa.*

Genetic correlations among birth weight and the respective behavioural traits generally did not exceed their standard errors, while phenotypic correlations accorded with literature cited. The former result stemmed from the relatively small size of the data sets used. Against this background, it may be advisable to postpone judgement on the sign and magnitude of genetic correlations between traits until larger data sets become available.

Acknowledgement

We wish to express our sincerest gratitude to those assisting with the collection of data, and Mr. J.E. Fourie, who was responsible for the care and maintenance of the breeding flocks.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay D.R., Pearce D.T., (Eds.). Reproduction in sheep. Australian Academy of Science in Conjunction with the Australian Wool Corporation, Canberra, Australia. pp. 199 - 209.

Alexander, G., 1988. What makes a good mother? *Proceedings of the Australian Society of Animal Production* 17: 25 - 41.

Alexander, G., Stevens, D., Bradley, L.R., 1990a. Intensive observations during lambing in a goitre-affected flock, with special reference to the behaviour of lambs. *Australian Journal of Experimental Agriculture* 30: 749 - 757.

Alexander, G., Stevens, D. and Bradley, L.R., 1993. Effect of age and parity on maternal behaviour in single-bearing Merino ewes. *Australian Journal of Experimental Agriculture* 33: 721 - 728.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990b. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27 - 38.

Arnold, G.W., Morgan, P.D., 1975. Behaviour of the ewe and lamb at lambing and its relationship to lamb mortality. *Applied Animal Ethology* 2: 25 - 46.

Brand, A.A., Cloete S.W.P., De Villiers, T.T., 1985. Factors that influence mortality amongst lambs in the Elsenburg Dormer and SA Mutton Merino flocks (in Afrikaans). *South African Journal of Animal Science* 15: 155 - 161.

Cloete, S.W.P., 1992. Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and SA Mutton Merino ewes. *South African Journal of Animal Science* 22: 214 - 221.

Cloete, S.W.P., 1993. Observations on neonatal progress of Dormer and SA Mutton Merino lambs. *South African Journal of Animal Science* 23: 38 - 42.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2001. Environmental and genetic aspects of survival and early liveweight in Western Australian Merino sheep. *South African Journal of Animal Science* 31: 123 - 130.

Cloete, S.W.P., Olivier, J.J., Scholtz, Anna J., 1998a. Aspects of lambing and neonatal behaviour of dual-purpose sheep. *Proceedings of the 6th World Congress on Genetic Applied Livestock Production.* Armidale, NSW, Australia. 27: 39 - 42.

Cloete, S.W.P., Scholtz, Anna J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Scholtz, Anna J., ten Hoope, J.M., Lombard, P.J.A., Franken, M.C., 1998b. Ease of birth in relation to pelvic dimensions, litter weight and conformation in sheep. *Small Ruminant Research* 31: 51 - 60.

Cloete, S.W.P., van Halderen, A., Schneider, D.J., 1993. Causes of perinatal mortality amongst Dormer and SA Mutton Merino lambs. *Journal of the South African Veterinary Association* 64: 121 - 125.

Conington, J., Bishop, S.C., Waterhouse, A., Simm, G., 1995. A genetic analysis of early growth and ultrasonic measurements in hill sheep. *Animal Science* 61: 85 - 93.

Fahmy, M.H., Robert, S., Castonguay, F., 1997. Ewe and lamb behaviour at parturition in prolific and non-prolific sheep. *Canadian Journal of Animal Science* 77: 9 - 15.

Faure, J.M., 1994. Behavioural genetics – an overview. *Proceedings of the 5th World Congress on Genetic Applied Livestock Production.* Guelph, Ontario, Canada. 20: 129.

Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R., 1999. ASREML – Reference manuel. NSW Agriculture Biometric Bulletin No. 3. NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia.

Hall, D.G., Fogarty, N.M., Gilmour, A.R., 1995. Performance of crossbred progeny of Trangie fertility Merino and Booroola Merino rams and Poll Dorset ewes. 1.

Lamb birth weight, survival and growth. *Australian Journal of Experimental Agriculture* 35: 1069 - 1074.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361 - 363.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Hinch, G.N. 1997. Genetics of behaviour. In: Piper, L., Ruvinsky, A., (Eds.). The genetics of sheep. CAB International, Wallingford, Oxon, UK. pp. 353 - 374.

Hohenboken, W.D., 1986. Inheritance of behavioural characteristics in livestock. A review. *Animal Breeding Abstracts* 54: 623 - 639.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259 - 271.

Kuchel, R.C., Lindsay, D.R., 1999. Maternal behaviour and the survival of lambs in superfine wool sheep. *Reproduction Fertility and Development* 11: 391 - 394.

Lindsay, D.R., Nowak, R., Putu, I.G., McNeil, D., 1990. Behavioural interactions between the ewe and her young at parturition. In: C.M. Oldham, G.B. Martin and I.W. Purvis (Eds.), Reproductive Physiology of Merino sheep. School of Agriculture, University of Western Australia. pp. 191 - 205

Lopez-Villalobos, N., Garrick, D.J., 1999. Genetic parameter estimates for lamb survival in Romney sheep. *Proceedings of the New Zealand Society of Animal Production* 59: 121 - 124.

Morris, C.A., Hickey, S.M., Clarke, J.N., 2000. Genetic and environmental factors affecting lamb survival at birth and through to weaning. *New Zealand Journal of Agricultural Research* 43: 515 - 524.

Owens, J.L., Bindon, B.M., Edey, T.N., Piper, L.R., 1985. Behaviour at parturition and lamb survival of Booroola Merino sheep. *Livestock Production Science* 13: 359 - 372.

Ramirez, A., Quilles, A., Hevia, M., Sotillo, F., 1995. Observations on the birth of goats. *Canadian Journal of Animal Science* 75: 165 - 167.

Slee, J., Springbett, A., 1986. Early post-natal behaviour in lambs of ten breeds. *Applied Animal Behaviour Science* 15: 229 - 340.

Snyman, M.A., Olivier J.J., Olivier W.J., 1996. Variance components and genetic parameters for body weight and fleece traits of Merino sheep in an arid environment. *South African Journal of Animal Science* 26: 11 - 14.

PART 3

Responses to selection for ewe multiple rearing ability

Chapters 8 to 16

CHAPTER 8

A NOTE ON SEPARATION FROM ONE OR MORE LAMB(S) IN MERINO LINES DIVERGENTLY SELECTED FOR EWE MULTIPLE REARING ABILITY

Short communication

S.W.P.Cloete, A.J.Scholtz and J.M.Ten Hoope

Elsenburg Agricultural Development Institute,
Private Bag X1, Elsenburg 7607, South Africa

Published in:
Applied Animal Behaviour Science (1998) 58: 189 - 195

Reproduced with permission of:
Applied Animal Behaviour Science

A note on separation from one or more lamb(s) in Merino lines divergently selected for ewe multiple rearing ability

S.W.P. Cloete, Anna J. Scholtz, J.M. Ten Hoope

Elsenburg Agricultural Development Institute, Private Bag X1, Elsenburg 7607, South Africa

Accepted 17 June 1997

The time that ewes remained on their respective birth sites and proportions of postparturient separation from one or more lamb(s) were studied in 370 Merino ewes of lines subjected to divergent selection for multiple rearing ability. In the high line, ram and ewe replacements were mostly descended from dams that reared more than one lamb per mating, mostly after ≥ 2 lambing opportunities. Progeny of ewes that reared fewer than one lamb per mating were preferred in the low line. Depending on the average reproduction of the flocks and number of replacements required, progeny of ewes that reared one lamb per mating were occasionally accepted as ewe replacements within both lines. Higher proportions of permanent separation were recorded in maiden ewes compared to mature ewes (0.144 *vs*. 0.073; P = 0.06) and in ewes caring for viable multiples compared to those caring for singles (0.147 *vs*. 0.034; $P <$ 0.01). Ewes that cared for viable multiples remained on their birth sites for longer periods as compared to ewes caring for singles (7.81 ± 0.49 h *vs*. 6.66 ± 0.38 h; P = 0.05). The proportion of ewes separated from one or more lamb(s) was similar in the high and low lines (0.090 *vs*. 0.096). The proportion of maiden high line ewes caring for a viable single lamb and getting separated from it was lower (P = 0.075) than in low line contemporaries (0.023 *vs*. 0.143). A similar tendency was recorded in maiden high line ewes caring for multiple lambs (0.292 *vs*. 1.000; P = 0.111). Interference with or by other ewes was found to be more likely to predispose to separation of one or more lamb(s) in high line ewes than in low line contemporaries (respective proportions of 0.500 and 0.167 per ewe separated from at least one lamb; P = 0.074). Desertion of one or more lamb(s) tended to be more prevalent in low line ewes (respective proportions of 0.667 and 0.364; P = 0.151). These results imply that selection for ewe multiple rearing ability may have led to behavioral adaptations in the sheep flock studied.

Keywords: Sheep-maternal behaviour; Postpartum separations; Interference, Desertion; Lambing site; Maternal-filial bond.

Introduction

Inadequate maternal care of newborn lambs was reported to contribute markedly to perinatal lamb mortalities, particularly in multiple-bearing Merino ewes (Stevens *et al.*, 1982; Alexander *et al.*, 1983*a*). Against this background, Alexander (1988) listed behavioral patterns conducive to lamb survival. These include, among others, absence of interference with or by other parturient ewes, the ewe remaining on her birth site for at least 5 h, a lack of separation from a lamb(s) and concern at the absence of a lamb(s). Alexander (1988) contended that at least some of these attributes may be controlled by gene action, making selection a proposition to be considered.

Against this background, we observed Merino ewes subjected to divergent selection for multiple rearing ability, to determine whether the selection resulted in changes in the behavioral patterns mentioned previously.

Material and Methods

A total of 370 mixed age (2 - 6 yrs) Merino ewes lambing during the period 1993 to 1995 at the Elsenburg Agricultural Development Institute served as experimental animals. The ewes formed part of a selection experiment involving divergent selection on maternal ranking values for number of lambs weaned per lambing opportunity (Cloete and Durand, 1994). A lambing opportunity was defined as a year during which an ewe was exposed to a fertile ram. For ease of comprehension, this will be referred to as a mating in this paper. Selection decisions were mostly based on performance over ≥ 2 matings. More details regarding the determination of ranking values may be found in the paper by Cloete and Durand (1994). The two lines were selected from the same base population since 1986. In the high line, replacements of both sexes were preferably descended from dams that reared more than one lamb per mating (i.e., reared twins at least once). Progeny from dams that reared fewer than one lamb per mating (i.e., failed to lamb or lost all lambs born at least once) were preferred in the low line. Depending on the average reproduction of the flocks and number of replacements required, progeny of ewes that reared one lamb per mating were occasionally accepted as ewe replacements in both lines. The two lines were managed as a single flock throughout the year, except during mating in single sire groups to 4 - 5 rams during January - February.

Winter lambing during June-July took place on 10 kikuyu paddocks of 0.5 ha each. Five paddocks were used during daylight hours, while the other five were floodlit for use at night (Cloete, 1992). The lambing flock was observed continuously for a period of approximately three weeks during peak lambing. Ewes were side-branded with stock-marker spray to facilitate identification without undue disturbance. Teams of two trained observers recorded interest of parturient ewes in other lambing ewes and/or newborn lambs. Interest was defined as the licking of amniotic fluid and the genitalia of other parturient ewes, and the persistent, vigorous grooming of neonates given birth to by other ewes. Nonpermanent interest displayed for periods shorter than 30 s was not recorded. The birth sites of individual lambed ewes were identified with a peg, mostly after the dam attended to the neonate(s) for a period of at least 15 min. Movement of ewes from their birth sites was recorded at 30 - min intervals. Ewes were regarded as having left their respective birth sites permanently after having moved more than 15 m away from the site for more than 2 h. Estimation of distances was aided by a grid system consisting of iron poles within paddocks and fluorescent markers placed on paddock fences at 20m intervals. Separation of ewes from at least one lamb was regarded as permanent after 6 h with no contact, with the ewe being apparently unaware of the location of her lamb(s). Typically, distances between the dam and neonate(s) of > 10 to 15 m would be observed at this stage. Circumstances leading to the separation of ewes from their lamb(s) were noted. The main predisposing causes of separation were reduced to interference by or with other parturient ewes, desertion and the straying of lambs from the proximity of the birth site when left momentarily unattended. Lambs not fostered by other ewes were reunited with their mothers after 6 h of separation. Ewes not accepting their lamb(s) at this stage were forced to do so by confining them to pens of 2.5 x 1.5 m with their offspring, for at least 5 days. Lambs not accepted at this stage were removed for hand-rearing. Lamb mortalities were recorded, but it was not related to the behavioral patterns studied, since human intervention would have changed these relationships.

The period that ewes remained on their respective birth sites was expressed in hours, and subjected to least squares analysis of variance (Harvey, 1990). A preliminary analysis on 221 ewes that were observed two or more times revealed that the between ewe variance component for the period spent by ewes on their respective birth sites approached significance ($P = 0.09$). The repeatability coefficient (Turner and Young, 1969) derived from this analysis was, however, low (0.121; *SE* = 0.091). On this basis, it was decided that individual measurements on ewes observed repeatedly was sufficiently uncorrelated to satisfy assumptions for analysis of variance. The fixed model subsequently fitted included the effects of lambing year (1993 to 1995) selection line (high or low), ewe age (2 – yr - old maiden or mature), number of viable lambs cared for (single or multiple) and the interactions, which were not significant.

The occurrence of separation of a ewe from her lamb(s) in a given year could not be related to subsequent or previous performance. Cases where separation were recorded were thus expressed as proportions of ewes observed and pooled for lines, ewe age groups and litter size groups. Ewes separated from one or more lamb(s) due to a specific cause were also expressed as proportions of the total number of separations per ewe observed. These proportions were assessed statistically by either Chi^2 procedures or Fisher's exact test (Siegel, 1956) depending on the number and distribution of observations. The latter test was used for 2 x 2 contingency tables when the total count was ≤ 100. Given that the total number of ewes separated from one or more lamb(s) was relatively low, a significance level of $P < 0.10$ was accepted for these tests.

Results

Parturient high line ewes tended ($P = 0.113$) to be more interested in other lambing ewes than low line contemporaries (respective proportions 0.045 *vs*. 0.008 per ewe observed; $Chi^2 = 2.51$; $df = 1$). Interest of parturient ewes in newborn lambs did not differ for the two lines (0.094 *vs*. 0.056, respectively, $Chi^2 = 1.13$; $P = 0.29$).

The period that ewes remained on their respective birth sites was not significantly ($P > 0.10$) related to lambing year, selection line or dam age (Table 1). Ewes caring for viable multiples remained on their respective birth sites for longer ($P = 0.05$) periods than contemporaries with singles. The proportion of ewes permanently separated from one or more lamb(s) did not differ between lambing years and selection lines, but was higher ($P < 0.10$) in maiden ewes and in ewes caring for multiples.

The proportion of observed high line ewes caring for viable multiples after parturition was markedly higher ($P < 0.01$) compared to that of their low line contemporaries (141/245 = 0.576 *vs*. 50/125 = 0.400; $Chi^2 = 9.51$). Line differences were thus compared within age and caring status groups, to account for the fact that high line ewes were more likely to care for multiples. One of 43 maiden high line ewes caring for single lambs (a proportion of 0.023) were separated from it, compared to four in 28 maiden low line contemporaries (0.143; Fisher's exact probability = 0.075). A similar tendency was observed in 24 high line maidens caring for multiples relative to 2 low line contemporaries (respective proportions 0.292 *vs*. 1.00; Fischer's exact probability = 0.111). No line differences were observed for mature ewes.

Table 1. Stay of ewes on birth sites and levels of permanent separation from at least one lamb (expressed as proportions) in relation to lambing year, line, ewe age and number of viable lambs cared for

Effects	**Number of observations**	**Stay on birth site (h)** **Mean ± *SE***	**Permanent separation / ewe observed**
Overall mean	370	7.23 ± 0.33	0.092
Year		NS*	NS*
1993	136	7.97 ± 0.47	0.103
1994	91	6.54 ± 0.56	0.109
1995	143	7.19 ± 0.49	0.070
Line		NS	NS*
High line	245	7.32 ± 0.36	0.090
Low line	125	7.14 ± 0.55	0.096
Ewe age		NS	0.061
Maiden	97	7.02 ± 0.58	0.144
Mature	273	7.15 ± 0.32	0.073
Number of lambs		0.05	0.001
Single	179	6.66 ± 0.38	0.034
Multiple	191	7.81 ± 0.49	0.147

*Represents actual significance level for $P < 0.10$. The caption NS denotes significance levels of $P > 0.10$.

In total, separation from at least one lamb was recorded in 22 high line ewes and 12 low line ewes. There was a suggestion that the etiology of separation from one or more lamb(s) differed between lines. The predisposing cause of separation was recorded as interference in a higher ($P < 0.10$) proportion of high line ewes when compared to low line contemporaries (11/22 = 0.500 *vs.* 2/12 = 0.167; Fischer's exact probability = 0.07). Three of the eight mature high line ewes (a proportion of 0.375) that were separated from at least one lamb rejected one of their own multiple lambs after having bonded with a lamb born to an ewe interfered with. Both low line ewes that got separated from at least one lamb through interference was interfered with by high line ewes. One incident involved a high line ewe that adopted the second multiple of a low line contemporary after delivering a single lamb that died shortly after birth due to a severe umbilical hernia. There was a tendency for low line ewes to be more likely to desert one or more lam(s) than high line contemporaries (8/12 = 0.667 *vs.* 8/22 = 0.364, respectively; Fisher's exact probability = 0.15). Separations due to lambs straying from the birth site occurred at similar proportions in both lines (3/22 = 0.136 in the high line *vs.* 2/12 = 0.167 in the low line).

Ewes (n = 29) that remained on their respective birth sites for less than 2 h were more ($P < 0.001$) likely to be separated from at least one lamb than 345 contemporaries that remained for longer periods (9/29 = 0.310 *vs*. 29/345 = 0.072; Chi^2 = 15.27). This was mainly due to a shorter ($P < 0.01$) mean (± *SE*) period spent on their respective birth sites by 16 ewes deserting one or more lamb(s), compared to 336 contemporaries not separated from any offspring (3.22 ± 1.21 h *vs*. 7.56 ± 0.33 h). Ewes (n = 18) where other causes of separation (interference, straying of the lamb from the birth site) were recorded, remained on their respective birth sites for a period corresponding to that of contemporaries not separated from any offspring (6.99 ± 1.16 h *vs*. 7.56 ± 0.33 h).

Discussion and conclusions

Separation of Merino ewes from one or more lamb(s) was somewhat lower in our study than the > 46% separations reported previously in twin-bearing Merino ewes (Stevens *et al.*, 1982; Alexander *et al.*, 1983*a*), but consistent with the report of Alexander *et al.* (1990) where 1 to 9% permanent separations were found. Pasture conditions in the present study were probably adequate, as suggested by the average ewe leaving her birth site after more than 7 h. Results pertaining to the effects of age of the ewe and number of lambs cared for accorded with literature reports; levels of separation generally being higher ($P < 0.05$) in primiparous ewes (Putu *et al.*, 1986; Alexander *et al.*, 1993) and in ewes caring for multiple lambs (Alexander *et al.*, 1983*a*,*b*, 1990; Cloete, 1992). Inadequate maternal care has often been related to ewes voluntarily leaving the vicinity of their birth site within 1 - 2 h after birth (Alexander *et al.*, 1983*a*,*b*; Cloete, 1992) or disturbed from it (Putu *et al.*, 1988). Murphy *et al.* (1994a) recently showed that ewes drifted and penned 25 m from their birth sites had a similar proportion of permanent separations compared to ewes penned on the birth site, suggesting that the benefit arises from isolation with their lamb(s) rather than an attribute of the birth site itself.

The high line appeared to differ from the low line with regard to factors leading to separation from one or more lamb(s). There was a suggestion that parturient high line ewes were more likely to be interested in other lambing ewes. This was reflected in a predisposition towards higher levels of separation from one or more lamb(s) as a result of interference. The greater likelihood of high line ewes being separated from one or more lamb(s) due to interference poses a challenge for management. Interference by parturient ewes can be limited by a decreased stocking rate, as proposed by Winfield (1970), Alexander *et al.* (1983*b*) and Cloete (1992). There is, however, no guarantee that interference will be eliminated. We found separations due to interference with only two lambed ewes on a lambing paddock at two different occasions. Barring very intensive lambing management, which is prohibitive from an economic point of view, it remains the only viable option to alleviate the problem of interference in paddock lambing ewes.

No difference was found in either time spent on the birth site or permanent separation from one or more lamb(s) in the high line relative to the low line. Given that the high line was at a higher risk of separation from one or more lamb(s) because of their higher birth rate, this result is satisfactory. There was, in fact, evidence that maternal care of primiparous, maiden high line ewes was improved relative to low line contemporaries. Although it has been implicated that improved maternal care of Marshall Romney ewes relative to control Romneys contributed to improved survival of their offspring (Knight *et al.*, 1988), no other supporting evidence of responses to selection for multiple rearing ability was found in the literature. Emotivity of ewes was shown to be repeatable and related to maternal ability (Murphy *et al.*, 1994b). Divergent selection for emotivity resulted in an improvement in lamb survival (Lindsay, 1996) as well as peri-parturient behaviour conducive to lamb survival. Given the behavioral patterns conducive to lamb survival listed by Alexander (1988), it seems to be reasonable that some of the tendencies observed in this investigation resulted from purposeful selection for ewe multiple rearing ability.

Acknowledgements

We are indebted towards Mr. PJA Lombard and Miss Farida Martin, as well as University of Stellenbosch students (A Venter, L Burger, J Cloete) assisting with the observations. The experiment was furthermore supported financially by the SA Wool Board.

References

Alexander, G., 1988. What makes a good mother? Components and comparative aspects of maternal behaviour in ungulates. *Proceedings of the Australian Society of Animal Production* 17: 25 - 41.

Alexander, G., Stevens, D., Kilgour, R., De Langen, H., Mottershead, B.E., Lynch, J.J., 1983*a*. Separation of ewes from twin lambs: incidence in several sheep breeds. *Applied Animal Ethology* 10: 301 - 317.

Alexander, G., Stevens, D., Mottershead, B., 1983*b*. Problems in accurate recording of lambing data. *Australian Journal of Experimental Agriculture and Animal Husbandry* 23: 361 - 368.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester-derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27 - 38.

Alexander, G., Bradley, L.R., Stevens, D., 1993. Effect of age and parity on maternal behaviour in single-bearing Merino ewes. *Australian Journal of Experimental Agriculture* 33: 721 - 728.

Cloete, S.W.P., 1992. Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and SA Mutton Merino ewes. *South African Journal of Animal Science* 22: 214 - 221.

Cloete, S.W.P., Du Rand, A., 1994. Reproduction of Merino sheep subjected to divergent selection on maternal values for lambs weaned per ewe joined. *South African Journal of Animal Science* 24: 27 - 29.

Harvey, W.R., 1990. User's Guide for LSMLMW and MIXMDL. PC2 version, MIMEOGRAPH.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259 - 271.

Lindsay, D.R., 1996. Environment and reproductive behaviour. *Animal Reproduction Science* 42: 1 - 12.

Murphy, P.M., Lindsay, D.R., Purvis, I.W., 1994a. The importance of the birthsite on the survival of Merino lambs. *Proceedings of the Australian Society of Animal Production* 20: 251 - 254.

Murphy, P.M., Purvis, I.W., Lindsay, D.R., Le Neidre, P., Orgeur, P., Poindron, P., 1994b. Measures of temperament are highly repeatable in Merino sheep and some are related to maternal behaviour. *Proceedings of the Australian Society of Animal Production* 20: 248 - 250.

Putu, I.G., Poindron, P., Oldham, C.M., Gray, S.J., Ballard, M.J., 1986. Lamb desertion in primiparous and multiparous ewes induced to lamb with dexamethasone. *Proceedings of the Australian Society of Animal Production* 16: 315 - 318.

Putu, I.G., Poindron, P., Lindsay, D.R., 1988. Early separation of lambs from the birth site increases lamb separations and mortality. *Proceedings of the Australian Society of Animal Production* 17: 298 - 301.

Siegel, S., 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, NY.

Stevens, D., Alexander, G., Lynch, J.J., 1982. Lamb mortality due to inadequate care of twins by Merino ewes. *Applied Animal Ethology* 8: 243 - 252.

Turner, H.N., Young, S.S.Y., 1969. Quantitative Genetics in Sheep Breeding. Ithaca, NY.

Winfield, C.G., 1970. The effect of stocking density at lambing on lamb survival and ewe and lamb behaviour. *Proceedings of the Australian Society of Animal Production* 8: 291 - 296.

CHAPTER 9

MUTUAL IDENTIFICATION OF EWES AND LAMBS, AS AFFECTED BY DIVERGENT SELECTION FOR EWE MULTIPLE REARING ABILITY

S.W.P.Cloete, Anna J. Scholtz and J.J.E.Cloete

Elsenburg Agricultural Centre, Private Bag X1, Elsenburg 7607, South Africa

Submitted at:
Australian Journal of Experimental Agriculture

Mutual identification of ewes and lambs, as affected by divergent selection for ewe multiple rearing ability

S.W.P. Cloete, Anna J. Scholtz and J.J.E. Cloete

Elsenburg Agricultural Centre, Private Bag X1, Elsenburg 7607, South Africa

Abstract. Lambs and ewes from two lines that were selected divergently from the same base population for multiple rearing ability were assessed for mutual identification under various contrived situations. Selection began in 1986, and data for the study were obtained from 1998 to 2002. Overall and post-parturient lamb mortality for lambs born during 1998 - 2001 were lower ($P < 0.05$) in multiple born H line lambs than in L line contemporaries. No line difference was found for singles. When tethered 20 m away from their dams at 1 day of age, lambs in the High (H) line tended ($P \leq 0.10$) to be more likely to bleat and tug on the tethering rope than Low (L) line contemporaries. Ewes in the H line were quicker ($P < 0.05$) to reach a tethered lamb than L line ewes. Further divergence between the two lines in the period required by ewes to reach their lambs was evident during the course of the experiment. In an experiment conducted in pens at and age of 3 days, the vast majority (99.1%) of ewes bleated for their lamb(s) when put in a 1.5m X 1.5m pen within sight of a group of lambs. The nonlinear component of the spline for birth year interacted with selection line for the time required by ewes to reach and identify their lamb or litters from a choice of three at 3 days of age. In absolute terms, means for the intervals required by L line dams to reach their lambs or litters were slightly above those required by H line ewes during 1998 and 1999. During 2000, H line ewes took longer ($P < 0.05$) to reach their lambs or litters than L line contemporaries. During 2002, however, H line ewes had a distinct advantage ($P < 0.050$) compared to those in the L line. When lambs were assessed in the same way, the vast majority (88.8%) was able to find their dams within 5 minutes, with no evident line difference ($P > 0.05$). When turned loose from the pens, 95% of single-bearing ewes returned for their lambs, the proportion of H line ewes tending ($P < 0.10$) to be higher than in the L line. No line difference was found for multiples, where ewes returned for 73% of the lambs tested. When following their dams when chased away, H line lambs were more ($P < 0.01$) likely to follow level to the front legs of the ewe. Direct heritability (± *SE*) estimates for birth weight, the intervals required for ewes to reach a tethered lamb at 1 day and to establish contact with all individual litter mates, the intervals required by ewes to reach their lambs at 3 days and the interval required by lambs to reach their dams at 3 days were 0.19 ± 0.08, 0.05 ± 0.05, 0.08 ± 0.09, 0.09 ± 0.07 and 0.04 ± 0.05 respectively. Maternal genetic effects (m^2) were not significant for the interval required by ewes to reach their lambs in the pen tests at 3 days of age. Estimates of m^2 were 0.38 ± 0.04, 0.23 ± 0.05, 0.24 ± 0.07 and 0.15 ± 0.05 respectively for birth weight, the intervals required for ewes to reach a tethered lamb at 1 day and to establish contact with all individual litter mates, as well as the interval required by lambs to reach their dams at 3 days. Behavioral adaptations in the H line appeared to be conducive to lamb survival when compared to performance in the L line.

Keywords: Behaviour, discriminate, follow, lamb vitality, Merino, parameter estimates

Introduction

Lamb mortality is regarded as one of the most important sources of reproductive wastage in sheep (Alexander, 1988; Haughey, 1991). A 'core' level of lamb losses remain, even if managerial inputs are optimised (Alexander, 1984). A better understanding of the nature of the problem is required to deal with it under paddock lambing conditions (Lindsay *et al.*, 1990).

Lambs are very precocious in the neonatal stage, and are able to follow their dams shortly after birth (Le Neidre and Poindron, 1990). Their survival, however, depends strongly on an exclusive bond between dam and offspring that is established shortly after birth (Alexander, 1988; Lindsay *et al.*, 1990). The physiological control of maternal behaviour in ewes was reviewed by Le Neidre and Poindron (1990), and will not be discussed in detail. Visual, olfactory and auditory clues contribute to the ability of dams to identify offspring that they have bonded to during the neonatal phase (Alexander, 1988; Le Neidre and Poindron, 1990; Lindsay *et al.*, 1990).

It is of importance to note that the ability of lambs to identify and stay with their dam is also of importance (Stevens *et al.*, 1984). According to the findings of Nowak and Lindsay (1990) lambs are attracted to ewes as soon as 12 hours after birth. Some lambs are also able to discriminate between their own mothers and alien dams at this stage. In this respect, crossbred lambs performed better than purebred Merinos (Stevens *et al.*, 1984; Nowak and Lindsay, 1990). The way in which such discrimination is accomplished evolves rapidly from birth to three days of age (Poindron *et al.*, 1996).

Selective breeding was advocated by a number of authors as a means of improving the lamb survival, and thus overall flock reproductivity rate (Le Neidre and Poindron, 1990; Lindsay *et al.*, 1990; Haughey, 1991). Selective breeding was shown to be effective in reducing lamb mortality, particularly in multiples (Cloete and Scholtz, 1998). Differences in behaviour conducive to lamb survival were observed in medium wool Merino lines divergently selected for and against the ability to rear multiples (Cloete and Scholtz, 1998). This study extends previous research at this institution by investigating the ability of ewes and lambs to identify each other in various contrived situations.

Material and methods

Animals, management and location

Two lines of Merino sheep were divergently selected from the same base population since 1986, using maternal ranking values (Turner, 1977) for lambs reared per joining.

Details with regard to the selection procedure of replacements can be found in the literature (Cloete and Scholtz, 1998). In short, ewe and ram progeny of ewes rearing more than 1 lamb per joining (i.e. reared twins at least once) were preferred as replacements in the High (H) line. Replacements were preferably descended from ewes rearing fewer than 1 lamb per joining (i.e. ewes were barren or lost all lambs born at least once) in the Low (L) line. Depending on the average reproduction of the lines and the replacement needs, progeny of ewes that reared 1 lamb per joining were occasionally accepted in both lines. Selection decisions were mostly based on ≥ 3 maternal joinings, especially in the case of rams. Once selected, ewes remained in the breeding flock for at least 5 joinings, unless in the case of death or severe teeth or udder malfunction. The H line was augmented by 28 ewe progeny born as a result of a program involving multiple ovulation and embryo transfer during 1991 and 1992 (Cloete *et al.*, 1998). The mean performance of these ewes was similar to that recorded in the H line, and they were treated as a single group. Since 1996 small numbers of 6.5 year - old dams were also annually screened into both the H and L lines from the other selection lines maintained at the Tygerhoek experimental farm (Cloete *et al.*, 2001). Ewes rearing 7+ lambs from 5 opportunities and rearing at least 1 lamb per opportunity were screened into the H line. Ewes rearing 1 to 3 lambs from five opportunities were selected in the L line.

Since their establishment, the 2 lines have been maintained as a single flock, except during joining in single sire groups to 4 - 5 rams. For the duration of this study, the lines were maintained on the Elsenburg experimental farm near Stellenbosch in the south-western part of South Africa (latitude 33° 51' S; longitude 18° 50' E). The experimental site and husbandry of the animals are detailed in the literature (Cloete and Scholtz, 1998; Cloete *et al.*, 2002b), and will not be elaborated upon.

Lamb birth weight and mortality

Lamb birth weights of 1281 lambs were obtained within 24 h of birth. Lamb mortality was recorded for 1089 of these lambs born from 1998 to 2001. Lambs born in 2002 have not been weaned yet, and mortality is thus not known. Lamb mortality was expressed as proportions, and classified as deaths occurring in the post-parturient stage (from birth to weaning). Overall lamb mortality (including parturient deaths) was also assessed. Based on results obtained previously (Cloete and Scholtz, 1998), single and multiple lambs were assessed separately.

The recording of behavioural data

The study was conducted over a 5 - year period (1998 - 2002). The paddocks used, and management of ewes at lambing were described (Cloete and Scholtz, 1998; Cloete *et al.*, 2002*b*). Data for this study were recorded at two stages, namely at approximately 1 day (between 12 and 36 hours after birth) and at approximately 3 days (between 60 and 84 hours after birth). The treatment of experimental animals was closely related to procedures previously used by Alexander *et al.* (1990*b*). All procedures involved two persons. The handler worked with the animals, while the recorder observed ewe and lamb behaviour and recorded the applicable data. These data were collected annually over a period of approximately three weeks during peak lambing, and approximately 64% of all lambs born were assessed. Recordings at 1 day of age involved the following:

- ☐ The handler approached ewes cautiously, to minimise disturbance. A lamb was then removed from the ewe. The lamb was tethered, using a peg stuck firmly in the ground, approximately 20 m away. The estimation of distances was aided by a grid reference system in the paddock (Cloete and Scholtz, 1998). The handler hid lambs from the sight of the ewe behind his body. In some cases (particularly in the case of singles) ewes followed the handler closely. Such ewes were put off track by the handler and the recorder moving in a criss-cross pattern. After tethering, the handler moved away at least 20 m from the lamb, to limit interference. The activity of the tethered lamb (standing still, lying, bleating, tugging on the tethering rope) was recorded. The time that ewes took to reach individual lambs was recorded to the nearest second.
- ☐ Multiple lambs were tethered in sequence. Additional recordings, including the following of ewes by litter members not tethered, were made. Waiting of ewes for such lambs on their way to the tethered lamb was also recorded. The time after reaching the tethered lamb that ewes took to establish contact with all members of a

litter was recorded. Contact with other litter members was defined as looking back to lambs following within 2 m, or the nosing/licking/nuzzling of such lambs.

For the recordings carried out at 3 days, a set of movable pens erected near the experimental site was used. The pen consisted of a reception area, consisting of two 3m x 6m pens. Gates with corrugated iron sides were fitted to the side of these pens leading to the rest of the facility. A third pen of dimensions 6m x 6m separated these pens from three smaller 1.5m x 1.5 m pens. A second external pen of 6m x 6m was erected next to this facility in order to be visible from the smaller pens, but removed from it by at least 3 m. This facility was used to gather the following information:

- ☐ Sets of three ewes were put individually in the smaller pens, while the remaining ewes were kept in the first reception pen. The lambs belonging to these ewes were put in the external facility next to the main pen, to be visible from the smaller pens. The activity of the ewe was recorded over a period of at least 1 minute. Behaviour patterns identified were grazing, bleating and the seeking of lambs within the confined space of the pen. The latter behaviour was characterised by fairly rapid turning in the pen and sniffing at the ground and sides.
- ☐ The lambs were moved from the external pen to the second reception pen. They were then individually placed in the third pen. The time they took to identify and reach their dams was recorded. Reaching their dams was defined as remaining in close contact for at least 10 seconds, nuzzling the head of the ewe, and attempts to pass through the bars of the small pen to be with the dam.
- ☐ The positions of the ewes and the lambs were subsequently reversed, with the ewes being put in the second reception pen. Individual lambs or all members of a litter were subsequently put in the smaller pens. These proceedings were conducted out of sight of the ewes. The ewes were then individually allowed out in the third pen, and the interval required to identify and reach their lambs was recorded. An attempt was regarded as successful when an ewe remained in close contact, nuzzling or sniffing at the lamb(s) for at least 10 seconds, and attempted to pass her head through the bars of the gate to groom her lamb(s).

- Individual ewes were then returned to the second reception pen. The lamb(s) belonging to specific ewes were placed in the pen next to the outlet of the facility. Ewes were then chased to the outlet of the facility, and left to go. If they returned to the smaller pens searching for their offspring and establishing contact, their lambs were passed over the sides of the pen. In multiple bearing ewes, this process was repeated for each individual lamb.
- After this test, lambs were chased with their dams over a distance of at least 10 m. The position they adopted in following their dams was recorded as next to the front legs, next to the middle or next to or behind the hind legs of the ewe.

In all cases where time intervals were recorded, 5 minutes were regarded as a cut-off time. In ewes or lambs failing to achieve the objective in time, this value was recorded. It was also used in the appropriate statistical analyses. In total, behavioural data at 1 day of age were available for 812 lambs. The number of records at 3 days of age numbered 791.

Statistical analysis

Differences in proportions were assessed for statistical significance by *Chi*^{2} procedures (Siegel, 1956). Data based on time intervals were skewed. These data were thus transformed to natural logarithms prior to analysis. Seeing that these data were mostly unbalanced, least-squares procedures were used to analyse continuous variables (Gilmour *et al.*, 1999). All analyses were conducted from the perspective of the lamb. Fixed effects in these analyses included selection line, birth year, gender (ram or ewe), age of dam (2 to 7 years) and birth type (single or multiple). Trends in time intervals attributable to dam age and birth year were modelled by using cubic splines (Gilmour *et al.*, 1999). The fixed linear and random non-linear components of the splines were interacted with selection line where appropriate, to establish possible differences. Complete pedigrees of 2702 animals born over a 10 - year period from 1993 to 2002 were available, and used to compute random animal and dam effects. Log likelihood ratios were used to determine goodness of fit of different models, where the maternal variance was partitioned into genetic and permanent environmental components, or where the correlation between direct and maternal effects were computed.

Results

Lamb mortality

Approximately two thirds of 762 H line lambs that were assessed were multiples. In the low line, slightly below 50% of 327 lambs were born as multiples (Table 1). Lamb mortality of single lambs was independent of selection line. In multiples, however, H line progeny had a marked advantage ($P < 0.01$) compared to L line contemporaries (Table 1). This resulted in a corresponding advantage ($P < 0.05$) in overall lamb mortality in favour of the H line.

Table 1. Post-parturient (deaths from birth to weaning, excluding parturient deaths) and overall lamb mortality of single and multiple born H and L line ewes during 1998 to 2001. Lamb mortality is expressed as proportions.

Classification	**Selection line**		*Chi²*
	H line	**L line**	
Singles:			
Number of lambs	235	156	
Post-parturient deaths	0.115	0.164	0.37
Number of lambs	246	164	
Overall deaths	0.154	0.183	0.39
Multiples:			
Number of lambs	494	148	
Post-parturient deaths	0.251	0.412	13.64**
Number of lambs	516	163	
Overall deaths	0.283	0.466	18.09**
Overall:			
Number of lambs	729	304	
Post-parturient deaths	0.207	0.273	5.46*
Number of lambs	762	327	
Overall deaths	0.241	0.324	7.59**

- Significant ($P < 0.05$); ** Significant ($P < 0.01$)

Observations at one day of age

Lamb birth weight was independent of selection line ($P > 0.10$; Table 2). Ram lambs and singles were respectively 6.0 and 30.4 % heavier ($P < 0.01$) than ewes and multiples.

Lamb birth weight increased curvilinearly ($P < 0.01$) with an increase in dam age, reaching a maximum in 4 - 5 year-old dams.

Table 2. Least squares means (± *SE*) for birth weight and the measures of behaviour considered at one day of age. The latter traits were analysed after transformation to natural logarithms, and included the interval between the tethering of the lamb and the dam reaching it (ewe to lamb) and from reaching the tethered lamb to establish contact with all lambs in a litter. The latter trait was only considered in multiples. Back transformed means are given in parentheses.

Fixed effects	**Birth weight (kg)**	**Ewe to lamb (Seconds)**	**Establish contact (Seconds)**
Number of observations	1281	812	455
Overall mean	3.96 ± 0.08	3.48 ± 0.10 (32.5)	3.27 ± 0.22 (26.3)
Birth year	*	**	NS
Selection line	NS	*	*
H line	3.97 ± 0.09	3.28 ± 0.11 (26.6)	2.92 ± 0.24 (18.2)
L Line	3.95 ± 0.11	3.68 ± 0.14 (39.6)	3.62 ± 0.31 (37.3)
Birth type	**	**	**n.a.**
Single	4.48 ± 0.09	2.77 ± 0.11 (16.0)	
Multiple	3.44 ± 0.08	4.20 ± 0.11 (66.7)	
Gender	**	NS	NS
Ram	4.08 ± 0.08	3.52 ± 0.11 (33.8)	3.19 ± 0.24 (24.3)
Ewe	3.84 ± 0.08	3.44 ± 0.11 (31.2)	3.34 ± 0.23 (28.2)
Age of dam (years)	**	**	**
2	3.50 ± 0.10	3.97 ± 0.13 (53.0)	4.18 ± 0.31 (65.4)
3	3.77 ± 0.09	3.78 ± 0.11 (43.8)	3.77 ± 0.24 (43.4)
4	3.94 ± 0.08	3.46 ± 0.11 (31.8)	3.37 ± 0.22 (29.1)
5	3.97 ± 0.08	3.40 ± 0.10 (30.0)	3.16 ± 0.22 (23.6)
6	3.92 ± 0.08	3.30 ± 0.10 (27.1)	3.10 ± 0.22 (22.2)
7	3.80 ± 0.08	3.26 ± 0.12 (26.1)	3.06 ± 0.2 (21.3)

NS – Not significant ($P > 0.01$); * - Significant ($P < 0.05$); ** Significant ($P < 0.01$); **n.a.** - not applicable

When lambs were tethered, no marked line differences were observed in activity. Lambs from the H line, however, tended ($P = 0.09$) to be more likely to bleat than L line contemporaries (581/608 = 0.956 *vs.* 188/204 = 0.922; $Chi^2 = 2.88$; degrees of freedom = 1). There was also a tendency ($P = 0.10$) for lambs in the H line to tug on the tether rope more often than those in the L line (528/608 = 0.868 *vs.* 167/204 = 0.819; $Chi^2 = 2.68$; degrees of freedom = 1). Among multiple lambs not tethered, there was a suggestion ($P = 0.15$) for H line lambs to be more likely to follow their dams to their tethered sibling than their L line contemporaries (346/405 = 0.854 *vs*. 70/89 = 0.787; $Chi^2 = 2.04$; degrees of freedom = 1).

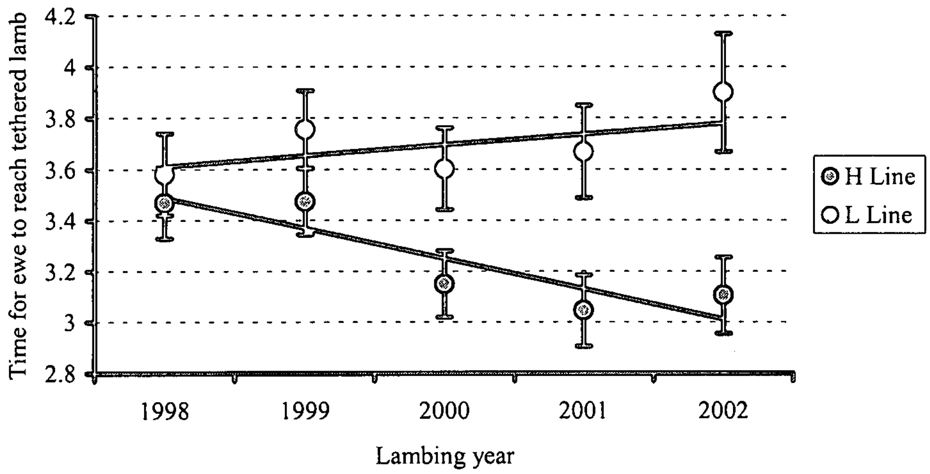


Fig. 1. The interaction between the fixed linear component of the spline for year and selection line regarding the time required for ewes to reach their tethered lambs at 1 day of age. Data were transformed to natural logarithms. Vertical lines about means depict standard errors. Means were derived from an analysis computing the interaction between fixed year and fixed selection line effects.

Tethered lambs in the H line were generally reached by their dams after a shorter ($P < 0.05$) interval than their L line contemporaries (Table 2). This generalisation was complicated by an interaction between selection line and the linear component of the spline for lamb birth year (Fig. 1). From Fig. 1, it is evident that the interval required to reach H line lambs decreased over years, while a slight increase was observed in L line lambs. Single lambs were reached much sooner ($P < 0.01$) than multiples (Table 2). This was true despite a small proportion of all multiple bearing ewes (172/494 = 0.348) that was observed to stop repeatedly, bleat and wait for siblings lagging behind on their way to a tethered lamb. Dams of tethered ram and ewe lambs reached them after similar intervals (Table 2). The interval required to reach a tethered lamb generally declined ($P < 0.05$) with an increase in ewe age.

Dams of multiple H line lambs were quicker ($P < 0.01$) to establish contact with all litter members after reaching a tethered lamb, than L line ewes (Table 2). Apart from a distinct age pattern, no other fixed effects were found to be significant. In total, dams of more ($P < 0.05$) H line lambs established contact with all litter members within 5 minutes of reaching a tethered lamb than dams of L line contemporaries (290/378 = 0.767 *vs*. 50/77 = 0.649; $Chi^2 = 4.10$; degrees of freedom = 1).

Observations at three days of age

When ewes were penned within sight of a group of lambs at three days of age, no distinct line differences in their activity were recorded. There was a suggestion for multiple-rearing ewes in the H line to search more for a lamb(s) in the confined area of the pen than L line contemporaries (83/193 = 0.570 *vs*. 23/42 = 0.452; $Chi^2 = 1.48$; degrees of freedom = 1; $P = 0.22$). Only one L line ewe out of a total of 567 ewes that were observed commenced grazing without apparent distress at being separated from her lamb. The vast majority of ewes (562/567 = 0.991) bleated for their lambs and looked in the direction of the pen containing them.

The intervals required by the dams of penned individual lambs or litters to reach these lambs were largely unaffected by the fixed effects recorded (Table 3). Selection line and the nonlinear component of the spline fitted to birth year were involved in a significant interaction (Fig. 2). In absolute terms, means for the intervals required by L line dams to reach their lambs or litters were slightly above those required by H line ewes for 1998 and 1999. During 2000, H line ewes took longer ($P < 0.05$) to reach their lambs or litters than L line contemporaries. During 2002, however, H line ewes again had a distinct advantage ($P < 0.05$) in this regard when compared to those in the L line. Overall, there was a suggestion ($P = 0.19$) for more H line ewes to reach their individual lamb or litter within the 5 minute deadline than L line ewes (571/595 = 0.960 *vs*. 183/196 = 0.934; $Chi^2 = 1.69$; degrees of freedom = 1). The averaged interval required by individual lambs to reach their dams was generally independent of the fixed effects analysed (Table 3). The exception was gender, where ewe lambs were found to be slightly quicker ($P < 0.05$) to reach their dams than ram lambs (Table 3).

When turned loose from the pens, the vast majority of single-bearing ewes (299/314 = 0.952) returned for their lambs. Ewes in the H line tended ($P = 0.08$) to be more likely to return for singles than L line contemporaries (196/202 = 0.970 *vs*. 103/112 = 0.920; $Chi^2 = 3.03$; degrees of freedom = 1). No line difference was found for multiples, ewes returning for 307 out of 418 lambs (0.734) at an age of three days.

Table 3. Least squares means (± *SE*) for the measures of behaviour considered at three days of age, as analysed after transformation to natural logarithms. Traits included the intervals between the dam being turned loose and reaching the lamb or litter (ewe to lamb or litter), and from individual lambs being turned loose and the reaching the dam (lamb to ewe). Back transformed means are given in parentheses.

Fixed effects	**Ewe to lamb or litter (Seconds)**	**Lamb to ewe (Seconds)**
Number of observations	561	786
Overall mean	2.09 ± 0.12 (8.1)	3.47 ± 0.11 (32.1)
Birth year	NS	NS
Selection line	NS	NS
H line	2.17 ± 0.14 (8.8)	3.44 ± 0.13 (31.2)
L Line	2.01 ± 0.19 (7.5)	3.49 ± 0.15 (32.8)
Birth type	NS	NS
Single	2.20 ± 0.13 (9.0)	3.46 ± 0.12 (31.8)
Multiple	1.97 ± 0.14 (7.2)	3.47 ± 0.12 (32.1)
Gender	NS	*
Ram	2.06 ± 0.14 (7.8)	3.56 ± 0.12 (35.2)
Ewe	2.11 ± 0.13 (8.2)	3.37 ± 0.12 (29.1)
Age of dam (years)	NS	**
2	2.46 ± 0.16 (11.7)	3.68 ± 0.14 (39.6)
3	2.24 ± 0.13 (9.4)	3.56 ± 0.12 (35.2)
4	2.10 ± 0.13 (8.2)	3.48 ± 0.11 (32.5)
5	2.08 ± 0.12 (8.0)	3.42 ± 0.11 (30.6)
6	2.15 ± 0.13 (8.6)	3.47 ± 0.11 (32.1)
7	2.28 ± 0.17 (9.8)	3.68 ± 0.15 (39.6)

NS- Not significant ($P > 0.01$); * - Significant ($P < 0.05$); ** Significant ($P < 0.01$)

When chased away together with their dams after the pen test, H line lambs followed their dams next to the front legs or midside more often ($P < 0.01$) than L line contemporaries (347/588 = 0.590 *vs*. 76/195 = 0.390; $Chi^2 = 22.8$; degrees of freedom = 1).

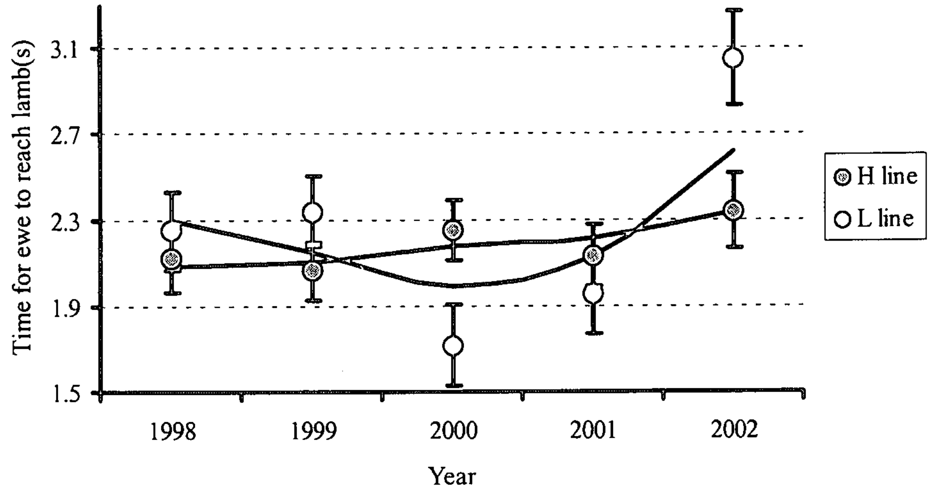


Fig. 2. The interaction between the random nonlinear component of the spline for year and selection line regarding the time required for ewes to reach their lambs or litters at 3 days of age. Data were transformed to natural logarithms. Vertical lines about means depict standard errors. Means included were derived from an analysis including the interaction between the fixed

Parameter estimates

The estimation of genetic parameters was not regarded as the main objective of the investigation. Direct h^2 estimates were not significant (more than double the corresponding *SE*) except in the case of birth weight (Table 4).

Table 4. Variance components and ratios for the traits considered. Components include the direct additive (σ^2_a), maternal additive (σ^2_m) and environmental (σ^2_e) variances respectively. Ratios include the direct heritability (h^2) and maternal heritability (m^2).

Trait	**Variance components**			**Variance ratios (± *SE*)**	
	σ^2_a	σ^2_m	Σ^2_e	h^2	m^2
Birth weight	0.0934	0.1822	0.2075	0.19 ± 0.08	0.38 ± 0.04
Traits at one day					
Ewe to lamb	0.0549	0.2525	0.8110	0.05 ± 0.05	0.23 ± 0.05
Establish contact	0.2164	0.6855	1.9137	0.08 ± 0.09	0.24 ± 0.07
Traits at three days					
Ewe to lamb	0.1151		1.2470	0.09 ± 0.07	
Lamb to ewe	0.0667	0.2344	1.2776	0.04 ± 0.05	0.15 ± 0.05

Effect not significant ($P < 0.05$) according to Log Likelihood

Estimates depicting maternal effects (m^2) were significant in most cases, with the exception of the interval required by ewes to reach their lamb(s) in the pens at an age of three days. Estimates of m^2 regarding to recordings made at an age of 1 day exceeded 0.20 in all instances. The partitioning of maternal variances in direct and permanent environmental components did not result in improvements in the acquired log likelihood ratios in cases where maternal effects were significant. The inclusion of the direct-maternal covariance components similarly did not result in improved log likelihood ratios.

Discussion

Lamb mortality

The survival of lambs was not compromised by selection for ewe multiple rearing ability, despite the fact that higher mortality levels are expected with an increase in multiple birth rate (Haughey, 1991). The survival of multiples, in particular, was improved substantially in the H line. Previous results obtained during the 5 - year period from 1993 to 1997 on the same resource population were similar to those obtained in the present investigation (Cloete and Scholtz, 1998). Similar advantages of selection for lamb survival and/or ewe rearing ability were reported in the literature (Atkins, 1980; Donnelly, 1982; Haughey, 1983; Knight *et al.*, 1988).

Behavioural observations

The impact of environmental factors upon birth weight was consistent with that expected from the literature. These results will thus not be discussed in detail. The behavioural attributes of dams generally improved with age (Tables 2 and 3). This result accords with literature reports that behaviour beneficial to lamb survival in ewes can be accrued over additional lambing opportunities as ewes gain more experience (Alexander *et al.*, 1984; Alexander, 1988; Alexander *et al.*, 1993). In a study involving 5 - year-old primiparous single-bearing ewes, results of Alexander *et al.* (1993) indicated that there was no evidence of improved maternal attributes with an increase in ewe age that could not be related to previous experience of giving birth to and the rearing of lambs.

Dams caring for multiple lambs at an age of one day were slower ($P < 0.05$) to reach a tethered lamb than those caring for singles (Table 2). This result was found despite the fact that relatively few of these ewes were seen to actively wait for a sibling lagging behind. No effect of birth type on the time required to reach a tethered lamb was found in the study of Alexander *et al.* (1990*b*). Triplet bearing ewes in the latter study were, however, slower to collect their litters together than twin bearers. The only other fixed effect (apart from selection line) that was significant was gender. Ewe lambs were quicker ($P < 0.05$) to reach their dams in the pen test at 3 days than ram lambs (Table 3). Although no comparable results were found in the literature, it is well-known that ewe lambs are more likely to survive to weaning than ram lambs (Alexander, 1984). An enhanced ability of ewes to identify the appropriate dam would be conducive to an improved survival rate (Lindsay *et al.*, 1990; Poindron *et al.*, 1996), possibly contributing to the observed gender difference.

Dams in the H line were quicker to reach a tethered lamb in the tests conducted at 1 day of age (Table 2). Moreover, results suggested that divergence between lines were present for this trait (Fig.1). Comparable results pertaining to different breeds that were investigated by Alexander *et al.* (1990*b*) were inconclusive. Merino, Border Leicester and a Border Leicester derived line selected for rearing ability (Glen Vale) were compared. Merino dams were quicker to reach tethered lambs than the other breeds, but a higher proportion of Merinos failed to reach a tethered lamb within the time allocated. Glen Vale ewes were quicker to reach their tethered lambs than Border Leicester ewes, and tended not to wait for siblings that were not tethered. Merino ewes that were able to collect their litters within 5 minutes, took longer to do so than either Glen Vale or Border Leicester ewes. At this stage it is uncertain whether this result can be related to the present findings pertaining to the quicker establishment of contact with all litter members in H line ewes compared to L line contemporaries.

Lambs in the H line tended ($P < 0.10$) to be more likely to vocalize than L line lambs when they were tethered. It is established in the literature that bleats by lambs are invariably followed by a bleat by the dam (Lindsay *et al.*, 1990). The ability of lambs to distinguish between their own mothers and alien ewes was related to their frequency of bleating (Nowak, 1989). It is thought that this continuous stimulus-response behaviour pattern facilitates the establishment of a strong dam-offspring bond (Lindsay, 1996). Lambs in the H line also tended ($P = 0.10$) to be more likely to tug upon the tether rope, while there was a suggestion that they were more likely to follow their dams at 1 day of age. The latter suggestion was augmented by results obtained at three days, when H line lambs were more ($P < 0.01$) likely to follow next to the front legs of their dams. These findings seem to indicate a greater vitality in H line lambs. In a goitre-affected flock, Alexander *et al.* (1990*a*) found that following behaviour and survival of lambs were impaired in lambs with higher thyroid scores. In the breed comparison of Alexander *et al.* (1990*b*), following behaviour was affected by breed at 1 day of age, but not at 2 to 3 days. At 1 day of age, fewer ($P < 0.05$) Merino singles and twins followed their dams than Border Leicester and Glen Vale lambs.

No consistent line difference was found for the time that ewes took to identify their 3-day-old lambs in the pen tests. Alexander *et al.* (1990*b*) correspondingly did not find breed differences at this age. No apparent explanation can be given for the interaction ($P < 0.05$) of the nonlinear components of the spline for year with selection line (Fig. 2). The result may be co-incidental, since the two years with the largest leverage on the shape of the curve for L line ewes (2000 and 2002) were characterised by a small number of observations in this line. Only respectively 38 and 33 % of all the L line lambs born in these years were tested at 3 days of age compared to 51 - 64% in other years. These percentages were much more stable in the H line, between 59 and 73 % of all lambs born being tested in the respective years. Nearly 90 % of all lambs used in the pen tests at 3 days of age were able to identify the correct dam within 5 minutes, with no difference between lines. In this regard, Nowak and Lindsay (1990) reported that more Border Leicester X Merino lambs were able to identify their Merino dams at 12 hours of age than purebred Merinos. The formation of an exclusive dam-offspring bond evolves rapidly during the first 3 days of life (Poindron *et al.*, 1996). It is possible that initial line differences in this behavioural attribute could be masked at 3 days, since the formation of an exclusive dam-offspring bond are well-developed at this stage. In the study of

Alexander *et al.* (1990*b*), no breed differences were found for lamb traits, when assessed at an age of 3 days. In goitre-affected single lambs studied by Alexander *et al.* (1990*a*), intervals required to cover 6 m to their dams increased with an increased thyroid score.

Various strategies were proposed for the utilisation of behavioural information, with the intention to improve lamb survival. In New Zealand, the maternal behaviour score was considered in this role (O'Connor *et al.*, 1985). The scoring system is based on the distance that ewes retreat from their lamb or litter at tagging. Heritability estimates for these scores vary from low (Everett-Hincks *et al.*, 2002) to moderate (Lambe *et al.*, 2001). In a recent application of this system to a New Zealand flock with a high lamb survival (litter survival in excess of 90%), it was concluded that limited progress was to be expected from the usage of this index (Everett-Hincks *et al.*, 2002). In Australian Merinos, where a lower survival is expected, emotivity was considered as a possible means to improve lamb survival. It was hypothesized that quiet, unresponsive animals would have an advantage regarding the survival of their progeny (Lindsay, 1996). Ewes that were extremely nervous and reactive to new stimuli would be at a disadvantage. Emotivity was assessed in a test devised by Murphy *et al.* (1994). Divergent selection of lines of Merino sheep were subsequently undertaken, leading to an advantage in lamb survival in favour of the quiet, unresponsive line (Lindsay, 1996; Murphy *et al.*, 1998). This line also exhibited better maternal behaviour in the study of Murphy *et al.* (1998). The approach in the present study was rather to select for multiple rearing ability, which is a composite trait. Lamb survival is included as a component. It is reassuring to find that this selection strategy generally resulted in behaviour conducive to lamb survival (see also Cloete and Scholtz, 1998). A very similar objective, namely total weight of lamb weaned per ewe per parity, is being strived for in general for the sheep breeds participating in the South African Small Stock Improvement Scheme (Olivier, 1999). It is contended that selection for litter weight at weaning would keep reproduction traits within optimum fitness bounds for a particular environment (Ercanbrack and Knight, 1998).

Parameter estimates

Differences between breeds and lines are often regarded as indicative of genetic variation in behavioural traits, while very few formal estimates of genetic parameters are available (Hinch, 1997). Recent analyses at this institute indicated direct and/or maternal genetic variation in length of parturition as well as the intervals from birth to standing and from standing to suckling in lambs of dual-purpose breeds (Cloete *et al.*, 2002*a*). It thus comes as no surprise to find significant maternal variance components for the majority of the traits analysed in this study. Significant maternal variances for the time required by ewes to reach their lambs at 1 day and the establishment of contact with all litter mates were expected, owing to the major contribution of the ewe to these traits. It was surprising to find a significant maternal component for the time required by individual lambs to reach their dams in the pen tests at 3 days of age. It thus seems as if the contribution of the dam to the formation of a strong bond enabling the lamb to identify the correct dam at 3 days is important. No comparable estimates to test these against were found in the literature.

Conclusions

Results from the study generally supported a hypothesis that ewes and lambs in the H line underwent behavioural adaptations conducive to lamb survival when compared to L line contemporaries, according to the classification by Alexander (1988). Previous studies on the same resource population largely came to the same conclusion concerning other behavioural traits (Cloete and Scholtz, 1998; Cloete *et al.*, 2002*b*). Significant maternal variance components for mutual identification of ewes and lambs were found. These findings support a contention that at least some aspects of maternal and neonatal behaviour will respond to selection, provided that a feasible selection strategy could be devised. Similar conclusions pertaining to other components of behaviour were arrived at earlier during the analysis of data from dual-purpose breeds (Cloete *et al.*, 2002*a*). Parameter estimates of these and comparable other studies fulfil a need in the scientific literature, that was identified in the 1980's (Hohenboken, 1986). According to the most recent review in this respect, very limited progress has been made since (Hinch, 1997), and further studies are indicated.

Acknowledgements

The inputs of Mr. J.E. Fourie regarding the maintenance and care of the breeding flock are appreciated. The gates needed for the pen study at 3 days of age were obtained free of charge from BKB, Klapmuts. The research would have been impossible without access to these resources.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay, D.R., Pearce, D.T.,(Eds.). Reproduction in sheep. pp. 199 - 209. Australian Academy of Science in conjunction with the Australian Wool Corporation: Canberra, Australia.

Alexander, G., 1988. What makes a good mother? *Proceedings of the Australian Society for Animal Production* 17: 25 - 41.

Alexander, G., Bradley, L.R., Stevens, D., 1993. Effect of age and parity on maternal behaviour in single-bearing Merino ewes. *Australian Journal of Experimental Agriculture* 33: 721 - 728.

Alexander, G., Kilgour, R., Stevens, D., Bradley, L.R., 1984. The effect of age and experience in twin care in New Zealand Romney sheep. *Applied Animal Ethology* 12: 363 - 374.

Alexander, G., Stevens, D., Bradley, L.R., 1990a. Intensive observations during lambing in a goitre-affected flock, with special reference to behaviour of lambs. *Australian Journal of Experimental Agriculture* 30: 749 - 757.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990b. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27 - 38.

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of the Australian Society for Animal Production* 13: 174 - 176.

Cloete, S.W.P., Olivier, J.J., Du Toit, E., 2001. Blowfly strike of Merino sheep in relation to selection strategy, as well as to objective and subjective wool traits. *Proceedings of the Flystrike and Lice IPM Control Strategy Conference*, 22 - 25 June 2001, Launceston, Tasmania. pp 395 - 401.

Cloete, S.W.P., Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Scholtz, A.J., Gilmour, A.R., Olivier, J.J., 2002a. Genetic and environmental effects on lambing and neonatal behaviour of Dormer and South African Mutton Merino lambs. *Livestock Production Science*, in press.

Cloete, S.W.P., Scholtz, A.J., Taljaard, R., 2002b. Lambing behaviour of Merino lines subjected to divergent selection for multiple rearing ability from the same base population. *South African Journal of Animal Science* 32: 57 - 65.

Cloete, S.W.P., Van Niekerk, F.E., Rust, J.M., 1998. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *Sheep and Goat Research Journal* 14: 11 - 12.

Donnelly, F.B., 1982. A practical attempt to breed for better lamb survival. *Proceedings of the Australian Society of Animal Production* 14: 30 - 32.

Ercanbrack, S.K., Knight, A.D., 1998. Responses to various selection protocols for lamb production in Rambioullet, Targhee, Columbia and Polypay sheep. *Journal of Animal Science* 76: 1311 - 1325.

Everett-Hicks, J.M., Lopez-Villalobos, N., Blair, H.T., Stafford, K.J., 2002. Genetic variation in maternal behaviour score and lamb survival. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production*, 19 - 23 August 2002, Montpellier, France. 32: 63 - 66.

Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R., 1999. ASREML – Reference manuel. NSW Agriculture Biometric Bulletin No. 3. NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, N.S.W., Australia.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361 - 363.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Hinch, G.N., 1997. Genetics of behaviour. In: Piper, L., Ruvinsky, A. (Eds.). The genetics of sheep. Pp. 353 - 374. CAB International, Wallingford, Oxon, United Kingdom.

Hohenboken, W.D., 1986. Inheritance of behavioural characteristics in livestock. A review. *Animal Breeding Abstracts* 54: 623 - 639.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259 - 271.

Lambe, N.R., Conington, J., Bishop, S.C., Waterhouse, A., Simm, G., 2001. A genetic analysis of maternal behaviour score in Scottish Blackface sheep. *Animal Science* 72: 415 - 425.

Le Neidre, P., Poindron, P., 1990. Physiological and sensory basis of the mother young relationship in sheep. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.), Reproductive Physiology of Merino sheep. Pp. 179 - 190. School of Agriculture, University of Western Australia.

Lindsay, D.R., 1996. Environment and reproductive behaviour. *Animal Reproduction Science* 42: 1 - 12.

Lindsay, D.R., Nowak, R., Putu, I.G., McNeil, D., 1990. Behavioural interactions between the ewe and her young at parturition. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.). Reproductive Physiology of Merino sheep. pp. 191 - 205. School of Agriculture, University of Western Australia.

Murphy, P.M., Purvis, I.W., Lindsay, D.R., Le Neidre, P., Orgeur, P., Poindron, P., 1994. Measures of temperament are highly repeatable in Merino sheep and some are related to maternal behaviour. *Proceedings of the Australian Society of Animal Production* 20: 248 - 250.

Murphy, P.M., Lindsay, D.R., Le Neidre, P., 1998. Temperament of Merino ewes influences maternal behaviour and survival of lambs. *Proceedings of the 32nd Congress of the International Society for Applied Ethology*, Clermond-Ferrand, France. p 131.

Nowak, R., 1989. Early recognition of the mother by the new-born lamb. Ph.D. dissertation, the University of Western Australia, Perth ,W.A.

Nowak, R., Lindsay, D.R., 1990. Effect of genotype and litter size on discrimination of mothers by their twelve-hour-lambs. *Behaviour* 117: 1 - 13.

O'Connor, C.E., Jay, N.P., Nicol, A.M., Beatson, P.R., 1985. Ewe maternal behaviour score and lamb survival. *Proceedings of the New Zealand Society of Animal Production* 45: 159 - 162.

Olivier, J.J., 1999. The South African Merino performance testing scheme. In: Rising to the challenge – Breeding for the 21st Century Customer. Beef Industry and CRC for Premium Quality Wool Industry Symposia. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 13: 119 - 124.

Poindron, P., Nowak, R., Oldham, C.M., Lindsay, D.R., 1996. The reproductive behaviour of prolific sheep. In: Fahmy, M.H., (Ed.), Prolific sheep. pp. 471 - 483. CAB International, Wallingford, Oxon, OX10 8DE, United Kingdom.

Siegel, S., 1956. Non parametric statistics for the behavioral sciences. McGraw-Hill Book Company Inc., New York.

Stevens, D., Alexander, G., Mottershead, B., Lynch, J.J., 1984. Role of the lamb in post-partum separation of ewes from twin lambs. *Proceedings of the Australian Society for Animal Production* 15: 751.

Turner, H.N., 1977. Australian sheep breeding research. *Animal Breeding Abstracts* 45: 9 - 33.

CHAPTER 10

LAMB SURVIVAL IN RELATION TO LAMBING AND NEONATAL BEHAVIOUR IN MEDIUM WOOL MERINO LINES DIVERGENTLY SELECTED FOR MULTIPLE REARING ABILITY

S.W.P. Cloete and A.J. Scholtz

Elsenburg Agricultural Development Institute,
Private Bag X1, Elsenburg 7607, South Africa

Published in:
Australian Journal of Experimental Agriculture (1998) 38: 801 - 811

Reproduced with permission of:
Australian Journal of Experimental Agriculture

Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for multiple rearing ability

S.W.P. Cloete and A.J. Scholtz

Elsenburg Agricultural Development Institute, Private Bag X1, Elsenburg 7607, South Africa;
e-mail: schalkc@wcape.agric.za

Abstract: Two lines of Merino sheep were divergently selected from the same base population since 1986 on maternal ranking values for multiple rearing ability. In the high (H) line, ewe and ram progeny were preferably descended from ewes that reared > 1 lamb per joining. In the low (L) line, replacements were the progeny of ewes that reared < 1 lamb per joining. Data on lamb mortality, lambing and neonatal behaviour as well as lamb production were obtained from these lines over 5 years (1993 - 97).Lamb survival was improved ($P < 0.01$) in the H line, mainly as a result of the improved survival of multiples. It was evident that the survival of lambs was not compromised by selection for ewe multiple rearing ability, despite the fact that higher mortality levels are expected with an increase in multiple birth rate. No line difference was found for the time lapse from birth to first standing for > 10 s, but H line lambs were quicker ($P < 0.01$) to progress from standing to suckling than L line contemporaries (28 *vs.* 38 min respectively). This line difference remained after adjustment for better co-operation of H line ewes with the first suckling attempts of their progeny. Ewes in the H line tended ($P = 0.18$) to remain longer on or near their birth sites than L line contemporaries (403 *vs.*362 min respectively). They also tended to be less ($P = 0.07$) likely to desert their lambs than L line ewes (12/424 = 0.028 *vs.* 14/230 = 0.061 respectively). After least-squares adjustment for their heavier ($P < 0.01$) litter weight, H line ewes experienced shorter ($P < 0.05$) births than their L line contemporaries (46 *vs.* 57 min respectively). Fewer ($P < 0.05$) H line lambs died during or shortly after parturition (respective proportions of 22/890 = 0.025 and 25/441 = 0.057), while maiden H line ewes were less ($P < 0.05$) likely to be assisted at lambing than L line contemporaries (4/107 = 0.037 *vs.* 8/61 = 0.131 respectively). With regard to overall lamb production, it was found that the number of lambs weaned per ewe present at lambing in the H line was improved ($P < 0.05$) in all years relative to that observed in the L line, the differences ranging from 25% in 1993 to 47% in 1997. Lamb weaning weight was correspondingly improved ($P < 0.05$) in H line lambs, the differences ranging from 8% in 1994 to 22% in 1996. Fairly high levels of production could thus be attained with predominantly pasture-fed ewes selected for multiple rearing ability.

Additional keywords: length of parturition, birth problems, neonatal lamb progress, desertion.

Introduction

Lamb mortality is regarded as a major constraint to efficient sheep production (Alexander, 1988; Haughey, 1991). A 'core' level of lamb losses remain, even if managerial inputs are optimised (Alexander, 1984). Even very intensive management failed to reduce lamb mortality in South African Mutton Merinos and Dormers to levels of below 15% (Brand *et al.*, 1985). The cost of intensification prohibits the improvement of lamb survival by, for instance, providing permanent supervision and confining ewes and lambs to indoor pens during the perinatal period. Selective breeding was advocated as a possible means of improving lamb survival and ewe rearing ability under paddock conditions (Lindsay *et al.*, 1990; Haughey, 1991). It was hypothesised that behavioural adaptations may contribute to selection responses in lamb survival (Alexander, 1988).

This paper reports on responses in lamb survival in South African medium wool Merino flocks that were divergently selected for multiple rearing ability. The assumption that behaviour was instrumental in the obtained responses was tested, by comparing behaviour in the flocks.

Material and methods

Animals, management and location

Two lines of Merino sheep were divergently selected from the same base population since 1986, using maternal ranking values (Turner, 1977) for lambs reared per joining. Details with regard to the selection procedure of replacements can be found in the literature (Cloete and Durand, 1994; Cloete *et al.*, 1998*b*). In brief, ewe and ram progeny of ewes rearing more than 1 lamb per joining (i.e. reared twins at least once) were preferred as replacements in the high (H) line. Replacements were preferably descended from ewes rearing fewer than 1 lamb per joining (i.e. barren or lost all lambs born at least once) in the low (L) line. Depending on the average reproduction of the lines and the replacement needs, progeny of ewes that reared 1 lamb per joining were occasionally accepted in both lines. Selection decisions were mostly based on ≥ 3 maternal joinings, especially in the case of rams. Once selected, ewes remained in the breeding flock for 5 joinings, unless in the case of death or severe teeth or udder malfunction. The H line was augmented by 28 ewe progeny born as a result of a program involving multiple ovulation and embryo transfer during 1991 and 1992 (Cloete *et al.*, 1998*c*). The mean performance of these ewes was similar to that recorded in the H line, and they were treated as 1 group.

Since their establishment, the 2 lines were being maintained as a single flock, except during joining in single sire groups to 4 - 5 rams. For the duration of the study, the lines were maintained on the Elsenburg experimental farm (33°51'S, 18°50'E) near Stellenbosch in the south-western region of South Africa. The climate for the experimental site is Mediterranean, with 78% of the average annual rainfall of 606 mm being recorded in the months from April to September. Irrigated kikuyu (*Pennisetium clandestinum*) paddocks were utilised during joining in summer (January - February) and lambing in winter (June - July). Dryland lucerne (*Medicago sativa*) and medic (*M. truncatula*) pastures were mostly utilised during the remainder of the year. An oat (*Avena sativa*) fodder crop was occasionally utilised in winter, while oat crop residues and standing hay were sometimes available during spring and early summer. Nutrition was mostly adequate throughout the year, and supplementary feeding was rarely needed. The ewes were shorn annually within 3 - 4 weeks of the commencement of lambing.

Lambing management and recording of production data

The study was conducted over 5 years (1993 - 97). Lambing occurred on 10, 0.5 ha kikuyu paddocks. Ewes were side-branded with stock-marker spray to facilitate identification without undue disturbance. Unlambed ewes were drifted from the previous night paddock to the next day paddock at 07h30 hours. At 18h00 hours unlambed ewes were drifted to the following night paddock. Care was taken not to disturb recently lambed ewes or their lambs during drifting. Groups of ewes were left on their lambing paddock for 2.5 - 3.0 days, before being placed out to lucerne pasture. Group sizes at this stage ranged from 20 to 30 ewes with their lambs. After tailing, larger flocks were formed to utilise the more extensive dryland lucerne pastures.

Lamb birth weight was obtained within 24 h of birth, and used to calculate total litter weight for ewes. Other data that were recorded on a flock basis included lamb survival, levels and causes of lamb mortality, overall ewe reproduction rate (lambs reared per ewe joined) and lamb weaning weight (at about 100 days). Lamb mortality was classified according to stage as follows: (i) peri-parturient mortalities (before, during and within 6 h of birth); (ii) > 6 h to 3 days of age; and (iii) > 3 days of age to weaning.

Lambs (113) which died during the perinatal period (before, during or within 7 days of birth) were collected and delivered to the Veterinary Diagnostic Centre at Stellenbosch once daily, or after storage in a cool room (4°C) over weekends and public holidays. Using the procedure described by McFarlane (1965) and Haughey (1991) lambs were classified as having died in the antenatal period (characterised by autolysis, subcutaneous oedema or mummification), in the parturient or postparturient period due to birth stress (characterised by oedema of the presenting portion, meconium staining, epicardial petechiae, ruptured liver, haemorrhages and congestion of the brain and the spinal chord), in the postparturient period with evidence of starvation – mismothering - exposure (SME, characterised by depleted fat reserves, inadequate milk ingesta) or due to other causes (lethal congenital malformations, infections acquired after birth, deformities, unknown causes). Age, number of lambs given birth to and selection line were known for individual ewes. Pedigree, selection line, sex and birth type (single, first multiple, subsequent multiple) were known for individual lambs.

Recording of behaviour at lambing

The lambing flock was observed continuously by 1 - 2 trained observers for a period of about 3 weeks during peak lambing. The ewes adapted to human presence within a short period, and could be approached closely (< 10 m) without undue disturbance. Five lambing paddocks were used during daylight hours, while the other 5 were floodlit for use at night (Cloete, 1992; Cloete *et al.*, 1998*b*).

In chronological order, recordings included the first definite sign of parturition (straining or the presentation of membranes in > 90% of cases) and length of parturition from the first definite sign to the birth of the last lamb. Length of parturition of individual lambs was calculated as the period between the first definite sign of parturition and the birth of that specific lamb. In multiples, the birth of the previous lamb was regarded as the beginning of parturition for subsequent litter mates. Ewes were assisted upon their failure to deliver a lamb within: (i) 3.5 - 4.0 h after the first definite sign; (ii) 2 h after the first sight of the presentation of the lamb at the vulva; (iii) 2 h after the birth of a preceding litter mate; or (iv) 30 min after the appearance of a part of the body (e.g. the head or a limb).

Lambs were identified with stock marker spray according to the order of birth within a litter after being groomed by their mother for at least 15 min. The birth site was simultaneously marked with a peg. Lamb progress, as reflected by the period from expulsion to standing for > 10 s and from standing to first apparently suckling was also recorded. Ewes that frustrated the first suckling attempts of their neonates by backing, circling or butting were recorded (Alexander, 1988). Active co-operation by standing still, adopting a slightly hunched posture to enable access to the udder and nudging the lamb in a position to facilitate suckling was also noted (Lynch *et al.*, 1992).

Movement of ewes from their birth sites was recorded at 30 - min intervals. Ewes were regarded as having left their birth sites permanently after having moved away more than 15 m for more than 2 h. Estimation of distances was aided by a grid system consisting of iron poles and fluorescent markers placed on the paddock fences at 20 m intervals. Interference of parturient ewes with neonatal lambs of other ewes was allowed during 1993 - 95 (Cloete *et al.*, 1998*b*). Interfering ewes were taken out of the paddock, to lamb in the corridor between paddocks in 1996 and 1997. This was done to prohibit the adoption of foreign lambs by ewes and to ensure the correct pedigrees as far as possible. The deserting of lambs by their dams was still recorded, and ewes were still forced to accept deserted lambs, as described by Cloete *et al.*, (1998*b*).

Statistical analyses

Differences in proportions were assessed for statistical significance by Chi^2 procedures (Siegel, 1956). Differences in lambs reared per ewe available at lambing were tested for significance between lines as described by Brown (1988). Since the data were mostly unbalanced, least squares procedures (Harvey, 1990) were used to analyse continuous variables. Length of parturition and periods indicating neonatal progress were negatively skewed and leptocurtic. A standard $\log_{10}$ transformation normalised these data. A square root transformation was required for the time spent on or near the birth site. Fixed effects in the analyses on lamb traits included selection line, birth year, sex (ram or ewe), age of dam (maiden or mature) and birth type (single, first multiple or subsequent multiple). The analyses on length of parturition, litter weight and time spent on the birth site in ewes were complicated by the fact that several ewes were observed repeatedly in different years. Since these observations could be correlated, the assumptions for analysis of variance were not necessarily satisfied. This limitation was overcome by including the random effect of ewes within selection lines (H or L) in these analyses. This approach enabled us to calculate repeatability coefficients for these traits from the between ewe and error variance components (Turner and Young, 1969). Other fixed effects included in these analyses included lambing year (1993 - 97), age (maiden or mature) as well as linear covariables where appropriate. Two-way interactions between main effects were relatively unimportant ($P > 0.1$) in the least squares analyses on ewe and lamb traits, and are thus not presented. Birth or lambing year means were only presented where they contributed to the discussion and conclusions. Ten triplet births (9 in the H line and 1 in the L line) were pooled with twins as multiples.

Results

Levels and causes of lamb mortality

In total, 1331 lambs were born in the study (890 in the H line and 441 in the L line). The proportion of multiple lambs in the H line was higher ($P < 0.01$) than in the L line (610/890 = 0.685 *vs.* 238/441 = 0.540; $Chi^2 = 26.5$). Overall lamb mortality was > 25%, the majority of lambs succumbing in the postparturient period (> 6 h after birth; Table 1). Total levels of lamb mortality and mortality at specific stages was independent ($P > 0.10$) of sex of the lamb and dam age. These values are thus not presented. Lamb mortality, and particularly mortality from > 3 days to weaning was affected ($P < 0.01$) by birth year. Multiples were also more ($P < 0.01$) likely to die during the postnatal stage than singles.

Lambs born in the H line were more ($P < 0.01$) likely to survive birth than L line contemporaries (Table 1). A similar tendency ($P = 0.07$) was observed as for postnatal deaths to 3 days. Closer scrutiny of the data indicated that the survival of multiples in particular contributed to the better survival of H line lambs. The overall proportion of single H line lambs that died before weaning was similar to that recorded in the L line (47/280 = 0.168 *vs.* 45/203 = 0.222; $Chi^2 = 1.88$; $P = 0.17$). The mortality of multiple-born H line lambs was lower ($P < 0.01$) than that of L line contemporaries (154/610 = 0.252 *vs.* 93/238 = 0.391; $Chi^2 = 15.20$; $P < 0.01$). This could be attributed to fewer ($P < 0.05$) deaths during or shortly after birth (13/610 = 0.021 *vs.* 14/238 = 0.059; $Chi^2 = 6.65$) and from birth to 3 days of age (44/610 = 0.072 *vs.* 28/238 = 0.118; $Chi^2 = 4.00$) in H line multiples. A corresponding tendency ($P = 0.07$) was observed in deaths occurring at > 3 days of age (97/610 = 0.159 *vs.* 41/238 = 0.214; $Chi^2 = 3.26$). When looking at individual years, the overall level of lamb mortality was lower ($P < 0.05$) in the H line, except during 1993 and 1995.

Table 1. Preweaning lamb mortalities (expressed as proportions) classified according to stage as affected by selection line, birth year and litter size

Effect	No. of Lambs	Total	Stage of mortality		
			Birth	Birth – 3 days	> 3 days
Overall mean	1331	0.255	0.035	0.069	0.150
Selection line		**	**	0.070	NS
H line	890	0.226	0.025	0.060	0.142
L line	441	0.313	0.057	0.088	0.168
Birth year		**	NS	*	**
1993	275	0.313	0.036	0.069	0.207
1994	259	0.224	0.050	0.108	0.066
1995	284	0.384	0.018	0.039	0.327
1996	251	0.163	0.032	0.076	0.056
1997	262	0.172	0.042	0.057	0.073
Litter size		**	NS	**	**
Single	483	0.190	0.041	0.041	0.108
Multiple	848	0.291	0.032	0.085	0.175

* $P < 0.05$; ** $P < 0.01$; NS, not significant.

Of the 113 lambs autopsied, 3 (2.7%) were found to have died before parturition (antenatal deaths). Birth stress was diagnosed in 42 lambs (37.2%), while 52 lambs (46.0%) showed evidence of starvation, mismothering and/or exposure. Other causes of mortality (infections, deformities etc.) were diagnosed in 16 lambs (14.1%). Causes were broadly similar in lines, but there was a tendency ($P \approx 0.10$) for a higher proportion of birth-stressed lambs autopsied in the L line relative to the H line (24/52 = 0.462 *vs.* 18/61 = 0.295; $Chi^2 = 2.66$). Slightly more H line lambs were diagnosed with SME (32/61 = 0.524) compared with L line contemporaries. (20/52 = 0.385) but significance could not be demonstrated ($Chi^2 = 2.66$; $P = 0.19$).

Neonatal lamb progress and co-operation of ewes with their first suckling attempts

Since the majority of lamb deaths occurred > 6 h after birth, behavioural patterns and other factors that could be involved at this stage are discussed first. After least squares adjustment for litter size, H line lambs were 3.7% heavier ($P < 0.01$) than L line contemporaries (Table 2).

Table 2. Least squares means (± *SE*) for birth weight (± *SE*) and the $\log_{10}$-transformed period from expulsion to first standing for > 10 s as affected by selection line, sex, age of dam and order of birth

Effect	**No. of Observations**	**Birth Weight (kg)**	**Expulsion – Standing (min)**	
			Mean ± *SE*	**Antilog**
Overall mean	975	3.85 ± 0.03	1.41 ± 0.02	26
Selection line		**	NS	
H line	661	3.93 ± 0.03	1.43 ± 0.02	27
L line	314	3.79 ± 0.04	1.40 ± 0.02	25
Sex		**	**	
Ram	472	3.99 ± 0.03	1.45 ± 0.02	28
Ewe	503	3.72 ± 0.03	1.38 ± 0.02	24
Age of dam		**	**	
Maiden	199	3.70 ± 0.05	1.41 ± 0.03	26
Mature	776	4.02 ± 0.02	1.41 ± 0.01	26
Order of birth		**	0.06	
Single	338	4.53 ± 0.04	1.41 ± 0.02	26
First multiple	319	3.60 ± 0.05	1.45 ± 0.02	28
Next multiple	318	3.44 ± 0.05	1.38 ± 0.03	24

**$P < 0.01$; NS, not significant

Birth weight was also affected ($P < 0.01$) by sex, age of dam and order of birth. The period from expulsion to standing was independent of selection line, but ram lambs were slower ($P < 0.01$) to progress to standing than ewe lambs. There was also a tendency ($P = 0.06$) for subsequent multiples to progress faster to standing than first multiples. Maiden H line ewes were less ($P < 0.05$) likely to back away from lambs attempting to suckle than their L line contemporaries (Table 3). A similar tendency was observed in mature ewes ($P < 0.10$). Mature H line ewes were less likely ($P < 0.01$) to frustrate the first suckling attempts of their lambs by circling than L line contemporaries. A higher ($P < 0.05$) proportion of maiden H line ewes co-operated actively (definition in Material and methods) with the first suckling attempts of their lambs than L line contemporaries. A similar tendency ($P < 0.10$) was observed in mature ewes. Lambs in the H line were quicker ($P < 0.01$) to progress from standing to suckling than L line contemporaries (Table 4). Lambs borne by mature ewes and as singles were correspondingly quicker ($P < 0.01$) to suckle than lambs with maiden dams and multiples. The inclusion of maternal co-operation as an effect in the model, to account for the better co-operation of H line and mature ewes with the first suckling attempts of their lambs, failed to remove the line and dam age differences. Log_{10}-transformed means for H and L line lambs after correction were 1.41 ± 0.02 and 1.52 ± 0.03 (antilogs being 26 and 33 min; $P < 0.01$). The difference between dam age classes was reduced ($\log_{10}$-transformed means being 1.42 ± 0.02 for lambs with mature dams and 1.51 ± 0.04 for lambs with maiden dams; antilogs being 27 and 33 min), but it remained significant ($P < 0.05$).

Table 3. Co-operation of maiden and mature ewes with the first attempts of their lambs to suckle in relation to selection line

Trait	**Line**		**χ^2 for line difference**[A]
	H line	**L line**	
	No. of ewes		
Maiden	96	50	
Mature	320	168	
	Proportion of ewes		
Backing			
Maiden	0.292	0.480	4.30
Mature	0.069	0.119	2.93
Circling			
Maiden	0.375	0.480	1.10
Mature	0.103	0.233	14.73
Butting			
Maiden	0.042	0.120	2.05
Mature	0.041	0.054	0.18
Co-operated activity			
Maiden	0.646	0.420	5.95
Mature	0.722	0.643	2.88

[A] Critical *Chi*^{2} values: $P < 0.10 = 2.71$; $P < 0.05 = 3.84$; $P < 0.01 = 6.63$

Table 4. Least squares means (± *SE*) for the $\log_{10}$-transformed period between standing and suckling in lambs (min), as affected by selection line, sex, age of dam and order of birth

Effect	**No. of observations**	**Mean ± *SE***	**Antilog**
Overall mean	940	1.51 ± 0.02	32
Selection line		**	
H line	642	1.45 ± 0.02	28
L line	298	1.58 ± 0.03	38
Sex		NS	
Ram	452	1.53 ± 0.03	34
Ewe	488	1.50 ± 0.03	32
Age of dam		**	
Maiden	183	1.60 ± 0.04	40
Mature	757	1.43 ± 0.02	27
Order of birth		**	
Single	330	1.42 ± 0.03	27
First multiple	304	1.54 ± 0.04	35
Next multiple	306	1.57 ± 0.04	38

** $P < 0.01$; N.S not significant

Period on or near the birth site and the desertion of lambs

A total of 678 parturitions were observed. After 654 of these, dams were found to care for at least 1 viable lamb. The latter parturitions were used to study desertion of lambs and the period ewes remained on or near their birth sites. The square-root-transformed average period that ewes spent on or near the birth site was independent of selection line and age (Table 5). The actual significance level for the effect of line was $P = 0.18$. Ewes caring for viable multiples tended ($P = 0.08$) to remain on or near their birth sites for longer periods than those caring for singles. There was a tendency ($P = 0.07$) for a higher proportion of L line ewes to desert at least one lamb when compared with their H line contemporaries. Desertions were also more common ($P < 0.05$) among maidens and ewes caring for viable multiples. A significantly higher ($P < 0.05$) proportion of L line ewes was found to desert a viable single than their H line contemporaries (7/150 = 0.047 *vs.* 1/199 = 0.005; $Chi^2 = 4.89$). No line difference was found in ewes caring for viable multiples (respectively 7/80 = 0.088 *vs.* 11/225 = 0.049; $Chi^2 = 0.96$).

Table 5. Least squares means (± *SE*) for the square-root-transformed period spent on or near the birth site and the proportion of ewes deserting one or more lambs, as affected by selection line, age, and number of viable lambs per ewe.

Effect	**No. of observations**	**Proportion of desertions**	**Stay on birth site (min)**	
			Mean ± *SE*	**Mean^2**
Overall mean	654	0.040	19.6 ± 0.04	384
Selection line		0.070	NS	
H line	424	0.028	20.1 ± 0.05	403
L line	230	0.061	19.0 ± 0.07	362
Age		*	NS	
Maiden	157	0.070	19.8 ± 0.08	393
Mature	497	0.030	19.3 ± 0.06	372
Litter size		*	0.08	
Single	349	0.023	18.7 ± 0.08	350
Multiple	305	0.059	20.4 ± 0.07	416

* $P < 0.05$; NS, not significant

Parturition process

The other stage where a line difference was implicated was during the process of parturition. The majority of parturitions in the H line were multiples (237/441 = 0.537), with fewer ($P < 0.001$; $Chi^2 = 17.3$; one degree of freedom) multiple births being observed in the L line (87/237 = 0.367). Of the total number of births, 38 (a proportion of 0.056) needed assistance. In 22 cases, assistance was rendered 3.5 - 4.0 h after the first definite sign of parturition or 2 h after presentation of a lamb or the birth of a preceding multiple. The remaining 16 ewes were assisted 30 min after the appearance of a part of the body (a head with only 1 or no front feet in 15 cases, hind limbs in one case). The recorded length of parturition was analysed in ewes assisted at birth, since only ewes having relatively long parturitions were assisted.

Repeatability coefficients (± *SE*) estimated from the analyses on litter weight at birth and length of parturition were 0.38 ± 0.05 and 0.21 ± 0.05. After least squares adjustment for their larger litter size, it was evident that H line ewes produced heavier ($P < 0.01$) litters than L line contemporaries (Table 6). The litters of mature and twin-bearing ewes were correspondingly heavier ($P < 0.01$) than litters of maiden and single-bearing ewes. In preliminary analyses on untransformed data, H line ewes had shorter ($P < 0.05$) parturitions than L line contemporaries. No line effect was, however, observed in the transformed data (Table 6).

Table 6. Least squares means (± *SE*) for litter weight and $\log_{10}$-transformed period of parturition, as affected by selection line, age and number of lambs born

Effect	No of observations	Litter weight (kg)	Period of parturition (min)	
			Mean ± *SE*	Antilog
Overall mean	678	5.80 ± 0.06	1.69 ± 0.02	49
Selection line		**	NS	
H line	441	5.94 ± 0.07	1.67 ± 0.03	47
L line	237	5.65 ± 0.10	1.71 ± 0.04	51
Age		**	NS	
Maiden	168	5.59 ± 0.10	1.73 ± 0.04	54
Mature	510	6.01 ± 0.08	1.64 ± 0.03	44
Litter size		**	**	
Single	354	4.45 ± 0.08	1.60 ± 0.03	40
Multiple	324	7.12 ± 0.09	1.79 ± 0.04	62

** $P < 0.01$; NS, not significant

After accounting for the heavier litters of H line ewes by analysis of covariance, a significant ($P < 0.05$) line difference was found, H line ewes having shorter parturitions than L line ewes. Log_{10}-transformed least squares means (± *SE*) were 1.66 ± 0.02 for the H line and 1.76 ± 0.04 for the L line (antilogs 46 and 57 min respectively). It was furthermore found that a higher proportion of maiden L line ewes required assistance at birth than their H line contemporaries (4/107 = 0.037 *vs.* 8/61 = 0.131; *Chi*² = 3.83; $P = 0.05$). Multiple births took longer ($P < 0.01$) than single births (Table 6). The same basic results were observed when length of parturition was analysed for individual lambs. The parturitions of single and first-born multiple lambs ($\log_{10}$-transformed least squares means = 1.59 ± 0.03 and 1.53 ± 0.03; antilogs being 39 and 34 min respectively) were longer ($P < 0.05$) than that of subsequent multiples (1.23 ± 0.03; 17 min).

Ewe performance and lamb weaning weight

The implications of selection on the productivity of the lines were considered next. Number of lambs born per ewe available at lambing was generally improved ($P < 0.10$) in the H line relative to the L line (Table 7). Expressed relative to the L line, these differences ranged from + 17% in 1993 to +32% in 1995. Corresponding differences ($P < 0.05$) in lambs weaned per ewe available at lambing ranged from + 25% in 1993 to + 47% in 1997. After least squares adjustment for their larger litter size, lamb weaning weight was also improved ($P < 0.05$) in the H line when compared with the L line. Expressed relative to the L line, these differences ranged from + 8% in 1994 to + 22% in 1996.

Table 7. Lambs born or weaned in relation to the number of ewes available at lambing, as well as lamb weaning weight (± *SE*), as classified by lambing year and selection line

Year and line	**Ewes available at lambing**	**No. of lambs per ewe**		**No. of lambs weaned**	**Lamb weaning weight (kg)**
		Born	**Weaned**		
1993		0.06	*		**
H line	131	1.366	0.962	126	21.2 ± 0.4
L line	82	1.171	0.768	63	18.8 ± 0.5
1994		NS	**		*
H line	118	1.475	1.203	142	22.7 ± 0.4
L line	65	1.308	0.908	59	21.1 ± 0.5
1995		**	**		**
H line	128	1.570	0.992	127	23.7 ± 0.4
L line	70	1.186	0.686	48	20.3 ± 0.6
1996		**	**		**
H line	124	1.531	1.169	145	23.7 ± 0.4
L line	78	1.103	0.821	65	19.5 ± 0.5
1997		**	**		**
H line	127	1.346	1.173	149	24.2 ± 0.4
L line	85	1.071	0.800	68	21.0 ± 0.5

* $P < 0.05$; **$P < 0.01$; NS, not significant.

Discussion

Levels and causes of lamb mortality

The overall level of lamb mortality in this study was higher than mean figures of 10 - 20% quoted in the reviews of Alexander (1984) and Haughey (1991). This could mainly be ascribed to higher ($P < 0.01$) levels of total lamb mortality as well as lamb mortality after 3 days during 1993 and 1995 (Table 1). These results require further comment. During August 1993 an outbreak of chronic, non-supperative arthritis resulted in the need to treat 92 lambs (33.5% of the lamb crop) with long-acting antibiotics. The organism *Erysipelotrix rhusiopatiae* was isolated from samples obtained from affected lambs. During 1995, the flock was harassed by stray dogs during the last fortnight of August. A total of 52 lambs (18.3% of the lamb crop) died as a direct result of dog bites.

It was evident that the survival of lambs was not compromised by selection for ewe multiple rearing ability, despite the fact that higher mortality levels are expected with an increase in multiple birth rate (Dalton *et al.*, 1980; Haughey, 1991). The survival of multiples, in particular, was indeed improved substantially in the H line. It was furthermore clear that fairly high levels of production could be attained with predominantly pasture-fed ewes. For that matter, higher levels of production could have been reached, had it not been for circumstances beyond our control (i.e. infections in 1993 and dog attacks in 1995). Similar advantages of selection for lamb survival and/or ewe rearing ability have been reported in the literature (Atkins, 1980; Donnelly, 1982; Haughey, 1983; Knight *et al.*, 1988).

Causes of perinatal lamb mortality were broadly similar to those reported in the literature, with the majority of lamb deaths being attributed to SME and stressful births (Dalton *et al.*, 1980; Alexander, 1984; Haughey, 1991; Cloete, 1992). Antenatal deaths, as well as perinatal deaths attributable to infections were less important, as was reported by the literature sources cited.

Neonatal lamb progress

Behavioural attributes that could be associated with postparturient survival (> 6 h after birth) will be considered first, since the majority of deaths were recorded during this period. No line difference was found for the period from expulsion to first standing for > 10 s. This aspect of behaviour could thus not be related to the improved postparturient survival of H line lambs in our study. In the literature, however, breed differences were reported for time lapses to standing (Slee and Springbett, 1986; Cloete *et al.*, 1998*a*), suggesting that it may be affected by gene action. The trait was also found to be heritable in a preliminary analysis on Dormer and South African Mutton Merino lambs (Cloete, 1993). In a later analysis on a larger data set it was possible to partition the variances. Both the direct genetic variance and the maternal permanent environmental variance amounted to about 10% of the overall phenotypic mean (Cloete *et al.*, 1998*a*).

Lambs born in the H line were quicker to progress from standing to suckling than L line contemporaries. This advantage in the behaviour of H line lambs remained, after accounting for the better co-operation of their mothers with their first suckling attempts. A study involving very few Marshall Romney (selected for lamb survival) and control Romney lambs yielded results very similar to ours, but significance could not be demonstrated (Knight *et al.*, 1989*a*). Forty-one Marshall Romney lambs first suckled 29 min after birth, while 17 control Romneys took 38 min. Our results are also very similar to those reported by O'Connor and Lawrence (1992), who reported that Mule (Bluefaced Leicester rams x Scottish Blackface ewes) lambs were as quick to stand as Scottish Blackface lambs, but that they progressed more slowly to suckling. This was attributed to a lack of udder directed behaviour in Mule lambs. This result implies that the lamb itself is born with an inherited ability to facilitate suckling. Our previous work has shown a relatively small amount of direct additive genetic variation (7% of the phenotypic mean) in the period taken to progress from standing to suckling in Dormer and South African Mutton Merino lambs (Cloete *et al.*, 1998*a*). A larger part of the phenotypic variation (19%) could be attributed to a maternal permanent environmental effect. This effect probably includes aspects of maternal behaviour, such as co-operation with the first suckling attempts and absence of aggressive behaviour towards the neonate (Alexander, 1988). The fact that H line ewes were more co-operative with the first suckling attempt of their lambs, supports this line of reasoning. This result could, however, not be substantiated from the literature. Alexander *et al.* (1990) found no breed differences in ewes avoiding the first suckling attempts of their lambs. The overall occurrence of circling in the latter study was, however, low. Only 4% of ewes circled to some degree, compared with the 18% of ewes that circled in our study. We also found that a higher proportion of primiparous maiden ewes circled, whereas Alexander *et al.* (1990) found no effect of parity. A New Zealand study found that lambs borne to ewes with a high maternal behaviour score (MBS) were quicker to suckle than lambs with low MBS dams (Parker and Nicol, 1993). Marshall Romney lambs were less likely to die from starvation than control Romneys (Knight *et al.*, 1988), while neonatal lamb survival was improved in an Australian line selected for rearing ability (Haughey, 1983). These results all support the reasoning that maternal behaviour may be improved in lines selected for rearing ability.

Stay on the birth site and desertion of lambs

Ewes in the H line tended ($P = 0.18$) to remain longer on or near their birth sites than L line contemporaries. Szantar-Coddington (1994) found that Fertility flock Merino ewes remained on their birth sites for 266 min compared with 251 min for control ewes ($P > 0.05$). Knight *et al.* (1989*b*) found that 41 Marshall Romney ewes grazed away from their birth sites 46 min after birth took place, while 16 control Romneys remained at their birth sites for 27 min after birth ($P > 0.05$). A general pattern emerged that ewes selected for rearing ability or lamb survival tended to remain on their birth sites for longer periods than control ewes, although none of these studies found a significant line effect. Keeping in mind that this type of behaviour facilitates the formation of a strong mother - offspring bond (Alexander, 1988), this change in behaviour may well be correlated response to selection. It may furthermore be reflected in a tendency ($P = 0.07$) towards fewer cases of lamb desertion in the H line. Knight *et al.* (1989*a*) found that Marshall Romney ewes were less likely to abandon their lambs after slippage on steep slopes than control Romneys, leading to a marked difference in lamb mortality (17 *vs.* 43% respectively). Permanent separation of ewes from multiple lambs was more prevalent in unselected Border Leicester ewes than in a strain selected for rearing ability (18 *vs.* 4%; Alexander *et al.*, 1990). Conversely, desertion of singles played an important role in the difference between the H and L lines reported in Table 5.

The role of the lamb in assuring that it is not separated from its dam and subsequent survival has been emphasised in recent studies (Lindsay *et al.*, 1990). It was demonstrated that lamb vigour was associated with maternal bonding and subsequent survival in Merinos (Lindsay, 1996; Murphy and Lindsay, 1996). The better survival of Border Leicester X Merino lambs was attributed to the fact that they were quicker to recognise their Merino dams (Nowak and Lindsay, 1990) and less likely to be separated from them (Stevens *et al.*, 1984) than pure Merino lambs. The possibility remains that more responsive H line lambs (judged from the fact that they were quicker to suckle) were less likely to be deserted by their dams. This hypothesis, however, needs to be tested.

Parturition

The other major cause of perinatal lamb deaths was stressful births. Multiple births took longer than singles, as was commonly reported in the literature (Owens *et al.*, 1985; Alexander *et al.*, 1990; Haughey, 1991; Cloete, 1992; Ramirez *et al.*, 1995). There was a strong suggestion that H line ewes experienced easier births than L line contemporaries, despite the fact that the line difference was not significant before adjustment for their heavier litters. Lambs born in the H line were more likely to survive birth and the period shortly after it (Table 1), while maiden H line ewes were less likely to be assisted during birth. Among the lambs autopsied during the study, birth stress tended to be a more likely factor contributing to perinatal lamb mortality in the L line. Length of parturition was previously found to be repeatable (Cloete, 1992) and different between breeds (Alexander *et al.*, 1990; Cloete, 1992; Fahmy *et al.*, 1997; Cloete *et al.*, 1998*a*). Fewer deaths due to dystocia (Knight *et al.*, 1988) and during or near to birth (Haughey, 1983) were also reported as responses to selection programs for increased lamb survival or ewe rearing ability. Szantar-Coddington (1994) found no significant difference between the parturitions of a line selected for rearing ability (the Trangie Fertility flock) and an unselected control line, although Fertility flock ewes tended to experience slightly shorter births (31 *vs.*37 min respectively).

These findings support the contention that a mechanism associated with long and stressful parturitions, which are commonly linked to parturient deaths in lambs (Arnold and Morgan, 1975; Alexander, 1988; Haughey, 1991), is genetically controlled. A contributing factor may be pelvic size, which is related to rearing ability on a flock basis (Haughey *et al.*, 1985; Cloete, 1994). Further support stems from the findings that selection for rearing ability resulted in increases in pelvic size in Marshall Romneys (Knight *et al.*, 1988) and Trangie Fertility Merinos (Kilgour and Haughey, 1993). A preliminary genetic analysis on Dormer and South African Mutton Merino lambs found that the between family variation in length of parturition was mostly associated with a maternal permanent environmental effect accounting for 17% of the total phenotypic variation (Cloete *et al.*, 1998*a*). This finding confirmed the repeatable nature of length of parturition that was reported earlier (Cloete, 1992), and observed in this investigation also. From these results, maternal selection for easier births appears to be a possibility. Direct selection does not appear to be feasible, although Suffolk lambs had longer parturitions and were more likely to be assisted at birth than Scottish Blackface lambs (irrespective of ewe breed) in a crossover embryo transfer study on ewes and lambs of these breeds (Dwyer *et al.*, 1996).

Implications

The heritability of lamb survival is commonly estimated at essentially zero (Yapi *et al.*, 1992; Konstantinov *et al.*, 1994; Olivier, 1998; Fogarty and Gilmour, 1998), leading analysts to contend that genetic progress is unlikely. This paper reports responses in lamb survival after selection for maternal multiple rearing ability. It also provided insight into behavioural adaptations that could be instrumental in these responses. The response in the efficacy of lamb production is clearly illustrated in Table 7. Weight of lamb produced per ewe available at lambing was increased by 41.3 - 73.1% in the H line, when expressed relative to mean L line performance.

These findings pose some challenges with regard to a feasible selection strategy for the improvement of lamb survival in the industry. Recommendations in South Africa range from using a simple, low-cost technique like 'wet and dry' (Haughey, 1991; Fourie and Cloete, 1993) to more sophisticated selection systems based on a composite trait like weight of lamb weaned per ewe per year (Delport, 1989; Olivier, 1998; Snyman *et al.*, 1998). Recent work in Australia also provides a framework for selecting ewes on the basis of emotivity (Lindsay, 1996; Le Neidre *et al.*, 1998).

In conclusion, this study demonstrated that selection of sheep for multiple rearing ability was a viable method of improving lamb production. It is important to emphasise that it was possible to increase multiple birth rate without compromising lamb survival. The results were obtained under pasture conditions, and should be applicable to the pastoral sheep industries in the major sheep producing countries.

Acknowledgements

We are indebted to Messrs J.M. ten Hoope, J.E. Fourie and P.J.A. Lombard as well as Miss Farida Martin for assistance with the observations. Students of the University of Stellenbosch and other staff also played an important supportive role when employed temporarily. Resident veterinarians at the Stellenbosch Veterinary Diagnostic Centre (Drs D.J. Schneider, A. van Halderen, M.C. Franken, J.W. Wessels and T.A. Gouws) are also thanked for their contribution. The experiment was supported financially by the South African Wool industry.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay, D.R., Pearce, D.T. (Eds.), Reproduction in Sheep. Australian Academy of Science in Conjunction with Australian Wool Corporation, Canberra, Australia, pp. 199 - 209.

Alexander, G., 1988. What makes a good mother? *Proceedings of the Australian Society for Animal Production* 17: 25 - 41.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27 - 38.

Arnold, G.W., Morgan, P.D., 1975. Behaviour of the ewe and lamb at lambing and its relationship to lamb mortality. *Applied Animal Ethology* 2: 25 - 46.

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of the Australian Society for Animal Production* 13: 174 - 176.

Brand, A.A., Cloete, S.W.P., De Villiers, T.T., 1985. Factors that influence mortality amongst lambs in the Elsenburg Dormer and SA Mutton Merino flocks. *South African Journal of Animal Science* 15: 155 - 161. (in Afrikaans.)

Brown, G.H., 1988. The statistical comparison of reproduction rates for groups of sheep. *Australian Journal of Agricultural Research* 39: 899 - 905.

Cloete, S.W.P., 1992. Observations on litter size, parturition and maternal behaviour in relation to lamb mortality in fecund Dormer and SA Mutton Merino ewes. *South African Journal of Animal Science* 22: 214 - 221.

Cloete, S.W.P., 1993. Observations on neonatal progress of Dormer and SA Mutton Merino lambs. *South African Journal of Animal Science* 23: 38 - 42.

Cloete, S.W.P., 1994. Rearing performance of Merino, SA Mutton Merino and Dormer ewes in relation to live mass, reproduction and pelvic dimensions. *Journal of the South African Veterinary Association* 65: 10 - 17.

Cloete, S.W.P., Durand, A., 1994. A preliminary note on Merino sheep subjected to divergent selection on maternal values for lambs weaned per ewe joined. *South African Journal of Animal Science* 24: 27 - 29.

Cloete, S.W.P., Olivier, J.J., Scholtz, A.J., 1998*a*. Aspects of lambing and neonatal behaviour of dual-purpose sheep. In: Proceedings of the 6th World Congress of Genetics Applied to Livestock Production. Vol. 27: 11 - 16 January 1998, Armidale, NSW, Australia. pp. 39 - 42.

Cloete, S.W.P., Scholtz, A.J., Ten Hoope, J.M., 1998*b*. A note on separation of one or more lambs(s) in Merino lines divergently selected for ewe multiple rearing ability. *Applied Animal Behaviour Science* 58: 189 - 95.

Cloete, S.W.P., Van Niekerk, F.E., Rust, J.M., 1998*c*. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *Sheep and Goat Research Journal* 14: 173 - 179.

Dalton, D.C., Knight, T.W., Johnson, D.L., 1980. Lamb survival in sheep breeds on New Zealand hill country. *New Zealand Journal of Agricultural Research* 23: 167 - 173.

Delport, G.J., 1989. A mixed model approach for selecting Merino ewes. PhD Thesis, University of the Orange Free State, Bloemfontein, South Africa.

Donnelly, F.B., 1982. A practical attempt to breed for better lamb survival. *Proceedings of the Australian Society of Animal Production* 14: 30 - 32.

Dwyer, C.M., Lawrence, A.B., Brown, H.E., Simm, G., 1996. Effect of ewe and lamb genotype on gestation length, lambing ease and neonatal behaviour of lambs. *Reproduction Fertilisation and Development* 8: 1123 - 1129.

Fahmy, M.H., Robert, S., Castonguay, F., 1997. Ewe and lamb behaviour at parturition in prolific and non-prolific sheep. *Canadian Journal of Animal Science* 77: 9 - 15.

Fogarty, N.M., Gilmour, A.R., 1998. Effect of season on lambing performance of selection and control flock ewes tested in an 8 - monthly lambing system. In: Proceedings of the 6th World Congress of Genetics Applied to Livestock

Production, Vol. 27: 11 - 16 January 1998, Armidale, NSW, Australia. pp. 55-58.

Fourie, A.J., Cloete, S.W.P., 1993. Reproductive performance of commercial Merino, Dohne Merino and SA Mutton Merino flocks in the Southern Cape. *South African Journal of Animal Science* 23: 104 - 110.

Harvey, W.R., 1990. 'User's Guide for LSMLMW and MIXMDL. PC-2 Version. (MIMEOGRAPH: Columbus, Ohio, USA.)

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361 - 363.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Haughey, K.G., George, J., McGuirk, B.J., 1985. The repeatability of rearing performance of Merino and Dorset Horn ewes and its relationship with mature pelvic size. *Australian Journal of Experimental Agriculture* 25: 541 - 549.

Kilgour, R.J., Haughey, K.G., 1993. Pelvic size of Merino ewes selected for lamb rearing ability is greater than that of unselected Merino ewes. *Animal Reproduction Science* 31: 237 - 342.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259 - 271.

Knight, T.W., McMillan, W.H., Kilgour, R., Hockey, H-U.P., Hall, D.R.H., 1989*a*. Effect of slope of lambing site on lambs slipping and lamb mortality. *New Zealand Journal of Agricultural Research* 32: 199 - 206.

Knight, T.W., Wilson, L.D., Lynch, P.R., Hockey, H-U.P., 1989*b*. Slope and the choice of birth sites by ewes. *New Zealand Journal of Agricultural Research* 32: 193 - 198.

Konstantinov, K.V., Erasmus, G.J., Van Wyk, J.B., 1994. Evaluation of Dormer sires for litter size and lamb mortality using a threshold model. *South African Journal of Animal Science* 24: 119 - 121.

Le Neidre, P., Murphy, P.M., Boissy, A., Purvis, I.W., Lindsay, D.R., Orgeur, P., Bouix, J., Bibé, B., 1998. Genetics of maternal ability in cattle and sheep. In: Proceedings of the 6th World Congress of Genetics Applied to Livestock Production. Vol. 27: 11 - 16 January 1998, Armidale, NSW, Australia. pp. 23 - 30.

Lindsay, D.R., 1996. Environment and reproductive behaviour. *Animal Reproduction Science* 42: 1 - 12.

Lindsay, D.R., Nowak, R., Putu, I.G., McNeil, D., 1990. Behavioural interactions between the ewe and her young at parturition. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.), Reproductive Physiology of Merino Sheep. School of Agriculture, University of Western Australia, Perth, pp. 191 - 205.

Lynch, J.J., Hinch, G.N., Adams, D.B., 1992. Behaviour of the lamb. In: 'The Behaviour of Sheep: Biological Principles and Implications for Production'. pp. 153 - 77. (CAB International: Wallingford, UK.)

McFarlane, D., 1965. Perinatal lamb losses. 1. An autopsy procedure for investigation of perinatal losses. *New Zealand Veterinary Journal* 13: 116 - 135.

Murphy, P.M., Lindsay, D.R., 1996. The contribution of the activity of the newborn Merino lamb to the attachment to its mother and subsequent survival. *Proceedings of the Australian Society of Animal Production* 21: 486.

Nowak, R., Lindsay D.R., 1990. Effect of genotype and litter size on discrimination of mothers by their twelve-hour-lambs. *Behaviour* 117: 1 - 13.

O'Connor, C.E., Lawrence, A.B., 1992. Relationships between lamb vigour and ewe behaviour at parturition. *Animal Production* 54: 361 - 366.

Olivier, W.J., 1998. Evaluation of ewe productivity measures. MSc Agric Thesis, University of the Orange Free State, Bloemfontein, South Africa.

Owens, J.L., Bindon, B.M., Edey, T.N., Piper, L.R., 1985. Behaviour at parturition and lamb survival of Booroola Merino sheep. *Livestock Production Science* 13: 359 - 372.

Parker, R.J., Nicol, A.M., 1993. Ewe maternal behaviour score and ewe and lamb activity from birth to suckling. *Proceedings of the New Zealand Society of Animal Production* 53: 201 - 202.

Ramirez, A., Quilles, A., Hevia, M., Sotillo, F., 1995. Observations on the birth of goats. *Canadian Journal of Animal Science* 75: 165 - 167.

Szantar-Coddington, M.R., 1994. Genetic improvement of lamb survival in the Australian Merino: behavioural and physiological indicators of maternal ability. MRurSci. Thesis, University of New Zealand.

Siegel, S., 1956. Non Parametric Statistics for the Behavioural Sciences. (McCraw-Hill Book Company Inc.: New York.)

Slee, J., Springbett, A., 1986. Early post-natal behaviour in lambs of ten breeds. *Applied Animal Behaviour Science* 15: 229 - 340.

Snyman, M.A., Cloete, S.W.P., Olivier, J.J., 1998. Genetic and phenotypic correlations of total weight of lamb weaned with body weight, clean fleece weight and mean fibre diameter in three South African Merino flocks. *Livestock Production Science* 55: 157 - 162.

Stevens, D., Alexander, G., Mottershead, B., Lynch, J.J., 1984. Role of the lamb in post-partum separation of ewes from twin lambs. *Proceedings of the Australian Society for Animal Production* 15: 751.

Turner, H.N., 1977. Australian sheep breeding research. *Animal Breeding Abstracts* 45: 9 - 33.

Turner, H.N., Young, S.S.Y., 1969. Quantitative Genetics in Sheep Breeding. (Ithaca: New York.)

Yapi, V.V., Boylan, W.J., Robinson, R.A., 1992. Heritability and repeatability estimates and correlations of lamb mortality with birth weight and litter size. *World Review of Animal Production* 27: 55 - 60.

CHAPTER 11

LAMBING BEHAVIOUR OF MERINO EWES FROM LINES SUBJECTED TO DIVERGENT SELECTION FOR MULTIPLE REARING ABILITY FROM THE SAME BASE POPULATION

S.W.P. Cloete, A.J. Scholtz and R. Taljaard

Elsenburg Agricultural Centre,
Private Bag X1, Elsenburg 7607, South Africa

Published in:
South African Journal of Animal Science (2002) 32: 57 - 65

Reproduced with permission of:
South African Journal of Animal Science

Lambing behaviour of Merino ewes from lines subjected to divergent selection for multiple rearing ability from the same base population

S.W.P. Cloete[#], A.J. Scholtz and R. Taljaard*
Elsenburg Agricultural Centre, Private Bag X1, Elsenburg 7607, South Africa

Abstract: Timing of birth and birth site selection were investigated in two lines of grazing Merino sheep that had been divergently selected for multiple rearing ability. Time budgets in the neonatal phase were also compared between the two lines. Parturition was slightly more likely to commence during daylight hours (06h00 – 18h00) than at night (18h00 – 06h00) (0.548 *vs*. 0.452). Intervals between consecutive onsets of parturition in 685 ewes conformed to an exponential distribution, expected for intervals between consecutive, random occurring events. A significant excess of observed short intervals above those expected was found. This observation could either be coincidental, or indicative of an underlying mechanism that may operate as a trigger to synchronize the commencement of parturition. Recorded birth sites of 606 ewes not assisted at birth were found to differ from a random distribution in some of the 10 lambing paddocks used during the study. In four night paddocks, the frequency of birth sites in the 50% of the area situated on the boundaries was higher than in the middle portion. In the paddocks used during daytime an increased frequency of birth sites appeared to be associated with a tree on the boundary of two adjacent paddocks. In the five paddocks used at night, birth site frequencies differed when the paddocks were divided along the length in three blocks of equal size. In the paddock nearest to the base building, birth sites appeared to be concentrated along the boundary furthest from the building that served as base for the observers and the nearby floodlights. Selection line did not appear to influence the choice of a birth site. The period that ewes were observed to groom their lambs was lowly repeatable (0.13 ± 0.06). No line difference was observed in the period that ewes spent grooming. Ewes caring for viable multiples groomed their offspring for a longer period than those caring for singles. Mature ewes tended to groom their lambs for a longer period than primi-parous maidens. A higher proportion of High (H) line ewes groomed their progeny shortly after birth than Low (L) line ewes. Later on (90 - 120 min. postpartum), L line ewes were more likely than those in the H line to graze. The latter group of ewes was more likely to stand with their offspring at this stage.

Keywords: Birth site selection, diurnal variation, grooming, lambing behaviour, onset of parturition, sheep, time budget

*Present address: Agri Informatics, Postnet Suite 242, Private Bag X5061, Stellenbosch 7599, South Africa
[#]Corresponding author: E-mail address: schalkc@elsenburg.com

Introduction

Lamb mortality is regarded as a major constraint to efficient sheep production (Alexander, 1988; Haughey, 1991). A 'core' level of lamb losses remains, even if managerial inputs are optimised (Alexander, 1984). It is widely believed that human supervision and intervention will minimise maternal deaths and maximise offspring survival (Alexander *et al.*, 1993). This belief has prompted investigations into the distribution of lambings across the 24 hours of a day. Such comparisons are scarce for breeds adapted to South African environments.

The distribution of birth sites in lambing paddocks has not been studied in South African breeding flocks. Indications from elsewhere suggest that ewes prefer to lamb in higher lying areas and concentrate around the boundaries of paddocks (Alexander *et al.*, 1990). The latter observation was ascribed to attempts by ewes to seek isolation at birth. Differences in the survival of multiple lambs were recently demonstrated in South African Merino lines that were divergently selected for maternal multiple rearing ability (Cloete and Scholtz, 1998). Differences in behaviour conducive to lamb survival were also reported between the two lines, supporting the contention by Alexander (1988) that behavioural adaptations may contribute to selection responses in lamb survival.

Against this background, the diurnal variation in times of birth was studied in South African Merino ewes, as well as the synchrony of parturition within the flock. The distribution of birth sites in the lambing paddocks was also compared for Merino lines divergently selected for multiple rearing ability. The activities participated in by ewes caring for at least one viable lamb were also studied during the first 4 hours after lambing.

Material and Methods

Two lines of Merino sheep have been selected divergently from the same base population since 1986, using maternal ranking values for lambs reared per joining (Cloete and Scholtz, 1998). Ewe and ram replacements in the High (H) line were preferably the progeny of ewes rearing more than one lamb per joining (*i.e.* reared twins at least once). The progeny of ewes rearing fewer than one lamb per joining (*i.e.* barren or lost all lambs born at least once) were preferred as replacements in the Low (L) line. Depending on the average reproduction of the lines and the replacement needs, progeny of ewes that reared one lamb per joining were occasionally accepted in both lines. Selection decisions were mostly based on ≥ 3 maternal joinings, especially in the case of rams. Once selected, ewes normally remained in the breeding flock for five joinings. The H line was augmented by 28 ewe progeny born from an embryo transfer program during 1991 and 1992 (Cloete *et al.*, 1998). The mean performance of the ewes derived in this way was similar to that recorded in the H line, and they were treated as one group.

For the duration of the experiment, the two lines were maintained as a single flock, except during joining over a 6-week period in single sire groups to 4 - 5 rams during

January - February each year. For the duration of the present study, the lines were maintained on the Elsenburg experimental farm near Stellenbosch. Cloete and Scholtz (1998) detailed the locality and the management practices implemented, as well as the recording of behavioural data in the flock. The study was conducted over a 5-year period (1993 - 97). Lambing took place on 10 Kikuyu paddocks, which were generally rested for at least two months prior to the commencement of lambing. Ample feed was generally available. Ewes were side-branded with stock-marker spray to facilitate identification with minimal disturbance. Age (maiden or mature), number of viable lambs given birth (single or multiple) and selection line (H or L) were recorded for individual ewes.

The lambing flock was observed continuously by one to two trained observers for a period of approximately three weeks during peak lambing in June - July. The ewes adapted to human presence within a short period, and could be approached closely (<10 m) without disturbance. Five lambing paddocks were used during daylight hours, while the other five were floodlit for use at night (Cloete and Scholtz, 1998). Ewes were moved from day paddocks to the following night paddock at approximately 18h00, and from night paddocks to the following day paddock at approximately 07h00. Inclusive of the twilight time of dusk and dawn, detailed observations without supplementary lighting were possible from approximately 06h45 to 18h00. For the assessment of these data it was assumed that it would be feasible to observe ewes for the provision of assistance (when needed) from 06h00 to 18h00 (subsequently termed as daytime). The time of onset of lambing was recorded individually for 690 ewes during the experiment. Since the ewes were under continuous observation, it was possible to calculate the interval between onsets of parturition within the flock and to determine synchrony of parturition within production years. A total of 685 intervals between onsets of parturition was calculated for the duration of the experiment.

The sites of 647 births were recorded during the experiment. Estimation of distances was aided by a grid system consisting of iron poles and fluorescent markers placed on the paddock fences at 20 m intervals. Individual lambing sites were transferred to a map of the area, using a Geographic Information System. A detailed map of the area, indicating the major topographical features, is presented in Fig. 1. The size of individual paddocks ranged from 0.33 to 0.47 ha. Two blocks of five paddocks were used either for observations during daytime (situated on the eastern side of the map) or at night (on the western side). The floodlights used for illumination at night were situated on the northern side of the night paddocks. All paddocks were roughly rectangular, approximately 110 m in length (in a general east-west direction) and approximately 40 m in width (in a general north-south direction). The corridor between the paddocks was situated roughly along a ridge. Height contours indicated that altitude decreased from a north - westerly and south - westerly direction in the day paddocks. The lowest parts of these paddocks were thus on the eastern end of the centre day paddock. The night paddocks sloped gently in a south - westerly direction. Small to very large trees were scattered along the boundaries of individual paddocks.

Lambs were identified with stock marker spray according to the order of birth within a litter after being groomed by their mother for at least 15 min. The birth site was simultaneously marked with a peg. The behaviour of ewes and their lambs was recorded at 30 - min intervals during the first four hours postpartum. Behaviour patterns recorded in ewes included standing, lying, grooming or grazing. Ewes were observed for a period of approximately 30 seconds, and the activity engaged in for the majority of time was recorded. The time that individual ewes spent grooming their progeny was derived from these recordings. Grooming was assumed to have stopped for an individual ewe if this activity was not recorded for three consecutive 30 - min intervals, i.e. for 1.5 h.

Differences in proportions or frequencies were assessed for statistical significance by *Chi*^{2} procedures (Siegel, 1956). Seeing that the data for the time that ewes spent grooming their lambs were unbalanced, least-squares procedures (Harvey, 1990) were used. The data were positively skewed and leptocurtic. A standard square root transformation was required to normalise these data. The interpretation of results was complicated by the fact that repeat observations were made on several ewes in different years. Since these observations could be correlated, the assumptions for analysis of variance were not necessarily satisfied. This limitation was overcome by including the random effect of ewes within selection lines (H or L) in these analyses. This approach enabled us to calculate repeatability coefficients for these traits using the between ewe and error variance components (Turner and Young, 1969). Other fixed effects included in these analyses were lambing year (1993 - 97), age (maiden or mature) and number of live lambs cared for (single or multiple). Two-way interactions between main effects were relatively unimportant ($P > 0.1$) in the analyses, and are thus not presented. Lambing year means are similarly not presented, as they were not significantly different.

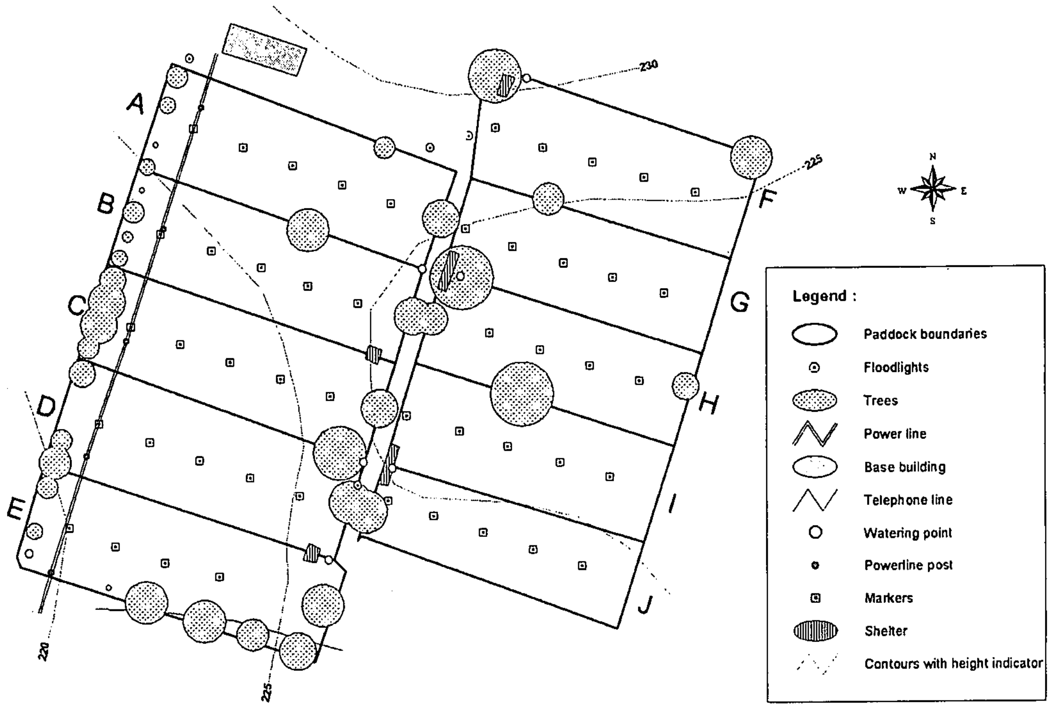


Fig. 1. Map of the trial location with the dominant topographical features depicted on it

Results

If the frequency of onset of parturition that was recorded during eight 3 - hour periods was independent of the time of the day, these proportions would be equal at 0.125. The observed proportions differed from a hypothetical equal distribution ($Chi^2 = 16.7$; degrees of freedom = 7; $P < 0.05$), showing a peak around noon (Fig. 2). Respective frequencies of onset of parturition for the periods from 06h00 to 09h00 and from 18h00 to 21h00 (the times of the morning and afternoon drifts) were 0.109 and 0.110. Onset of parturition of 378 ewes was observed between 06h00 and 18h00 (during daytime), while 312 ewes started lambing during the night (between 18h00 and 06h00). Expressed as deviations from equal frequencies, more ewes started to lamb during daylight hours ($Chi^2 = 6.3$; degrees of freedom = 1; $P < 0.05$). However, this difference was small, with 54.8% of the ewes commenced lambing during the day and 45.2% at night.

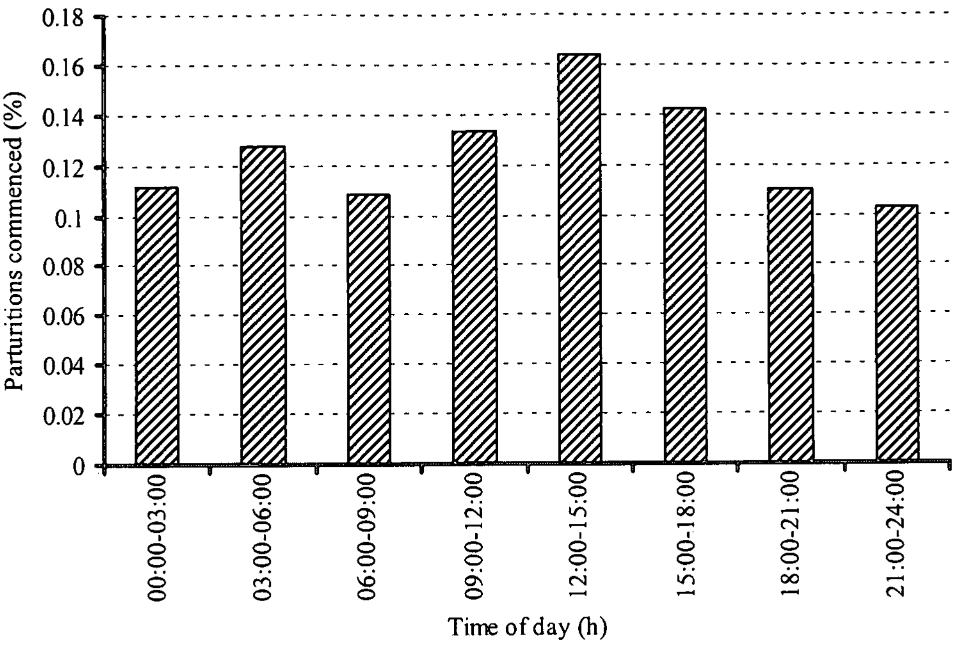


Fig. 2. Overall diurnal distribution of lambings for the period 1993 to 1997. If the occurrence of births was independent of time of the day, a proportion of 0.125 of the lambings would have been recorded for all intervals.

The frequency distribution of intervals between consecutive onsets of parturition over the 5 - year period showed a higher frequency of shorter intervals (Fig. 3).

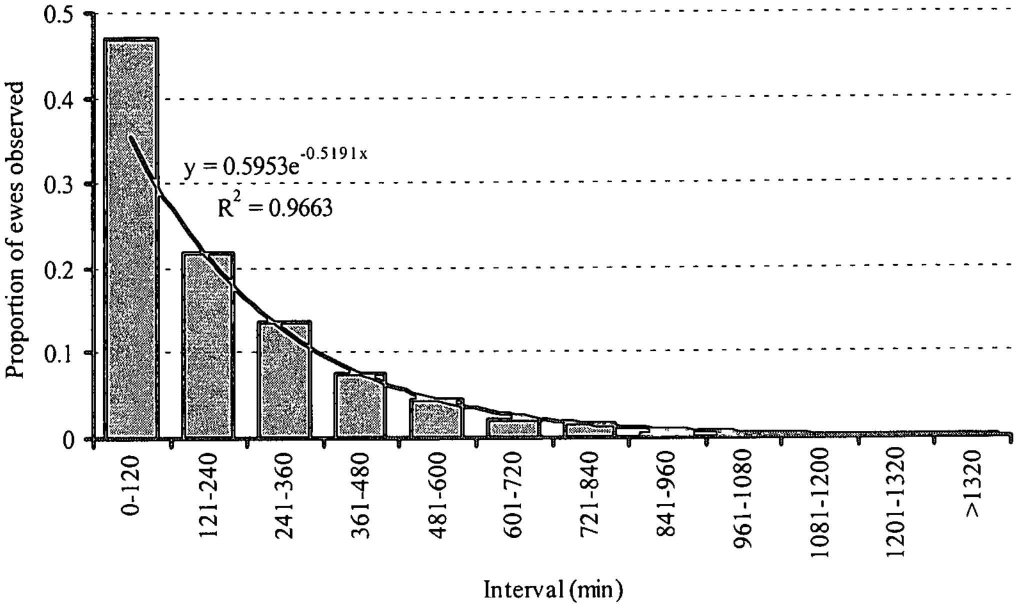


Fig. 3. Histogram depicting the proportion of onsets of parturition (n = 685 ewes) associated with time intervals between parturitions (1993 to 1997). A trendline depicting the theoretical exponential distribution for events occurring randomly is also included.

A map of the experimental location is given in Fig. 4, with individual lambing sites of 606 unassisted H and L line ewes depicted on it.

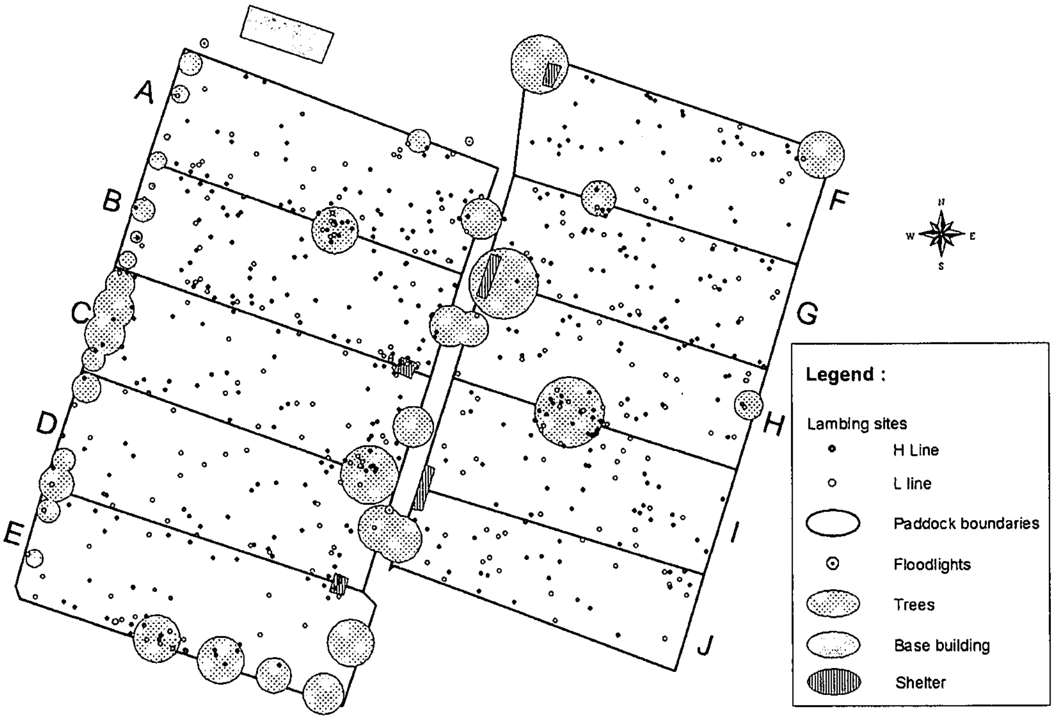


Fig. 4. Distribution of the lambing sites of ewes in the H and L lines across the lambing paddocks used in the investigation for the period 1993 to 1997. Paddock identification details are provided.

The sites of 41 assisted births were excluded. It was decided to test three hypotheses: The first of these was a concentration of birth sites along the boundaries of individual paddocks. Individual paddocks were divided in equal parts, with one part positioned along the boundaries and the other part in the centre of the paddock. A higher ($P < 0.05$) frequency of birth sites was found along the boundaries of paddocks A, B, C and E. No significant differences were found for the paddocks used during daytime. Overall, similar proportions of 400 H line ewes and 206 L line ewes gave birth in the portion of paddocks that was situated nearest to the boundaries (0.610 and 0.655 respectively; $Chi^2 = 1.01$; degrees of freedom = 1; $P > 0.05$). The hypothesis that the increased frequency of births along the boundaries of the paddocks was related to the seeking of shelter by ewes was subsequently tested. The half of the respective paddocks along the boundaries was divided into the part under trees and the remainder. Respective areas were computed and expected frequencies were related to the observed number of births, to assess if a disproportionately large frequency of births occurred in areas underneath trees and shelters in the paddocks, relative to the area occupied. This was found to be the case in paddock A (*Chi*^{2} = 7.94; degrees of freedom = 1; $P < 0.01$), paddock C (*Chi*^{2} = 10.33; degrees of freedom = 1; $P < 0.01$) and paddock H (*Chi*^{2} = 10.46; degrees of freedom = 1; $P < 0.01$).

Thirdly, frequencies for columns (across the width of paddocks, in a general north-south direction) and rows (along the length of paddocks, in a general east-west direction) in individual paddocks were assessed for deviations from a random distribution. Frequencies for columns deviated from a random distribution in paddocks A and H (Fig. 4). In paddock A, a higher frequency of birth sites was found in the eastern, higher part of the paddock (*Chi*^{2} = 12.07; degrees of freedom = 2; $P < 0.05$). Birth sites were more likely to occur in the middle column of paddock H, apparently in association with a tree on the boundary between paddocks H and I. When rows were compared for individual paddocks, significant ($P < 0.05$) deviations from a random distribution were found for seven paddocks (A, B, C, D, E, H and I; Fig. 4). In the floodlit paddocks used at night (A to E), birth sites were generally concentrated in the southern part of the paddock (furthest from the floodlights). In absolute terms, fewer births were occasionally found in the centre row of individual paddocks, although significant differences were not found. Birth sites in paddocks H and I were centred along the boundary between the two paddocks and appeared to be associated with the tree previously mentioned. Again, no significant association of selection line with specific birth site preference could be demonstrated.

The between ewe variance component for the time ewes spent grooming was significant ($P < 0.05$), but the repeatability (± *SE*) between years of the trait was fairly low at 0.13 ± 0.06. Time spent grooming was independent of selection line, although absolute means favoured the H line (Table 1). Mature ewes tended to spend longer ($P < 0.10$) periods grooming their offspring than primi-parous maidens. Ewes caring for more than one viable lamb spent longer ($P < 0.01$) periods grooming both lambs than ewes caring for singles.

Table 1. Least squares means for the square root transformed period spent grooming by individual ewes, as affected by selection line, age, and number of viable lambs cared for

Effect	**Number of Observations**	**Stay on birth site (min)**	
		Mean ± *SE*	**(Mean)^2**
Overall mean	654	6.30 ± 0.17	39.7
Selection line		NS	
High line	428	6.44 ± 0.19	41.5
Low line	226	6.15 ± 0.27	37.8
Lambing year		NS	
Age		$P = 0.08$	
Maiden	154	5.87 ± 0.33	34.5
Mature	500	6.73 ± 0.26	45.2
Number of lambs		**	
Single	350	5.66 ± 0.24	32.0
Multiple	304	6.94 ± 0.25	48.2

** $P < 0.01$; NS - not significant

Neo-natal activity was monitored in 428 H and 226 L line ewes during 1993 - 1997. At the first postpartum observation, H line ewes were more ($P < 0.05$) likely to be engaged in the grooming of their offspring than L line contemporaries (0.804 *vs.* 0.730 respectively; $Chi^2 = 4.32$; degrees of freedom = 1). A similar observation was made at the second observation, 30 minutes later (0.598 *vs.* 0.518; $Chi^2 = 7.58$; $P < 0.01$). Grooming behaviour subsequently declined rapidly, and no further line differences were found. Ewes in the L line were more likely to graze than H line contemporaries at 90 minutes (0.341 *vs.* 0.203; $Chi^2 = 14.15$; $P < 0.01$) and 120 minutes (0.310 *vs.* 0.224; $Chi^2 = 5.26$; $P < 0.05$) after lambing. A similar tendency ($P < 0.10$) was found 210 minutes after lambing (0.270 *vs.* 0.201; $Chi^2 = 3.65$). Ewes belonging to the H line were more ($P < 0.05$) likely to stand with their progeny than L line contemporaries at 90 minutes (0.638 *vs.* 0.531; $Chi^2 = 6.61$) and 180 minutes (0.640 *vs.* 0.535; $Chi^2 = 6.36$) postpartum. No line differences were observed with regard to the proportion of ewes lying.

Discussion

Substantial proportions of births were recorded in each of the eight 3-hour intervals throughout the day (Fig. 2), although slightly more ($P < 0.05$) births were recorded during daylight. Supervision of lambing to improve lamb survival would thus be only partly effective if restricted to daylight hours. Other authors reporting on paddock-lambing ewes came largely to the same conclusions (George, 1969; Arnold and Morgan, 1975; Alexander *et al.*, 1993). The work of Jilek *et al.* (1985) suggested that 42% of births occurred during the 12 - hour period from 18h00 to 06h00, which is in good agreement with the present results. The present results also accorded with those reported by Alexander *et al.* (1993) for Merinos under comparable conditions. In contrast, George (1969) found only 37% of births in the period from 08h00 to 18h00 in Merino ewes. Research on ewes that lambed in barns suggested that parturitions could be synchronised to an extent by manipulating feeding schedules and that feeding in the mornings, resulted in a relatively low proportion of late-night births, and more daytime births (Lindahl, 1964; Holmes, 1976; Gonyou and Cobb, 1986; Field *et al.*, 1998). In grazing animals, like those in the present investigation, varying feeding regimes is an unlikely option for managers.

Only the paper by Alexander *et al.* (1993) was available for comparison with the present results on the interval between consecutive lambings. Their results were very similar to those reported in the present paper, with the intervals between the onset of births found to conform to a theoretical exponential distribution. They also found that the observed distribution deviated significantly from the expected distribution for small intervals between consecutive lambings. They argued that small departures from the expected distribution could become significant if the observed sample is large (their study included roughly 1900 births). On the other hand, they contended that such a deviation could be biologically real. The endocrinological and physiological mechanisms involved in the commencement of parturition are known (Rice *et al.*, 1984). Yet, it may be possible that the parturition process in near-term ewes could be stimulated by pheromones or vision, facilitating the commencement of other births when one ewe has started lambing (Alexander *et al.*, 1993). The latter authors argued that such factors could be turned into an advantage from an animal husbandry perspective if it could be properly understood. The present knowledge only allows speculation in this regard, and further research is indicated.

The interpretation of data on birth sites is affected by a variety of interacting factors, complicating interpretation (Alexander *et al.*, 1990). The latter study found that Merino ewes would generally lamb on the high ground of a paddock. Very little evidence of such a trend was found in the present study, with the possible exception of paddock A, where more birth sites were found in the higher eastern part of the paddock. Alexander *et al.* (1990) also found that birth sites tended to be concentrated around the boundaries of paddocks in breeds other than the Merino. This finding was related to an attempt of ewes to seek isolation prior to birth (Alexander, 1988). In four night paddocks higher proportions of ewes were found to lamb in the half of the paddock nearest to the boundaries, but no such tendency was found in the day paddocks. This trend could have been associated with the preference of ewes for the southern parts of the night paddocks, furthest from the floodlights and the building used as base for the observers. This preference was particularly strong in paddock A, where respectively 16, 25 and 40 ewes lambed in the top third (the northernmost part of the paddock), middle third and bottom third. In most of the other paddocks, equal or higher (in absolute terms) numbers of ewes were seen to lamb in the top third when compared to the middle third. There was evidence that birth sites near to trees along the boundaries of paddocks A and C was associated with the preference ewes showed for the outer half of these paddocks. The significance of this finding is not clear, since these paddocks were used at night, when shelter from the sun would not be regarded as important. Results from the present study thus neither supported nor refuted the contention of Alexander *et al.* (1990) that Merino ewes did not prefer birth sites along the boundary fences. The distribution of birth sites in our day paddocks would support such a contention, but not those in the night paddocks. The only outstanding feature of the paddocks that could be related to a concentration of birth sites was trees on the boundaries of paddocks A, C and H, as was stated previously. In the study of Alexander *et al.* (1990), Merino ewes were generally not attracted to birth sites that were characterised by logs, rock piles, individual trees, clumps of trees or contrived shelters. The distribution of birth sites in our study was much closer to random compared to the results of Alexander *et al.* (1990). This difference probably results from much smaller paddocks used (averaging approximately 0.4 ha), compared to 8 to 9 ha in the latter study. In general, patterns with regard to birth site preference were not associated with selection line.

Alexander (1988) reported that grooming is usually intense at first, but that it becomes spasmodic within approximately half an hour of birth. Bouts of grooming can be interspersed with grazing or eating hay (Edwards and Broom, 1982). A similar pattern can be discerned in this study (Table 2). Literature results indicated that single lambs were groomed more intensively than individual twins (O'Connor and Lawrence, 1992). When the total amount of grooming was considered, it was clear that an increased litter size was associated with an increase in overall grooming behaviour by the ewe. When the time-budget of ewes for the first 4 hours after lambing was considered, it was clear that a higher proportion of H line ewes groomed their lambs at first than L line contemporaries (Table 2). No conclusive line difference could be discerned about an hour after the first recording. It has previously been demonstrated that mild sedation of lambs led to less activity shortly after birth (Murphy and Lindsay, 1996). Ewes caring for these lambs spent less ($P < 0.05$) time grooming their progeny, and longer periods separated from them. Although the effect of sedation was only temporary, the survival of sedated lambs to 9 weeks was lower ($P < 0.05$) relative to their contemporaries. Murphy and Lindsay (1996) contended that the poor vigour induced by sedation disrupted the formation of a strong dam - offspring bond, thus compromising subsequent lamb survival. Maternal and neonatal behaviour of superfine wool lambs born as part of an embryo transfer program to either superfine or medium wool ewes was considered in a later study (Kuchel and Lindsay, 1999). Medium wool ewes spent more time grooming and less time separated from their superfine progeny than superfine ewes. Neonatal progress in the progeny of superfine ewes was slower, as reflected by fewer standing attempts, a longer interval to progress from birth to suckling and shorter periods spent standing or suckling. Lamb survival was correspondingly compromised in the superfine progeny of superfine ewes. Progeny from the H line that was assessed in the present study were quicker to suckle than contemporaries in the L line, and also had a higher survival to weaning (Cloete and Scholtz, 1998). This led the latter authors to hypothesise that higher levels of lamb vigour in the H line possibly stimulated maternal interest, thus enhancing the probability of survival. The greater initial interest of H line ewes in their lambs supports this line of reasoning, although it cannot be proved beyond doubt.

There was evidence that L line ewes were more likely to resume grazing more rapidly after birth than their H line contemporaries. The latter ewes appeared to be more content just to stand with their offspring at this stage. These results could possibly be related to the longer period that ewes caring for sedated offspring spent apart from their progeny, as reported in the study of Murphy and Lindsay (1996).

Conclusions

If the supervision of Merino ewes in South Africa was to be confined to daylight hours in intensive systems, a substantial proportion of births would not be supervised. If further research substantiates the contention that births trigger each other under certain conditions, it would be of benefit to identify the mechanism involved. This knowledge could facilitate the synchronisation of natural births in pasture lambing flocks, where it is impractical to alter the distribution of births by nutrition. Although relatively few line differences were found in the present study compared to earlier work on other behavioural characteristics (Cloete and Scholtz, 1998), it could be mentioned that behavioural adaptations in the H line would generally facilitate lamb survival, as was found previously.

Acknowledgements

We are indebted to J.M. ten Hoope, P.J.A. Lombard and Farida Martin for assistance with the observations. Students of the University of Stellenbosch and other staff also played an important supportive role when employed temporarily. The maintenance of the experimental animals was supported financially by the South African Wool industry. We also wish to express our sincerest gratitude to Liezl Landman for the preparation and editing of the maps of the experimental area.

References

Alexander, G., 1984. Constraints to lamb survival. In: Lindsay, D.R. & Pearce, D.T., (Eds.) Reproduction in Sheep, Australian Academy of Science in Conjunction with the Australian Wool Corporation, Canberra, Australia. pp. 199 - 209.

Alexander, G., 1988. What makes a good mother? *Proceedings of the Australian Society of Animal Production* 17: 25 - 41.

Alexander, G., Stevens, D., Baker, P., Bradley, L.R., 1993. The timing of birth in grazing Merino sheep. *Australian Journal of Experimental Agriculture* 33: 557 - 560.

Alexander, G., Stevens, D., Bradley, L.R., 1990. Distribution of field birth-sites of lambing ewes. *Australian Journal of Experimental Agriculture* 30: 759 - 767.

Arnold, G.W., Morgan, P.D., 1975. Behaviour of the ewe and lamb at lambing and its relationship to lamb mortality. *Applied Animal Ethology* 2: 25 - 46.

Cloete, S.W.P., Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Van Niekerk, F.E., Rust, J.M., 1998. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *Sheep and Goat Research Journal* 14: 11 - 12.

Edwards, S.A., Broom, D.M., 1982. Behavioural interactions of dairy cows with their newborn calves and the effects of parity. *Animal Behaviour* 30: 525 - 530.

Field, R.A., Taylor, N.A., Riley, M.L., Russell, W.C., 1998. The proportion of lambs born at night is not changed by lighting. *Sheep and Goat Research Journal* 14: 191 - 193.

George, J.M., 1969. Variation in the time of parturition of Merino and Dorset Horn ewes. *Journal of Agricultural Science, Cambridge* 73: 295 - 299.

Gonyou, H.W., Cobb, A.R., 1986. The influence of time of feeding on the time of parturition in ewes. *Canadian Journal of Animal Science* 66: 569 - 574.

Harvey, W.R., 1990. User's guide for LSMLMW and MIXMDL. PC - 2 version, MIMEOGRAPH.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Holmes, R.J., 1976. Relationship of parturient behaviour to reproductive efficiency of Finn sheep. *Proceedings of the New Zealand Society of Animal Production* 36: 253 - 257.

Jilek, A.F., Pope, R.J., Vatthauer, X., Erickson, R.A., 1985. Influence of feeding time on parturition in ewes. *Journal of Animal Science* 61(Suppl. 1): 84.

Lindahl, I.L., 1964. Time of parturition in ewes. *Animal Behaviour* 12: 231 - 234.

Kuchel, R.C., Lindsay, D.R., 1999. Maternal behaviour and the survival of lambs in superfine wool sheep. *Reproduction Fertility and Development* 11: 391 - 394.

Murphy, P.M., Lindsay, D.R., 1996. The contribution of the activity of the newborn Merino lamb to the attachment to its mother and subsequent survival. *Proceedings of the Australian Society of Animal Production* 21: 486.

O'Connor, C.E., Lawrence, A.B. 1992. Relationship between lamb vigour and ewe behaviour at parturition. *Animal Production* 54: 361 - 366.

Rice, G.E., Leach Harper, C.M., Hooper, S., Thorburn, G.D., 1984. Endocrinology of pregnancy and parturition. In: Lindsay, D.R. & Pearce, D.T., (Eds.), Reproduction in Sheep. Australian Academy of Science in Conjunction with the Australian Wool Corporation, Canberra, Australia. pp. 165 - 173.

Siegel, S., 1956. Non parametric statistics for the behavioral sciences. McGraw-Hill Book Company Inc., New York, USA.

Turner, H.N., Young, S.S.Y., 1969. Quantitative Genetics in Sheep Breeding. MacMillan Publ. Co, Melbourne, Australia.

CHAPTER 12

GENETIC AND ENVIRONMENTAL PARAMETERS FOR LAMBING AND NEONATAL BEHAVIOUR IN MERINO LINES DIVERGENTLY SELECTED FOR EWE MULTIPLE REARING ABILITY

S.W.P.Cloete[1,2], J.B.Van Wyk[2], Anna J.Scholtz[1], A.R.Gilmour[3]

[1]Elsenburg Agricultural Centre, Private Bag X1, Elsenburg, 7607. South Africa
[2]University of the Free State, PO Box 339, Bloemfontein, 9300, South Africa
[3]NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange, 2800, NSW, Australia

Submitted at:
Australian Journal of Experimental Agriculture

Genetic and environmental parameters for lambing and neonatal behaviour in Merino lines divergently selected for ewe multiple rearing ability

S.W.P. Cloete[12], J.B. van Wyk[2], Anna J. Scholtz[1] and A.R. Gilmour[3]

[1]Elsenburg Agricultural Centre, Private Bag X1, Elsenburg 7607, South Africa
[2]University of the Free State, PO Box 339, Bloemfontein 9300, South Africa
[3]NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia

Abstract: Data were recorded for birth weight, lambing and neonatal behaviour of approximately 1600 Merino lambs born over a 10 - year interval from 1993 to 2002. Corresponding data were obtained from approximately 1000 ewe lambing records over the same period. The resource population has been divergently selected from the same base population since 1986, either for (H line) or against (L line) maternal multiple rearing ability. Behaviour traits were expressed as time intervals in minutes. In lambs, length of parturition was defined as the period between the first definite sign of impending parturition in the ewe to the birth of a specific lamb. In multiples, the birth of the preceding litter mate was regarded as the beginning of parturition for subsequent litter mates. Data for individual lambs were summed to obtain length of parturition for specific parity records in ewes. Other observations on lambs included the intervals from birth to standing for > 10 seconds and from standing to apparently suckling. Ewes were given a maternal score for cooperation with the first suckling attempts of lambs which was averaged for specific parities and also analysed as a trait of the ewe. The intervals that ewes spent on the birth site were also recorded. Single and male lambs were heavier than multiples and singles. Subsequent multiple lambs had shorter parturitions than singles and first-born multiples in both lines. Ram lambs experienced longer parturitions than ewes. Lamb birth weight was curvi-linearly related to dam age, while length of parturition generally decreased with an increasing dam age in both ewes and lambs. The interval from standing to suckling and maternal cooperation score were curvi-linearly related to dam age. Line differences ($P < 0.05$) favoured H line ewes and lambs for length of parturition, the interval from standing to apparently suckling and maternal cooperation score. Direct heritability estimates ($h^2 \pm SE$) in lambs were 0.18 ± 0.06, 0.05 ± 0.03, 0.23 ± 0.06 and 0.07 ± 0.04 respectively for birth weight, length of parturition, and the intervals from birth to standing and from standing to suckling. The inclusion of the maternal genetic variance ratio (m^2) resulted in an improvement in the log likelihood ratio for birth weight, length of parturition and the interval from standing to suckling, yielding estimates of respectively 0.23 ± 0.04, 0.10 ± 0.03 and 0.07 ± 0.03. Maternal permanent environment variance ratios (c^2) were 0.13 ± 0.05 for birth weight, 0.09 ± 0.03 for the interval from standing to apparently suckling and 0.23 ± 0.03 for maternal cooperation score. Heavier birth weights were generally associated with longer parturitions, particularly at the maternal genetic level (0.49 ± 0.14). Higher maternal cooperation scores were associated with shorter intervals between first standing and apparently suckling. This correlation was particularly strong for the maternal permanent environment (0.42 ± 0.14). When assessed as a trait of the ewe, h^2 was estimated at 0.17 ± 0.04 for length of parturition, 0.11 ± 0.04 for maternal cooperation score and 0.20 ± 0.04 for the interval ewes remained on or near the birth site. A small service sire effect for length of parturition in ewes amounted to 0.03 ± 0.02. Maternal cooperation score was genetically related to the time spent on or near to the birth site (0.53 ± 0.18). Differences between lines in behaviour, generally favouring the H line, would generally be conducive to lamb survival. Genetic trends suggested divergence between lines with regard to maternal breeding values for length of parturition and the interval from birth to standing in lambs. Genetic divergence between lines was also detected in all three traits assessed in ewes. Based on these results and the parameter estimates obtained, it was contended that selection for improved multiple rearing ability was feasible in paddock-reared sheep flocks.

Keywords: Selection, lamb survival, maternal ability, breeding values.

Introduction

Lamb mortality is a major constraint to efficient sheep production (Haughey, 1991). The cost of intensification prohibits the improvement of lamb survival by the provision of permanent supervision and confinement of breeding ewes to indoor pens during the perinatal period in the pastoral sheep production areas of the world. Selective breeding was advocated as a means of improving lamb survival and ewe rearing ability under paddock conditions (Le Neindre *et al.*, 1990; Lindsay *et al.*, 1990; Haughey, 1991). Behavioural adaptations were suggested to contribute to selection responses in lamb survival in the pastoral areas (Alexander, 1988). So far, very few published estimates of genetic (co)variances for peri-parturient behaviour in sheep have been published (Hinch, 1997). Breed and line differences in some traits (e.g. length of parturition and neonatal progress of lambs – for example see Alexander *et al.*, 1990*b*; Cloete and Scholtz, 1998; Kuchel and Lindsay, 1999) may be indicative of genetic variation. Genetic (co)variances for lambing and neonatal behaviour of South African dual-purpose breeds were reported recently (Cloete *et al.*, 2002*c*). Low to medium levels of direct and maternal genetic variation were found in this study. Nevertheless, as is commonly found when new traits are being analysed, genetic correlations were associated with large standard errors and were inconsistent between breeds. It was thus impossible to arrive at robust conclusions, generally applicable to the industry, in this regard.

This study reports results pertaining to environmental factors associated with peri-parturient behaviour of sheep, as well as genetic (co)variances among traits. The resource population used in the study was divergently selected for maternal multiple rearing ability over a number of years (Cloete and Scholtz, 1998). The larger size of the data set used, allowed the estimation of genetic (co)variances between traits, which were not estimated previously.

Materials and Methods

Animals and location

Two lines of Merino sheep were divergently selected from the same base population since 1986, using maternal ranking values for lambs reared per joining. Details of the procedure for selection of replacements can be found in the literature (Cloete and Scholtz, 1998). In short, ewe and ram progeny of ewes rearing more than 1 lamb per joining (i.e. reared twins at least once) were preferred as replacements in the High (H) line. Replacements were preferably descended from ewes rearing fewer than 1 lamb per joining (i.e. barren or lost all lambs born at least once) in the Low (L) line. The H line was augmented by 28 ewes from a multiple ovulation and embryo transfer program, that were born during 1991 and 1992 (Cloete *et al.*, 1998*b*). Progeny of mature ewes screened into the respective lines from other lines were also available since the 1996 lambing season. The screening process was detailed by Cloete *et al.* (2002*b*).

Since their establishment, the 2 lines were maintained as a single flock, except during joining in single sire groups to 4 - 5 rams. For the duration of this experiment, irrigated kikuyu (*Pennisetium clandestinum*) paddocks were utilised during joining in summer (January - February) and lambing in winter (June – July). Dryland lucerne (*Medicago sativa*) and medic (*M. truncatula*) pastures were mostly utilised during the remainder of the year. An oat (*Avena sativa*) fodder crop was occasionally utilised in winter, while oat crop residues and standing hay were sometimes available during spring and early summer. Nutrition was mostly adequate throughout the year, and supplementary feeding was rarely needed. The ewes were shorn annually within 3 - 4 weeks of the commencement of lambing. The study was conducted over a 10 - year period (1993 - 2002). Lambing took place on 10 kikuyu paddocks of approximately 0.3 to 0.5 ha each, as described by Cloete *et al.* (2002*d*).

Observations and recordings

The lambing flock was watched by 1 - 2 trained observers continuously for a period of approximately 3 weeks during peak lambing. The ewes soon adapted to human presence and could be approached closely (< 10 m) without undue disturbance. Five lambing paddocks were used during daylight hours and another five with floodlights were used at night (Cloete and Scholtz, 1998). Behavioural recordings included length of parturition of individual lambs (calculated as the period between the first definite sign of parturition and the birth of that specific lamb). In multiples, the birth of the previous lamb was regarded as the beginning of parturition for subsequent litter mates. Ewes that experienced difficult births and had not delivered 3.5 hours after parturition started, were assisted (Cloete *et al.*, 2002*c*). A few ewes were assisted if they had not delivered 2 hours after presentation or 30 minutes after obvious malpresentation of body parts (Cloete and Scholtz, 1998). Since assistance was based on time intervals, the time prior to assistance was accepted as the length of parturition. Other observations on the lambs included the time from birth to first standing for 10 seconds, and from standing to apparently suckling. After being groomed by their dams for at least 15 minutes, lambs were identified with stock marker spray according to their dam and order of birth. Birth weight was recorded to the nearest 0.1 kg within 24 hours of the birth of individual lambs.

The birth site was marked with a peg. Movement of ewes from their birth sites was recorded. Ewes were regarded as having left their birth sites permanently after having moved away more than 15 m for more than 2 h. Estimation of distances was aided by a grid system consisting of iron poles and fluorescent markers placed on the paddock fences at 20 m intervals (Cloete and Scholtz, 1998). Ewes that frustrated the first suckling attempts of their neonates by backing, circling or butting were recorded (Alexander, 1988). Active co-operation by standing still, adopting a slightly hunched posture to enable access to the udder and nudging the lamb in a position to facilitate suckling, was also noted. These recordings were combined to obtain an overall ewe maternal cooperation score on a 6 - point scale. Length of parturition and maternal behaviour score were also analysed as a trait of the ewe. For this purpose, the births of individual lambs were totalled for specific parities (Cloete and Scholtz, 1998). Maternal behaviour scores for individual lambs were correspondingly averaged to obtain a single value for individual lambing opportunities.

Statistical analysis

The ASREML program (Gilmour *et al.*, 1999) was used for the estimation of the fixed effects, and also subsequently to derive variance components for birth weight and the behavioural traits in univariate analyses. Fixed effects that were considered for lambs were year of birth (1993 - 2002), selection line (H and L), gender (ram or ewe), age of dam (2 - 7+ years) and birth type (single or multiple) or birth order (single, first multiple or second multiple), depending on the trait considered. Trends with regard to birth year and age of dam were modelled, using cubic splines (Verbyla *et al.*, 1999). Linear and non-linear components of the splines were interacted with selection line, to obtain indications of differences in these trends between lines. The first analyses involved fitting various combinations of fixed effects, random spline components and interactions between them to obtain an operational model. Effects found to be significant ($P < 0.05$) in these preliminary analyses were retained in subsequent analyses. Random terms were then added to the operational model, resulting in the following genetic models for analyses (in matrix notation):

$$y = Xb + Z_1a + e \qquad (1)$$

$$y = Xb + Z_1a + Z_2c + e \qquad (2)$$

$$y = Xb + Z_1a + Z_3m + e \qquad (3)$$

[Covariance (a,m)=0]

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad (4)$$

[Covariance (a,m)=0]

$$y = Xb + Z_1a + Z_3m + e \qquad (5)$$

[Covariance $(a,m)=A\sigma_{am}$]

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad (6)$$

[Covariance $(a,m)= A\sigma_{am}$]

In these analyses, y was a vector of observations for lamb birth weight or behavioural traits, b, a, m and c were vectors of fixed effects, direct genetic variances, maternal genetic variances and maternal permanent environmental variances respectively, X, Z_1, Z_2, and Z_3 were the corresponding incidence matrices relating the respective effects to y, e the vector of residuals, A the numerator relationship matrix, and σ_{am} the covariance between direct genetic and maternal effects.

It was assumed that:

$V(a) = A\sigma^2_a$; $V(m) = A\sigma^2_m$; $V(c) = I\sigma^2_c$; $V(e) = I\sigma^2_e$,

with I being an identity matrix; σ^2_a, σ^2_m, σ^2_c and σ^2_e direct genetic variance, maternal genetic variance (as a trait of the lamb) and the maternal permanent environmental variance and environmental (residual) variance respectively.

Similar procedures were followed when data recorded on ewes were considered. Fixed effects in this case were year of lambing (1993 - 2002), selection line (H and L), number of lambs given birth to (single or multiple) and ewe age (2 - 7+ years). Trends with regard to birth year and age of dam were modelled, using cubic splines (Verbyla *et al.*, 1999). Operational models were obtained as described earlier. Random terms were then added, resulting in the following models for analyses:

$$y = Xb + Z_1a + e \qquad (1)$$

$$y = Xb + Z_1a + Z_2c_{PE} + e \qquad (2)$$

$$y = Xb + Z_1a + Z_3c_{sire} + e \qquad (3)$$

In these models, y was a vector of observations for ewe behavioural traits as in the analyses on lamb traits, b, a, c_{PE} and c_{sire} were vectors of fixed effects, direct genetic variances, ewe permanent environmental variances and random service sire variances respectively, X, Z_1, Z_2, and Z_3 were the corresponding incidence matrices relating the respective effects to y, and e the vector of residuals. The assumptions were as before. All analyses included the full pedigree file, consisting of 4351 individuals, the progeny of 216 sires and 1107 dams.

Log likelihood tests were conducted to determine the most suitable model for each trait in univariate analyses. The random effects models that fitted the data for each trait best were identified, using the log likelihood ratios obtained from the respective analyses (Snyman *et al.*, 1996). Subsequently, 2 - trait animal models were fitted, both on lamb and ewe traits. These analyses allowed the calculation of all relevant direct and maternal correlations between traits, together with their appropriate standard errors.

Direct and maternal breeding values for traits were obtained and averaged within birth years for lambs. Trends were also obtained for traits that were assessed in ewes. Genetic trends were inspected for divergence between the lines, using standard errors obtained for the regression coefficients. The breeding values used for this were obtained from analyses where selection line and its interactions with other traits were excluded from the operational model. The inclusion of selection line as fixed would reduce the breeding values for genetic differences between lines that accrued as a result of selection.

Results

Fixed effects

Results pertaining to the analyses on lambs are presented first. Lamb birth weight was independent of selection line ($P > 0.10$; Table 1). Ram lambs and singles were respectively 7.4 and 28.8 % heavier ($P < 0.01$) than ewes and multiples. Lamb birth weight increased curvilinearly ($P < 0.01$) with an increase in dam age, reaching a maximum in 4 - 6 year-old dams.

Selection line and order of birth interacted ($P < 0.05$) as far as length of parturition was concerned (Table 2). In H line lambs, the births of first multiples tended ($P < 0.10$) to be 6.1% shorter than that of singles. Subsequent multiples had even shorter ($P < 0.05$) births, being 20% shorter than that of singles. The births of singles and first multiples in the L line were similar in length ($P > 0.10$). The births of subsequent multiples were approximately 23% shorter ($P < 0.05$). Overall, H line lambs tended to have shorter births than L line contemporaries (Table 1). The line difference in favour of the H line amounted to 10.6% in firstborn singles ($P < 0.05$), when expressed relative to the mean for L line lambs (Table 2). Ewe lambs experienced shorter births than rams ($P < 0.05$; Table 1). Length of parturition also tended ($P < 0.10$) to decline linearly with an increase in age of the dam. The fixed effects considered did not affect the interval from birth to standing in lambs.

Table 1. Least squares means (± *SE*) for birth weight, length of parturition and the interval from birth to first standing for > 10 seconds. The latter traits were analysed after transformation to natural logarithms. Back transformed means are given in parentheses.

Fixed effects	**Birth weight (kg)**	**Length of parturition (minutes)**	**Birth to standing (minutes)**
Number of observations	1644	1621	1578
Overall mean	4.21 ± 0.07	3.38 ± 0.07 (29.4)	3.02 ± 0.16 (20.5)
Birth year	**	*	*
Selection line	NS	*	NS
H line	4.27 ± 0.09	3.27 ± 0.08 (26.3)	3.04 ± 0.18 (20.9)
L Line	4.14 ± 0.10	3.50 ± 0.10 (33.1)	3.01 ± 0.18 (20.3)
Birth type or order	**	**	NS
Single	4.74 ± 0.08	3.69 ± 0.07 (40.0)	3.01 ± 0.17 (20.3)
Multiple/First Multiple	3.68 ± 0.08	3.57 ± 0.08 (35.5)	3.03 ± 0.17 (20.7)
Second multiple	-	2.89 ± 0.08 (18.0)	-
Gender	**	*	NS
Ram	4.36 ± 0.08	3.47 ± 0.07 (32.1)	3.08 ± 0.17 (21.8)
Ewe	4.06 ± 0.08	3.30 ± 0.07 (27.1)	2.97 ± 0.17 (19.5)
Age of dam (years)	**	$P = 0.10$	NS
2	3.83 ± 0.08	3.47 ± 0.08 (32.1)	3.04 ± 0.17 (20.9)
3	4.12 ± 0.08	3.43 ± 0.07 (30.9)	3.01 ± 0.17 (20.3)
4	4.21 ± 0.08	3.39 ± 0.07 (29.7)	3.04 ± 0.17 (20.9)
5	4.24 ± 0.07	3.35 ± 0.07 (28.5)	3.01 ± 0.17 (20.3)
6	4.23 ± 0.07	3.31 ± 0.07 (27.4)	3.02 ± 0.17 (20.5)
7	4.05 ± 0.10	3.27 ± 0.08 (26.6)	3.18 ± 0.19 (24.0)

NS– Not significant ($P > 0.01$); * - Significant ($P < 0.05$); ** Significant ($P < 0.01$); - No mean available

Table 2. Least squares means depicting the interaction between selection line and birth order

Order of birth	Selection line	
	H Line	L Line
Single	3.59 ± 0.09 (36.2)	3.80 ± 0.11 (44.7)
First multiple	3.37 ± 0.09 (29.1)	3.77 ± 0.12 (43.4)
Subsequent multiple	2.86 ± 0.09 (17.5)	2.93 ± 0.13 (18.7)

The linear component of the spline for age of dam interacted ($P < 0.05$) with selection line as far as the interval from standing to first apparently suckling was concerned. In two-tooth maidens, this interval was substantially shorter in H line lambs than in L line lambs ($P < 0.05$; Fig. 1). The interval declined with an increase in age in both lines, but the decline was more pronounced in the L line. In older dams (> 5 years of age) no line difference was found. Multiple lambs took longer to progress from standing to suckling than singles ($P < 0.01$; Table 3). Maternal cooperation score was higher ($P < 0.01$) in dams of H line lambs, but was unaffected by birth type and gender. Maternal cooperation score improved curvi-linearly with dam age ($P < 0.01$), with no significant differences between dam age groups exceeding three years of age.

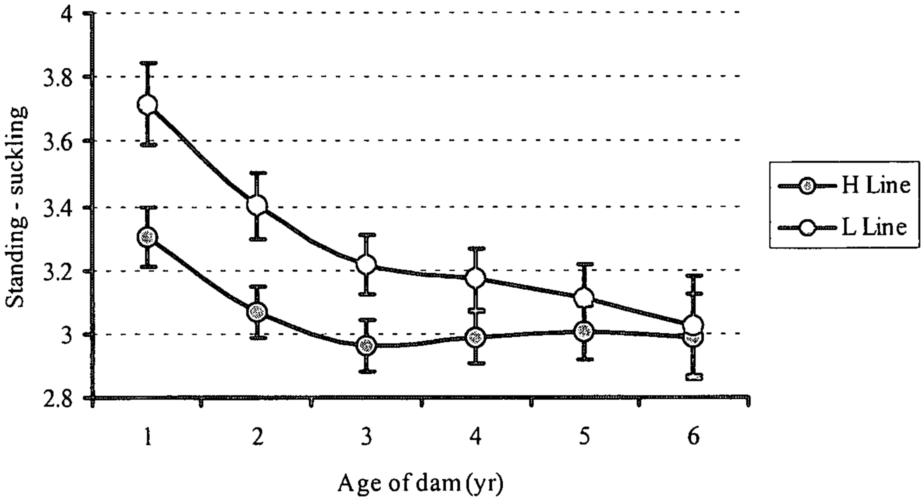


Fig. 1. The interaction between selection line and age of dam for the interval between standing and suckling in minutes. Data were transformed to natural logarithms prior to analysis. Vertical lines about means depict standard errors.

Table 3. Least squares means (± *SE*) for the interval from standing to first apparently suckling and maternal cooperation score. The former trait was transformation to natural logarithms prior to analysis. Back transformed means are given in parentheses.

Fixed effects	**Standing – suckling (min)**	**Maternal cooperation**
Number of observations	1495	1495
Overall mean	3.08 ± 0.07 (21.8)	5.45 ± 0.07
Birth year	*	NS
Selection line	*	**
H line	2.97 ± 0.08 (19.5)	5.59 ± 0.07
L Line	3.20 ± 0.09 (24.5)	5.31 ± 0.08
Birth type	**	NS
Single	2.87 ± 0.08 (17.6)	5.48 ± 0.08
Multiple	3.29 ± 0.07 (26.8)	5.42 ± 0.07
Gender	NS	NS
Ram	3.09 ± 0.07 (22.0)	5.40 ± 0.07
Ewe	3.08 ± 0.07 (21.8)	5.50 ± 0.07
Age of dam (years)	**	**
2	3.47 ± 0.08 (32.1)	4.57 ± 0.08
3	3.21 ± 0.07 (24.8)	5.18 ± 0.07
4	3.08 ± 0.07 (21.8)	5.45 ± 0.07
5	3.09 ± 0.07 (22.0)	5.45 ± 0.07
6	3.08 ± 0.07 (21.8)	5.42 ± 0.07
7	3.04 ± 0.12 (20.9)	5.52 ± 0.13

NS– Not significant ($P > 0.01$); * - Significant ($P < 0.05$); ** Significant ($P < 0.01$)

In the assessment of behavioural traits of the ewe, no significant ($P < 0.05$) interactions were found between fixed effects. The births of H line ewes were 6.3% shorter ($P < 0.05$) than those of their L line contemporaries (Table 4). Multiple-bearing ewes took 11.7% longer to give birth than ewes bearing singles ($P < 0.01$). Length of parturition declined linearly with an increase in ewe age.

Maternal cooperation score was higher in H line ewes ($P < 0.01$) and in ewes caring for singles ($P < 0.05$ – Table 4). It improved curvi-linearly with ewe age to 4 years ($P < 0.01$), after which little further improvement was seen. The period that ewes remained on the birth site was independent of selection line, although H line ewes tended to remain longer ($P < 0.25$). Ewes caring for multiples stayed longer ($P < 0.05$) on or near their birth sites than ewes caring for singles. The period ewes stayed on or near to their birth sites increased linearly ($P < 0.01$) with age.

Table 4. Least squares means (± *SE*) for length of parturition (as a trait of the ewe), cooperation score and the interval that ewes remained on or within 15 m from their birth sites. The time intervals were analysed after transformation to natural logarithms. Back transformed means are given in parentheses.

Fixed effects	**Length of parturition (minutes)**	**Cooperation with first suckling attempts**	**Stay on birth site (minutes)**
Number of observations	1117	1034	1003
Overall mean	3.97 ± 0.07 (53.0)	5.37 ± 0.07	5.63 ± 0.06 (279)
Birth year	NS	*	*
Selection line	*	**	NS
H line	3.84 ± 0.08 (46.5)	5.54 ± 0.08	5.71 ± 0.08 (302)
L Line	4.10 ± 0.09 (60.3)	5.20 ± 0.09	5.56 ± 0.09 (260)
Number of lambs born	**	*	**
Single	3.75 ± 0.07 (42.5)	5.46 ± 0.08	5.54 ± 0.07 (255)
Multiple	4.19 ± 0.07 (66.0)	5.28 ± 0.08	5.73 ± 0.07 (308)
Ewe age (years)	*	**	**
2	4.05 ± 0.08 (57.4)	4.52 ± 0.09	5.52 ± 0.08 (250)
3	4.01 ± 0.07 (55.1)	5.12 ± 0.07	5.58 ± 0.07 (265)
4	3.97 ± 0.06 (53.0)	5.37 ± 0.07	5.64 ± 0.06 (281)
5	3.92 ± 0.06 (50.4)	5.40 ± 0.07	5.69 ± 0.06 (296)
6	3.88 ± 0.07 (48.4)	5.44 ± 0.07	5.75 ± 0.07 (314)
7	3.83 ± 0.08 (46.1)	5.51 ± 0.09	5.81 ± 0.08 (334)

NS– Not significant ($P > 0.01$); * - Significant ($P < 0.05$); ** Significant ($P < 0.01$); - No mean available

Random effects

In the analyses on the lamb data, the model that fitted the data best for birth weight included direct additive, maternal additive and maternal permanent environmental effects (Table 5). The inclusion of direct and maternal additive variance components resulted in an improved ($P < 0.05$) log likelihood ratio in the case of length of parturition and the interval between birth and standing. The best model for the interval from standing to suckling and maternal cooperation score contained direct additive and maternal permanent environmental variance components.

Table 5. Log likelihood ratios for birth weight and the behavioural traits in Merino lambs of the H and L lines under seven different models of analysis. The "best' models are denoted in bold, italic figures.

Model fitted	Birth weight	Length of parturition	Birth – standing	Standing – suckling	Maternal cooperation
Fixed effects only	-121.115	-862.63	-442.33	-773.29	-680.95
+ h^2	5.672	-850.32	-411.56	-766.31	-664.05
+ h^2 + c^2	69.469	-842.80	-409.78	***-760.08***	***-638.98***
+ h^2 + m^2	77.858	***-841.14***	***-408.08***	-764.55	-642.06
+ h^2 + c^2 + m^2	***81.442***	-840.66	-407.04	-760.08	-637.50
+ h^2 + m^2 + r_{am}	77.927	-839.11	-408.05	-764.55	-641.93
+ h^2 + c^2 + m^2 + r_{am}	81.497	-838.65	-407.02	-760.20	-637.13

Direct heritability (h^2) estimates for birth weight (0.18) and the interval from birth to standing (0.23) were more than twice the corresponding standard errors (Table 6). Significant ($P < 0.05$) maternal additive variance ratios (m^2) were obtained for birth weight (0.23), length of parturition (0.10) and the interval from birth to standing (0.07). Maternal permanent environmental variance ratios (c^2) were 0.09 for the interval from standing to suckling and 0.23 for maternal cooperation score.

Table 6. Variance components and estimates of the direct genetic (h^2), maternal genetic (m^2) and maternal permanent environmental ($PE - c^2$) variance ratios (± *SE*) for birth weight and the respective behavioural traits in Merino lambs of the H and L lines

Model fitted	Birth weight	Length of parturition	Birth – standing	Standing – suckling	Maternal cooperation
<u>Variance components</u>					
Residual (σ^2_e)	0.1879	0.8793	0.4464	0.8467	0.6627
Direct additive (σ^2_a)	0.0750	0.0550	0.1475	0.0680	0.0181
Maternal genetic (σ^2_m)	0.0928	0.1019	0.0462	-	-
Maternal *PE* (σ^2_c)	0.0518	-	-	0.0910	0.2031
Total phenotype (σ^2_p)	0.4075	1.0362	0.6401	1.0067	0.8839
<u>Variance ratios</u>					
h^2	0.18 ± 0.06	0.05 ± 0.03	0.23 ± 0.06	0.07 ± 0.04	0.02 ± 0.03
m^2	0.23 ± 0.04	0.10 ± 0.03	0.07 ± 0.03	-	-
c^2	0.13 ± 0.05	-	-	0.09 ± 0.03	0.23 ± 0.03

- Effect not significant according to log likelihood ratio

Direct genetic correlations of birth weight with the other traits were high to very high, but were generally associated with large standard errors, making them unreliable (Table 7). This was also true for genetic correlations of the interval from birth to standing and maternal cooperation score with length of parturition. A notable maternal genetic correlation of 0.49 was found between birth weight and length of parturition. The maternal permanent environmental correlation of -0.42 between the interval from standing to suckling and maternal cooperation score is similarly of interest. When environmental and phenotypic correlations were considered, heavier birth weights were generally associated with longer births and shorter intervals from standing to suckling (Table 7). Lambs with longer parturitions were slower to stand. Lambs that took longer to stand were generally quicker to suckle, as were lambs with dams with higher maternal cooperation scores.

Table 7. Correlations among the respective behavioural traits in Merino lambs of the H and L lines

Model fitted	**Direct genetic**	**Maternal genetic**	**Maternal PE**	**Environment**	**Phenotypic**
Birth weight X					
Length of parturition	0.85 ± 0.25	0.49 ± 0.14	-	0.11 ± 0.04	0.23 ± 0.03
Birth – standing	0.56 ± 0.18	-0.29 ± 0.21	-	-0.08 ± 0.06	0.03 ± 0.03
Standing – suckling	-0.52 ± 0.32	-	0.28 ± 0.22	-0.10 ± 0.05	-0.09 ± 0.03
Maternal cooperation	0.54 ± 0.50	-	-0.03 ± 0.15	0.06 ± 0.04	0.06 ± 0.03
Length of parturition X					
Birth – standing	0.50 ± 0.28	0.22 ± 0.24	-	0.17 ± 0.04	0.20 ± 0.03
Standing – suckling	0.12 ± 0.43	-	-	-0.04 ± 0.04	-0.03 ± 0.03
Maternal cooperation	0.74 ± 0.99	-	-	-0.01 ± 0.04	0.01 ± 0.02
Birth – standing X					
Standing – suckling	0.26 ± 0.25	-	-	-0.19 ± 0.05	-0.10 ± 0.03
Maternal cooperation	0.08 ± 0.48	-	-	-0.01 ± 0.04	0.01 ± 0.03
Standing – suckling					
Maternal cooperation	0.10 ± 0.80	-	-0.42 ± 0.14	-0.26 ± 0.03	-0.27 ± 0.03

- Effect not estimated because not significant in at least one trait according to log likelihood ratio

Log likelihood ratios for the behavioural traits assessed in ewes are presented in Table 8. The inclusion of direct additive variance components improved ($P < 0.05$) the log likelihood ratio in all cases, when compared to fixed effects only models. A further improvement was found in the case of length of parturition when random permanent environmental effects of the service sire were fitted.

Table 8. Log likelihood ratios for the behavioural traits in Merino ewes of the H and L lines under four different models of analysis. The "best' models are denoted in bold, italic figures.

Model fitted	Length of parturition	Maternal cooperation	Stay on birth site
Fixed effects only	-477.275	-501.547	441.398
+ h^2	-460.030	***-494.300***	***421.507***
+ $h^2 + c^2_{PE}$	-459.223	493.840	419.900
+ $h^2 + c^2_{ram}$	***-457.293***	493.300	421.507

Assessed as a trait of the dam, h^2 was estimated at 0.17 for length of parturition (Table 9). Service sire, although resulting in a significant ($P < 0.05$) improvement in the likelihood ratio, accounted for only 3% of the observed phenotypic variance. Further h^2 estimates were 0.11 for maternal cooperation score and 0.20 for the period that ewes remained on or near to the birth site.

Table 9. Variance components and estimates of the direct genetic (h^2) and service sire permanent environmental ($PE - c^2_{sire}$) variance ratios (± *SE*) for the respective behavioural traits assessed in Merino ewes of the H and L lines

Component or ratio	Length of parturition	Maternal cooperation	Stay on birth site
Variance components			
Residual (σ^2_e)	0.6602	0.8220	0.6817
Direct additive (σ^2_a)	0.1406	0.0974	0.1676
Service sire PE (σ^2_{sire})	0.0258	-	-
Total phenotype (σ^2_p)	0.8265	0.09194	0.8494
Variance ratios			
h^2	0.17 ± 0.04	0.11 ± 0.04	0.20 ± 0.04
c^2_{sire}	0.03 ± 0.02	-	-

- Effect not significant according to log likelihood ratio

Genetic, phenotypic and environmental correlations between the traits measured on ewes were relatively low (Table 10). The exceptions were the genetic and phenotypic correlations between dam cooperation score and the period that ewes stayed on or near their birth sites.

Table 10. Correlations among the respective behavioural traits in Merino ewes of the H and L lines

Correlation	**Genetic**	**Phenotypic**	**Environmental**
Length of parturition X:			
Cooperation by dam	0.14 ± 0.21	0.01 ± 0.03	-0.01 ± 0.04
Stay on birth site	0.19 ± 0.17	0.01 ± 0.03	-0.03 ± 0.04
Cooperation by dam X:			
Stay on birth site	0.53 ± 0.18	0.10 ± 0.04	0.02 ± 0.04

Predicted breeding values and genetic trends

Behavioural records on lambs were obtained only for the period from 1993 to 2002, when the study on lambing and neonatal behaviour took place. Ewes born as early as 1987 were observed at an age of 6 years when they lambed during 1993, thus contributing data to the study. Since the first, unselected progeny group born in the selection experiment was born during 1986, predicted breeding values for ewe traits were obtained for individuals born during the period from 1986 to 2002. These trends were derived over a longer period, and right from the commencement of selection. It is thus not surprising that the trends obtained for ewes were generally better than those acquired from the lamb analyses.

Most of the derived regressions of averaged breeding values upon birth year were not significant in lambs (Table 11). The exception were reductions in maternal breeding values for length of parturition and the interval from birth to first standing in H line lambs. Expressed relative to overall means for these traits, the genetic changes amounted to respectively 0.38 and 0.21% respectively ($P < 0.05$). Regression coefficients differed between lines with regard to maternal breeding values for length of parturition and for the interval from birth to standing (Table 11). Trends in the H line were negative in both cases, indicative of shorter time intervals. Absolute values in the L line were positive, suggesting longer intervals. Intercepts were found to differ ($P < 0.05$) between lines for direct and maternal breeding values for length of parturition, as well as direct breeding values for the interval from standing to first apparently suckling. Differences were generally in the same direction, namely shorter in the case of H line lambs and longer for L line lambs, and substantial in size for the interval from standing to suckling.

Table 11. Details of linear regression equations depicting genetic change as reflected by the regression of averaged predicted breeding values on years of birth for traits that were measured on lambs

Trait and line	**Slope** ($b \pm SE$)	**Intercept** (a $\pm SE$)	R^2	r
Birth weight – Direct				
H line	0.0003 ± 0.0033	0.0150 ± 0.018	0.00	0.03
L Line	-0.0024 ± 0.0086	0.0217 ± 0.0459	0.01	-0.10
Birth weight – Maternal				
H line	0.0021 ± 0.0063	-0.0210 ± 0.0334	0.01	0.12
L Line	-0.0066 ± 0.0063	-0.0060 ± 0.0334	0.12	-0.35
Length of parturition – Direct				
H Line	-0.0057 ± 0.0032	-0.0140 ± 0.0173 ^{a}	0.27	-0.52
L Line	-0.0013 ± 0.0036	0.0375 ± 0.0193 ^{b}	0.13	-0.13
Length of parturition – Maternal				
H Line	-0.0124 ± 0.0036 ^{a}	-0.0270 ± 0.0197 ^{a}	0.59	-0.77*
L Line	0.0054 ± 0.0043 ^{b}	0.0438 ± 0.0225 ^{b}	0.17	0.41
Birth to standing – Direct				
H Line	-0.0006 ± 0.0069	0.0027 ± 0.0370	0.03	-0.03
L Line	-0.0088 ± 0.0066	0.0210 ± 0.0351	0.18	-0.43
Birth to standing – Maternal				
H line	-0.0062 ± 0.0017 ^{a}	0.0177 ± 0.0090	0.63	-0.79*
L line	0.0010 ± 0.0032 ^{b}	-0.0038 ± 0.0172	0.01	0.11
Standing to suckling – Direct				
H Line	-0.0035 ± 0.0030	-0.0812 ± 0.0159 ^{a}	0.14	-0.38
L Line	-0.0060 ± 0.0044	0.1559 ± 0.0242 ^{b}	0.19	-0.43

$^{a, b}$ Denote significant ($P < 0.05$) differences between selection lines for slopes or intercepts

* Denotes significant regressions

Regressions applicable to ewe traits were significant ($P < 0.05$) in most cases (Table 12). At the worst, equations for maternal cooperation score in the L line and for the period that ewes remained on or near the birth site in the H line approached significance ($P = 0.06$). Breeding values for length of parturition in the H line declined at a rate of 0.29% of the overall mean, while it increased at 0.15% of the overall mean in the L line (Fig. 2). Genetic trends in maternal cooperation score reflected an improvement of 0.11% of the overall mean in the H line. A downward tendency ($P = 0.06$) amounting to 0.12% of the overall mean was found in the L line. Corresponding results were found in the period spent by ewes on the birth site. Breeding values for ewes in the H line tended ($P = 0.06$) to increase at 0.06 % of the overall mean, while the reduction detected in the L line amounted to 0.10% of the overall mean. Divergence between lines was detected for all these analyses. Intercepts were found to differ for maternal cooperation score, in the same direction that breeding values diverged (Fig. 3).

Table 12. Details of linear regression equations depicting genetic change as reflected by the regression of averaged predicted breeding values on years of birth for traits that were measured on ewes

Trait and line	**Slope** ($b \pm SE$)	**Intercept** ($a \pm SE$)	R^2	r
Length of parturition				
H line	-0.0116 ± 0.0020^a	-0.0103 ± 0.0189	0.69	-0.83*
L Line	0.0060 ± 0.0024^b	0.0138 ± 0.0222	0.30	0.55*
Maternal cooperation score				
H line	0.0058 ± 0.0017^b	0.0240 ± 0.0156^b	0.45	0.67*
L Line	-0.0066 ± 0.0033^a	-0.0593 ± 0.0313^a	0.21	-0.46
Stay on birth site				
H Line	0.0031 ± 0.0015^b	-0.0229 ± 0.0144^a	0.22	-0.47
L Line	-0.0056 ± 0.0024^a	0.0130 ± 0.0228^b	0.26	-0.51*

$^{a, b}$ Denote significant ($P < 0.05$) differences between selection lines for slopes or intercepts

* Denotes significant ($P < 0.05$) regressions

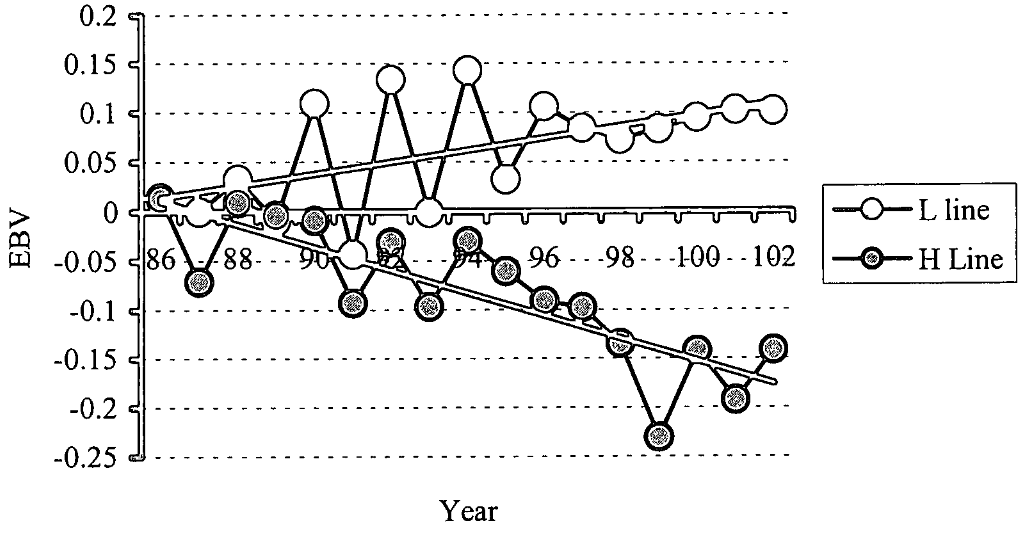


Fig. 2. Estimated direct breeding values (EBV) for length of parturition in H and L line ewes, averaged within birth years. The breeding values are expressed on a natural logarithmic scale. The year 1986 were regarded as the base year of the experiment, and coded as 0 for the regression analysis.

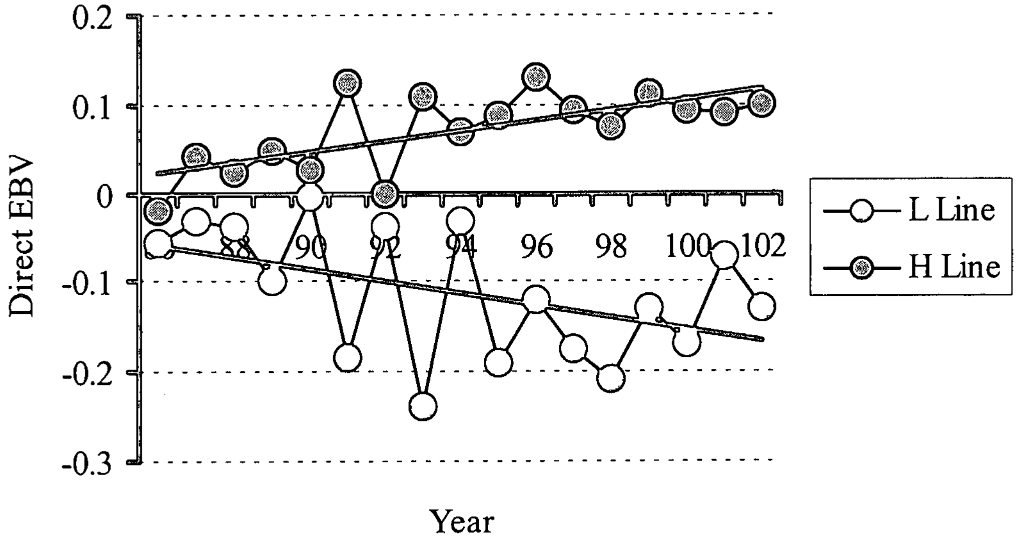


Fig. 3. Estimated direct breeding values (EBV) for maternal cooperation score of H and L line ewes, averaged within birth years. The year 1986 were regarded as the base year of the experiment, and coded as 0 for the regression analysis.

Discussion

Fixed effects

Although selection line was fitted as a fixed effect in the analyses, this effect is better discussed together with the random effects since the observed line differences were in response to the selection pressure applied to the respective lines even before the period of observations commenced. The effects of gender, birth type and dam age on birth weight were consistent with those obtained from comparable data sets in the literature, and need no further discussion. Subsequent lambs in multiple litters had shorter parturition than either singles or first-born lambs in both selection lines. Similar results in the literature (Arnold and Morgan, 1975; Cloete *et al.*, 2002*c*) were related to dilation of the cervix, facilitating the delivery of subsequent lambs (Arnold and Morgan, 1975). Haughey, (1991) also reported marked differences in length of parturition between first-born and second-born twins. In the study of Owens *et al.* (1985) it was also reported that second-born twins were quicker to appear at the vulva than first-born twins. No difference in the length of parturition for first-born and second-born twins was, however, reported in goats (Ramirez *et al.*, 1995).

Ram lambs had longer ($P < 0.05$) births than ewes. This result accords with previous results in other flocks and breeds (Alexander *et al.*, 1993; Cloete *et al.*, 2002*c*). Length of parturition decreased ($P < 0.05$) with an increase in dam age, when assessed both as a trait of the lamb or of the ewe. This finding accords with previous results for SA Mutton Merino lambs (Cloete *et al.*, 2002*c*). Conversely, no such effect was observed in Dormer lambs in the latter study. Alexander *et al.* (1993) found no effect of parity on length of parturition in progeny of ewes > 2 years of age. They did, however, report that length of parturition was longer in progeny of 2 - year old maiden ewes than in lambs with older dams.

The interval from birth to standing was generally independent of birth type, gender and age of dam. Multiple lambs took longer to progress to suckling than singles. Booroola Merino triplets and quadruplets were found to take longer to stand and apparently suckle than twins or singles (Owens *et al.*, 1985). In goitre-affected Merino lambs, Alexander *et* *al.* (1990*a*) found that twins generally progressed slower during the neonatal period than singles. Slee and Springbett (1986) reported that progress to standing was independent of birth type in lambs from a number of breeds. Birth type did, however, exert an influence on the time lambs took to reach the udder. Absolute differences in neonatal progress between singles and twins of Romanov, Finsheep and Suffolk lambs were comparatively large in the study of Fahmy *et al.* (1997). In the latter study, no significant differences were found, possibly owing to relatively few observations. Triplet lambs were slower to progress to apparently suckling than singles in a previous study at this institute (Cloete *et al.*, 2002*c*). No robust conclusion could be drawn with regard to twins, which differed between ram and ewe lambs of the SA Mutton Merino and Dormer breeds. Ewes caring for multiples had generally lower maternal cooperation scores than those caring for singles. This finding is probably related to distraction afforded by the birth process of siblings, or by the process of sharing attention between more than one offspring.

Early rate of expression of neonatal behaviour of lambs was independent of gender. Slee and Springbett (1986), Alexander *et al.* (1993) and Cloete *et al.* (2002*c*) similarly found no effect of gender on the interval from birth to standing. In the study of Alexander *et al.* (1993), ram lambs were found to progress slower ($P < 0.05$) from standing to apparently suckling than ewe contemporaries. The interval from standing to suckling was complicated by an interaction between selection line and age of dam. Although this interval was reduced with age in both H and L line lambs, the magnitude of the reduction was larger in L line lambs. An opposite trend was found for maternal behaviour score, assessed both as a trait of the lamb or the ewe. In the literature, it was commonly found that lambs of maiden ewes took a longer time to progress from standing to suckling than lambs cared for by mature ewes (Cloete and Scholtz, 1998; Cloete *et al.*, 2002*c*). Primiparous maiden ewes were more likely to engage in activities to discourage suckling (e.g. circling or backing) than experienced mothers (Alexander *et al.*, 1993; Cloete and Scholtz, 1998). These activities would also reflect in the maternal behaviour score used in this study. In a study involving 5 – year - old primiparous single-bearing ewes, results of Alexander *et al.* (1993) indicated that there was no evidence of improved maternal attributes with an increase in ewe age that could not be related to previous experience of giving birth to and the rearing of lambs. It is contended that experience that accrued from previous reproduction opportunities in higher reproducing H line ewes could have contributed to the advantage of H line lambs cared for by younger ewes over their L line contemporaries. This does, however, not account for the better performance of inexperienced maidens in the H line.

Random effects

Seeing that genetic parameters for birth weight are relatively scarce for Merino lambs, this aspect will be discussed briefly. Previous estimates of h^2 ranged from 0.18 to 0.23 for Merino lambs in animal model analyses (Mortimer and Atkins, 1995; Cloete *et al.*, 2001; Duguma *et al.*, 2002). Corresponding estimates of m^2 ranged from 0.14 to 0.25, and those for c^2 from 0.08 to 012. Our estimates of 0.18 for h^2, 0.23 for m^2 and 0.13 for c^2 accords very well with the literature values cited above. It is also consistent with those obtained from other sheep breeds, as was summarized from the literature by Duguma *et al.* (2002).

Estimates of h^2 and m^2 for length of parturition in lambs were 0.05 and 0.10 respectively. In a previous study on Dormer and SA Mutton Merino lambs, h^2 was estimated at 0.04 and 0.03 respectively (Cloete *et al.*, 2002*c*). Corresponding values for m^2 were 0.14 and 0.15. These results are in good agreement with those obtained in the present study. Moreover, length of parturition as a trait of the ewe was also heritable (0.17). There was also strong evidence of divergence in the breeding values pertaining to this trait in the two selection lines in the present study, particularly when assessed as a trait of the ewe. These results combine to strongly suggest that ease of birth can be manipulated genetically. This contention is supported by a vast body of indirect evidence reporting differences in ease of birth (and/or the occurrence of dystocia or parturient deaths) between breeds (Grommers *et al.*, 1985; Alexander *et al.*, 1990*b*; Fahmy *et al.*, 1997; Cloete *et al.*, 1998*a*), or between lines within breeds (Haughey, 1983; Knight *et al.*, 1988; Cloete and Scholtz, 1998).

Although the effect was small (3% of the overall phenotypic variance), it was interesting to note that service sire effects resulted in an improved log likelihood in the analysis on length of parturition as a trait of the ewe. No supporting evidence could be obtained from the literature, but it is known that small service sire effects exist for litter size at weaning in sheep (Bromley *et al.*, 2001; Cloete *et al.*, 2002*a*). It was also suggested that the heritability of deaths due to dystocia was higher than for other sources of death in US lambs when paternal halfsib procedures were applied (Smith, 1977). In a study involving Marshall Romney (selected for rearing ability) and Control Romney lines in New Zealand, parturient deaths were found to be higher in lambs sired by Control Romney rams than in those lambs sired by Marshall Romney rams (Knight *et al.*, 1988). This effect was, however, more pronounced in the Control Romney ram by Marshall Romney ewe combination, resulting in a significant interaction between ram line and ewe line.

Direct h^2 was estimated at 0.23 for the interval from birth to standing, while m^2 was estimated at 0.07. Corresponding h^2 estimates were 0.10 for SA Mutton Merino lambs and 0.22 for Dormer lambs (Cloete *et al.*, 2002*c*). No significant maternal effects for this trait were detected in the latter study. Differences between breeds accorded with a contention that early neonatal progress in lambs is partially under genetic control (Slee and Springbett, 1986; Alexander *et al.*, 1990*b*; Cloete *et al.*, 2002*c*). Other studies, however, reported no breed differences for early neonatal behaviour (Fahmy *et al.*, 1997).

For the interval from standing to apparently suckling, h^2 was estimated at 0.07 with a corresponding c^2 estimate of 0.09. There was also a clear difference between the two lines evaluated. In SA Mutton Merinos, h^2 of the interval between standing and apparently suckling was estimated at 0.08 with a c^2 estimate of 0.17 (Cloete *et al.*, 2002*c*). In the present study, c^2 of maternal cooperation score (as a trait of the lamb) was estimated as 0.23. These results suggest that the environment provided by the dam to facilitate suckling contributes to the ability of lambs to suckle successfully within a reasonable period of time. Supporting evidence stems from a study where super-ovulated superfine wool embryos were transplanted into either superfine wool or medium wool ewes (Kuchel and Lindsay, 1999). Fine wool lambs cared for by medium wool ewes showed faster neonatal progress than their contemporaries cared for by superfine wool ewes. Lambmarking percentages were correspondingly affected, and were markedly lower in superfine wool lambs cared for by superfine wool dams (Kuchel and Lindsay, 1999).

Maternal cooperation score appears to have a small genetic component when assessed as a trait of the dam. It may well be that the line differences in the interval from standing to suckling in this study and in previous work on the same resource population (Cloete and Scholtz, 1998), could partly result from the divergent selection pressure for multiple rearing ability in the lines on maternal cooperation score. This suggestion is supported by the divergence between lines in maternal cooperation score, assessed as a trait of the ewe. Our previous results indicated that H line ewes were less likely to circle and back than L line contemporaries. They were also more likely to adopt a posture to facilitate suckling. After this behaviour has been accounted for by analysis of covariance, the line difference still remained, leading to the contention by Cloete and Scholtz (1998) that lambs may also have an innate ability to quickly progress to suckling. The partitioning of variances that could be accomplished in the present study serves to strengthen these hypotheses.

Ewes in the H line tended ($P < 0.25$) to remain longer on or near their birth sites than L line contemporaries. When analysed as a trait of the ewe, the period that ewes remained on or near the birth site was also found to be heritable. There was also evidence of genetic divergence between lines for this trait. In this respect, Szantar-Coddington (1994) found that Fertility flock Merino ewes remained on their birth sites for 266 minutes compared to 251 minutes for control ewes ($P > 0.05$). Knight *et al.* (1989b) found that 41 Marshall Romney ewes grazed from their birth sites 46 minutes after birth, while 16 control Romneys did so after 27 minutes ($P > 0.05$). A general pattern emerged that ewes selected for rearing ability or lamb survival tended to remain on their birth sites for longer periods than control ewes, although none of these studies found a significant line effect. Keeping in mind that this type of behaviour facilitates the formation of a strong mother-offspring bond (Alexander, 1988), as well as the heritable nature of the trait, this change in behaviour may well be a correlated response to selection. In the study of Murphy *et al.* (1994), it was shown that the presence of the ewe at the birth site as such did not improve the dam-offspring bond, since similar advantages could be obtained by penning ewes for 6 hours on another site.

Covariances

Lambs that were heavier at birth were likely to have longer parturitions. This relationship was particularly strong at the maternal genetic level (0.49). Comparable figures in the literature were 0.71 for Dormers and 0.35 for SA Mutton Merinos. No other comparable results were found. On a phenotypic level, litter weight has previously been shown to be associated with length of parturition (Fahmy *et al.*, 1997; Cloete *et al.*, 1998*a*). On a phenotypic and environmental level, a heavier birth weight was shown to be associated with faster progress from birth to standing. This finding accorded with previous results in the literature (Owens *et al.*, 1985; Cloete *et al.*, 2002).

On a phenotypic level, it was found that lambs with longer births generally took longer to stand, while those that took long to stand were generally quicker to suckle. Corresponding correlations that were estimated in the study of Cloete *et al.* (2002*c*) were variable and inconsistent between breeds, and do not support or refute the correlations obtained in this study. At this stage, these trends can therefore not be considered as robust and generally applicable to sheep breeding ventures.

When assessed as a trait of the lamb, virtually no genetic covariation was detected between the interval from standing to apparently suckling and maternal cooperation score. This relationship was, however, particularly strong on the maternal permanent environmental level. This result is a further indication of the important role dams play as far as the facilitation of successful suckling by their offspring is concerned (Cloete and Scholtz, 1998).

In ewes, their was some evidence that maternal cooperation score was genetically related to the period that ewes remained on or near their birth site. No directly comparable results could be found in the literature. It is well established that the birth site is of utmost importance in the formation of a strong dam-offspring bond (Murphy *et al.*, 1994; Lindsay, 1996). Early neonatal lamb-ewe interactions are equally important in the formation of this bond (Lindsay *et al.*, 1990; Murphy and Lindsay, 1996). When assessed from this perspective, such a relationship seems to be reasonable.

Conclusions

The line differences and genetic trends obtained suggested that behaviour in the H line was adapted to enhance lamb survival, when patterns that were identified by Alexander (1988) as being of importance to lamb survival were considered. Previous studies on the same resource population also suggested advantages in favour of the H line in grooming behaviour of ewes (Cloete *et al.*, 2002*d*), and in recognition of lambs by their dams as well as neonatal lamb vigour (Cloete *et al.*, 2002*b*). Lamb survival, and in particular the survival of multiples, were correspondingly improved in the H line, for the period from 1993 to 1997 (Cloete and Scholtz, 1998) and from 1998 to 2001 (Cloete *et al.*, 2002*b*). This study thus contributes to a better understanding of factors associated with lamb survival, and possible mechanisms that are involved in the genetic improvement of rearing ability in pasture-fed ewes. It provides a basis for the further extension of contentions by several authors (see Lindsay *et al.*, 1990; Haughey, 1991; Le Neindre *et al.*, 1998) that the ultimate objective in pastoral systems should be the establishment of genotypes that are capable of rearing their offspring with minimal external inputs.

Acknowledgements

The inputs of Mr. JE Fourie regarding the maintenance and care of the breeding flock are appreciated. We are indebted to Messrs J.J.E. Cloete, J.M. ten Hoope, and P.J.A. Lombard as well as Miss Farida Martin for assistance with the observations. Other staff and students also played an important supportive role when employed temporarily. The experiment was supported financially by the South African Wool industry.

References

Alexander, G., 1988. What makes a good mother? *Proceedings of the Australian Society for Animal Production* 17: 25 - 41.

Alexander, G., Bradley, L.R., Stevens, D., 1993. Effect of age and parity on maternal behaviour in single-bearing Merino ewes. *Australian Journal of Experimental Agriculture* 33: 721 - 728.

Alexander, G., Stevens, D., Bradley, L.R., 1990*a*. Intensive observations during lambing in a goitre-affected flock, with special reference to behaviour of lambs. *Australian Journal of Experimental Agriculture* 30: 749 - 757.

Alexander, G., Stevens, D., Bradley, L.R., Barwick, S.A., 1990*b*. Maternal behaviour in Border Leicester, Glen Vale (Border Leicester derived) and Merino sheep. *Australian Journal of Experimental Agriculture* 30: 27 - 38.

Arnold, G.W., Morgan, P.D., 1975. Behaviour of the ewe and lamb at lambing and its relationship to lamb mortality. *Applied Animal Ethology* 2: 25 - 46.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J., 2002*a*. Responses of mature breeding ewes to selection for multiple rearing ability. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production* 30: 689 - 692. 18 - 23 August, Montpellier, France.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2001. Environmental and genetic aspects of survival and early liveweight in Western Australian sheep. *South African Journal of Animal Science* 31: 123 - 129.

Cloete, S.W.P., Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Scholtz, A.J., Cloete, J.J.E., 2002*b*. Mutual identification of ewes and lambs, as affected by divergent selection for ewe multple rearing ability. *Australian Journal of Experimental Agriculture*, submitted.

Cloete, S.W.P., Scholtz, A.J., Gilmour, A.R., Olivier, J.J., 2002*c*. Genetic and environmental effects on lambing and neonatal behaviour of Dormer and South African Mutton Merino lambs. *Livestock Production Science*, in press.

Cloete, S.W.P., Scholtz, A.J., Taljaard, R., 2002*d*. Lambing behaviour of Merino lines subjected to divergent selection for multiple rearing ability from the same base population. *South African Journal of Animal Science* 32: 57 - 65.

Cloete, S.W.P., Scholtz, A.J., ten Hoope, J.M., Lombard, P.J.A., Franken, M.C., 1998*a*. Ease of birth in relation to pelvic dimensions, litter weight and conformation in sheep. *Small Ruminant Research* 31: 51 - 60.

Cloete, S.W.P., Van Niekerk, F.E., Rust, J.M., 1998*b*. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *Sheep and Goat Research Journal* 14: 11 - 12.

Duguma, G.J., Schoeman, S.J., Cloete, S.W.P., Jordaan, G.F., 2002. Genetic parameter estimates of early growth traits in the Tygerhoek Merino flock. *South African Journal of Animal Science* 32: 66 - 75.

Fahmy, M.H., Robert, S., Castonguay, F., 1997. Ewe and lamb behaviour at parturition in prolific and non-prolific sheep. *Canadian Journal of Animal Science* 77: 9 - 15.

Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R., 1999. ASREML – Reference manuel. NSW Agriculture Biometric Bulletin No. 3. NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia.

Grommers, F.J., Elving, L., van Eldik, P., 1985. Parturition difficulties in sheep. *Animal Reproduction Science* 9: 365 - 374.

Haughey, K.G., 1983. Selective breeding for rearing ability as an aid to improving lamb survival. *Australian Veterinary Journal* 60: 361 - 363.

Haughey, K.G., 1991. Perinatal lamb mortality – its investigation, causes and control. *Journal of the South African Veterinary Association* 62: 78 - 91.

Hinch, G.N., 1997. Genetics of behaviour. In: Piper, L., Ruvinsky, A., (Eds.). The genetics of sheep. pp. 353 - 374. CAB International, Wallingford, Oxon, United Kingdom.

Knight, T.W., Lynch, P.R., Hall, D.R.H., Hockey, H-U.P., 1988. Identification of factors contributing to the improved lamb survival in Marshall Romney sheep. *New Zealand Journal of Agricultural Research* 31: 259 - 271.

Knight, T.W., Wilson, L.D., Lynch, P.R., Hockey, H-U.P., 1989. Slope and the choice of birth sites by ewes. *New Zealand Journal of Agricultural Research* 32: 193 - 198.

Kuchel, R.C., Lindsay, D.R., 1999. Maternal behaviour and the survival of lambs in superfine wool sheep. *Reproduction Fertility and Development* 11: 391 - 394.

Le Neindre, P., Murphy, P.M., Boissy, A., Purvis, I.W., Lindsay, D.R., Orgeur, P., Bouix, J., Bibé, B., 1998. Genetics of maternal ability in cattle and sheep. *Proceedings 6th World Congress of Genetics Applied to Livestock Production* 27: 23 - 30. 11 - 16 January 1998, Armidale, NSW, Australia.

Le Neindre, P., Poindron, P., 1990. Physiological and sensory basis of the mother young relationship in sheep. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.). Reproductive Physiology of Merino sheep. pp. 179 - 190. School of Agriculture, University of Western Australia.

Lindsay, D.R., 1996. Environment and reproductive behaviour. *Animal Reproduction Science* 42: 1 - 12.

Lindsay, D.R., Nowak, R., Putu, I.G., McNeil, D., 1990. Behavioural interactions between the ewe and her young at parturition. In: Oldham, C.M., Martin, G.B., Purvis, I.W., (Eds.). Reproductive Physiology of Merino sheep. pp. 191 - 205. School of Agriculture, University of Western Australia.

Mortimer, S.I., Atkins, K.D., 1995. Maternal effects influence growth traits in Merino sheep. *Proceedings of the Australian Association for Animal Breeding and Genetics* 11: 421 - 424.

Murphy, P.M., Lindsay, D.R., 1996. The contribution of the activity of the newborn Merino lamb to the attachment to its mother and subsequent survival. *Proceedings of the Australian Society of Animal Production* 21: 486.

Murphy, P.M., Lindsay, D.R., Purvis, I.W., 1994. The importance of the birthsite on the survival of Merino lambs. *Proceedings of the Australian Society of Animal Production* 20: 248 - 250.

Owens, J.L., Bindon, B.M., Edey, T.N., Piper, L.R., 1985. Behaviour at parturition and lamb survival of Booroola Merino sheep. *Livestock Production Science* 13: 359 - 372.

Ramirez, A., Quilles, A., Hevia, M., Sotillo, F., 1995. Observations on the birth of goats. *Canadian Journal of Animal Science* 75: 165 - 167.

Slee, J., Springbett, A., 1986. Early post-natal behaviour in lambs of ten breeds. *Applied Animal Behaviour Science* 15: 229 - 340.

Smith, G.M., 1977. Factors affecting birth weight, dystocia and preweaning survival in sheep. *Journal of Animal Science* 44: 745 - 753.

Szantar-Coddington, M.R., 1994. Genetic improvement of lamb survival in the Australian Merino: Behavioural and physiological indicators of maternal ability. M.Rur.Sci. thesis, University of New England, Armidale, Australia.

Verbyla, A.P., Cullis, B.R., Kenward, M.G., Welham, S.J., 1999. The analysis of designed experiments and longitudinal data using smoothing splines. *Journal of the Royal Statistical Society, Series C* 48: 269 - 311.

CHAPTER 13

GENETIC PARAMETERS AND TRENDS FOR BIRTH WEIGHT, BIRTH COAT SCORE AND WEANING WEIGHT IN MERINO LINES DIVERGENTLY SELECTED FOR MULTIPLE REARING ABILITY

S.W.P. Cloete[1,2], J.J. Olivier[3], J.B. van Wyk[1], G.J. Erasmus[1] and S.J. Schoeman[4]

[1]University of the Free State, PO Box 339,
Bloemfontein 9300, South Africa
[2]Elsenburg Agricultural Development Centre, Private Bag X1,
Elsenburg 7607, South Africa
[3]Irene Animal Improvement Institute, Private Bag X5013,
Stellenbosch 7599, South Africa
[4]University of Stellenbosch, Private Bag X1,
Matieland 7602, South Africa

Submitted at:
South African Journal of Animal Science

Genetic parameters and trends for birth weight, birth coat score and weaning weight in Merino lines divergently selected for ewe multiple rearing ability

S.W.P. Cloete[1,2], J.J. Olivier[3], J.B. van Wyk[1], G.J. Erasmus[1] and S.J. Schoeman[4]

[1]University of the Free State, PO Box 339, Bloemfontein 9300, South Africa
[2]Elsenburg Agricultural Development Centre, Private Bag X1, Elsenburg 7607, South Africa
[3]Irene Animal Improvement Institute, Private Bag X5013, Stellenbosch 7599, South Africa
[4]University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

Abstract: Data were recorded for birth weight, birth coat score and weaning weight of between 2018 and 4235 Merino lambs born over a 17-year interval from 1986 to 2002. The resource population was divergently selected from the same base population since 1986, either for (H line) or against (L line) maternal multiple rearing ability. Direct additive genetic variances – expressed as a ratio of the total phenotypic variance (h^2, direct heritability) – were estimated at 0.12 ± 0.03 for birth weight, 0.70 ± 0.05 for birth coat score and 0.13 ± 0.04 for weaning weight. Corresponding maternal genetic variance ratios (m^2) were estimated at 0.23 ± 0.04 for birth weight and 0.10 ± 0.04 for weaning weight. It was not significant for birth coat score. The maternal permanent environmental variance ratios (c^2) for the respective traits amounted to 0.08 ± 0.03 for birth weight, 0.04 ± 0.02 for birth coat score and 0.08 ± 0.03 for weaning weight. No consistent phenotypic or genetic differences in favour of either line were found for birth weight or birth coat score. Compared to L line lambs, phenotypic means for weaning weight were heavier ($P <$ 0.05) in favor of H line lambs from 1995. This trend was confirmed by divergence in yearly averaged direct breeding values in the H and L lines. Expressed as percentage of the overall phenotypic mean for weaning weight, genetic changes amounted to +0.23 % in the H line and –0.26 % in the L line. A corresponding maternal genetic trend amounting to –0.19 % of the overall phenotypic mean for weaning weight was found in the L line, while no maternal genetic change could be discerned in the H line.

Keywords: direct heritability, genetic trends, maternal heritability, parameter estimation, smoothing, splines

Introduction

Production in sheep reflects the genes that an animal has inherited from both its parents as well as a mixture of seasonal and husbandry factors peculiar to the environment an animal finds itself in (Lewis and Beatson, 1999). Maternal influences are evident early in the life of lambs, while it tends to disappear with an increase in age (Snyman *et al.*, 1995). Maternal influences can be derived from the genotype of the dam (maternal additive genetic effects) and those consistent between lambings but not genetic in origin, also referred to as maternal permanent environmental effects (Lewis and Beatson, 1999). The advent of sophisticated software enable analysts to fit extended models to data obtained from livestock breeding operations (Meyer, 1989).

This paper reports genetic and environmental influences on live weight at birth and weaning, as well as on birth coat score, in a Western Cape Merino resource flock. The flock has been subjected to divergent selection based on maternal multiple rearing ability (Cloete and Scholtz, 1998). Preliminary analysis indicated genetic divergence between the lines in several traits of economic importance (Cloete and Olivier, 1998). Birth coat score has so far not been assessed in a genetic analysis on South African Merinos. The trait is reported to be highly heritable (Ponzoni *et al.*, 1996), while it may also be related to the thermo-regulating ability of lambs (Alexander, 1964). In this sense, it may be of value as far as the prevention of lamb mortality is concerned (Purser and Karam, 1967; Obst and Evans, 1970). Since differential levels of lamb mortality were found between the two lines under study (Cloete and Scholtz, 1998; Cloete *et al.*, 2002), the resource population was considered to be extremely suitable for the study of genetic aspects of birth coat score.

Material and Methods

Two lines of Merino sheep were divergently selected from the same base population since 1986, using maternal ranking values for lambs reared per joining. Details of the selection procedure of replacements can be found in the literature (Cloete and Scholtz, 1998). In short, ewe and ram progeny of ewes rearing more than 1 lamb per joining (*i.e.* reared twins at least once) were preferred as replacements in the High (H) line. Replacements were preferably descended from ewes rearing fewer than 1 lamb per joining (i.e. barren or lost all lambs born at least once) in the Low (L) line. The H line was augmented by 28 ewes from a multiple ovulation and embryo transfer program, that were born during 1991 and 1992 (Cloete *et al.*, 1998). Progeny of mature ewes screened into the respective lines from other lines were also available since the 1996 lambing season. The screening process was detailed by Cloete *et al.* (2002).

Since their establishment, the two lines were maintained as a single flock. The flock was maintained at the Tygerhoek experimental farm at first (1986 to 1992). At the end of 1992 the animals were transferred to Elsenburg for studies on lambing behaviour (Cloete and Scholtz, 1998; Cloete *et al.*, 2002). During this period the lines were also kept in a single flock, except during joining in single sire groups to 4-5 rams. Further treatment of the experimental animals was fairly similar on both farms, except for the lambing season. At Tygerhoek, ewes were hand-mated in spring to lamb during autumn (March – April) of the following year. At Elsenburg, joining took place in summer, for lambing during the winter (June – July) of the same year. Dryland lucerne (*Medicago sativa*) and medic (*M. truncatula*) pastures were mostly utilised on both localities. Small grain fodder crops (mostly oats) were occasionally utilised in winter, while small grain crop residues and oat standing hay were seasonally available during spring and early summer. At Elsenburg, irrigated kikuyu (*Pennisetium clandestinum*) paddocks were utilised during joining and lambing (Cloete and Scholtz, 1998).

Lamb birth weight was recorded within 24 hours of birth, as described by Cloete *et al.* (2002). Birth coat score was scored on a linear scale, taking cognisance of halo hair and short, curly, woolly groups of fibres (Ponzoni *et al.*, 1996). The scale was at follows: 1 – Hairy; 2 – More hairy than woolly; 3 – Equally hairy and woolly; 4 – More woolly than hairy; 5 – Woolly. Half marks were given in cases where it was impossible to judge differences between adjacent classes. Weaning weight was recorded at an age of approximately 3.5 months, and corrected to an age of 100 days prior to analysis. The correction procedure described by Van der Merwe (1976) was applied. Environmental factors affecting the production traits included year of birth (1986 - 2002), gender (male or female), age of dam (2 to 7+ years) and birth type (single or pooled multiples). The identity of the sire and dam of lambs were known individually. This information enabled linkage back to the line they were born in.

The ASREML program (Gilmour *et al.*, 1999) were used for the analysis of the fixed effects, and also subsequently to estimate variance components in univariate analyses. The first analysis involved fitting various combinations of fixed effects to obtain an operational model. Random trends other than linear (splines) in year and age of dam means, as well as random deviations from linearity but not conforming to a smooth curve, were also fitted where applicable at this stage. Effects found to be significant ($P < 0.05$) in these preliminary analyses were included in subsequent analyses. Random terms were then added to the operational model, resulting in the following models for analyses (in matrix notation):

$$y = Xb + Z_1a + e \qquad (1)$$

$$y = Xb + Z_1a + Z_2\mathrm{c} + e \qquad (2)$$

$$y = Xb + Z_1a + Z_3m + e \qquad (3)$$

[Covariance (a,m)=0]

$$y = Xb + Z_1a + Z_3\mathrm{m} + Z_2c + e \qquad (4)$$

[Covariance (a,m)=0]

$$\mathrm{y} = Xb + Z_1a + Z_3m + e \qquad (5)$$

[Covariance $(a,m)=A\sigma_{am}$]

$$y = Xb + Z_3a + Z_3\mathrm{m} + Z_2c + e \qquad (6)$$

[Covariance $(a,m)= A\sigma_{am}$]

In these analyses, y was a vector of observations for birth weight, birth coat score or weaning weight, and b, a, m and c vectors of fixed effects, direct genetic variances, maternal genetic variances and maternal permanent environmental variances respectively. X, Z_1, Z_2 and Z_3 were the corresponding incidence matrices relating the respective effects to y, while e was the vector of residuals. A was the numerator relationship matrix, and σ_{am} the covariance between direct genetic and maternal genetic effects.

It was assumed that:

$V(a) = A\sigma^2_a$; $V(m) = A\sigma^2_m$; $V(c) = I\sigma^2_c$; $V(e) = I\sigma^2_e$,

with I being identity matrixes; σ^2_a, σ^2_m, σ^2_c and σ^2_e the direct genetic variance, maternal genetic variance and the maternal permanent environmental variance and environmental (residual) variance respectively. These analyses yielded estimates of genetic and permanent environmental variances. Ratios for direct additive genetic, maternal genetic as well as maternal permanent environmental variances were computed from these estimates. These variances were expressed relative to the total phenotypic variance. Log likelihood tests were conducted to determine the most suitable model for each trait in univariate analyses (Snyman *et al.*, 1996). Subsequently, 2-trait animal models were fitted, allowing the calculation of all relevant direct and maternal correlations between traits, together with the appropriate standard errors.

Direct and maternal breeding values for traits were obtained where applicable and averaged within birth years. Genetic trends derived in this way were inspected for divergence between lines, using standard errors obtained for the regression coefficients. Breeding values were obtained from analyses where selection line and its interactions with other traits were excluded from the operational model.

Results

Fixed effects

Overall, lamb birth weight was independent of selection line ($P > 0.10$; Table 1). Selection line interacted with both the linear component of the spline for birth year, as well as random deviations from linearity ($P < 0.05$). Phenotypic means for birth weight ranged between 2.9 kg and 3.9 kg for the period from 1986 to 1992 (Fig. 1). After 1992, means appeared to stabilise at a slightly higher level, between 3.8 kg and 4.3 kg. Birth weight phenotypic means generally did not differ between lines prior to 1993. There was a suggestion for H line lambs to be heavier at birth ($P < 0.10$) than L line lambs from 1993 to 1997. No subsequent line differences were found. Ram lambs and singles were respectively 6.7 and 27.8 % heavier ($P < 0.01$) than ewes and multiples. Lamb birth weight increased curvi-linearly ($P < 0.01$) with an increase in dam age, reaching a maximum in 4 to 6 year-old dams.

Table 1. Least squares means (± *SE*) for birth weight, birth coat score and weaning weight in lambs of the H and L lines

Fixed effects	**Birth weight (kg)**	**Birth coat score (n)**	**Weaning weight (kg)**
Number of observations	4235	2018	3116
Overall mean	3.85 ± 0.08	3.22 ± 0.10	21.8 ± 0.5
Birth year	**	NS	**
Selection line	NS	NS	*
H line	3.90 ± 0.09	3.20 ± 0.12	22.3 ± 0.5
L Line	3.80 ± 0.09	3.24 ± 0.14	21.3 ± 0.5
Birth type	**	NS	**
Single	4.32 ± 0.08	3.18 ± 0.10	23.6 ± 0.5
Multiple	3.38 ± 0.08	3.26 ± 0.10	20.0 ± 0.4
Gender	**	*	*
Ram	3.98 ± 0.08	3.33 ± 0.10	22.3 ± 0.5
Ewe	3.73 ± 0.08	3.11 ± 0.10	21.3 ± 0.5
Age of dam (years)	**	NS	*
2	3.47 ± 0.09	3.33 ± 0.10	20.6 ± 0.5
3	3.72 ± 0.08	3.27 ± 0.10	21.5 ± 0.5
4	3.85 ± 0.08	3.23 ± 0.10	21.8 ± 0.5
5	3.90 ± 0.08	3.21 ± 0.10	21.7 ± 0.5
6	3.89 ± 0.08	3.22 ± 0.09	21.4 ± 0.5
7	3.80 ± 0.09	3.25 ± 0.09	20.9 ± 0.5

NS – Not significant ($P > 0.10$); * Significant ($P < 0.05$); ** Significant ($P < 0.01$);

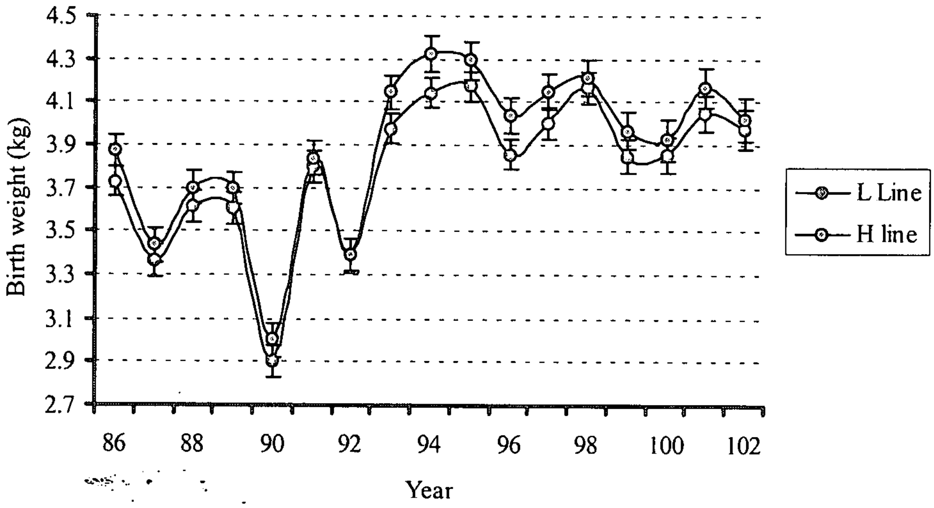


Fig. 1. Phenotypic trend for birth weight in the H and L lines for a 17-year period from 1986 to 2002. Vertical bars around the means denote standard errors.

Birth coat score was generally independent of the known sources of variation, except for gender (Table 1). Rams had slightly woollier coats than ewes ($P < 0.05$). Overall, H line lambs tended ($P < 0.10$) to be heavier at weaning than L line contemporaries. Selection line once more interacted with both the linear component of the spline for birth year, as well as random deviations from linearity ($P < 0.05$). Phenotypic means for weaning weight were generally not different at the commencement of the trial (Fig. 2), but consistent line differences in favour of the H line were observed after 1994. Selection line interacted with birth type for lamb weaning weight. In singles, H line lambs were 6.9 % heavier than L line contemporaries (24.4 ± 0.5 kg vs. 22.9 ± 0.5 kg respectively). The corresponding difference in multiples were not significant (20.1 ± 0:5 kg vs. 19.8 ± 0.5 kg respectively). Overall, ram lambs and singles were respectively 4.7 and 18.0 % heavier ($P < 0.05$) than ewes and multiples. Lamb weaning weight increased curvilinearly ($P < 0.01$) with an increase in dam age, reaching a maximum in 3 to 5 year-old dams.

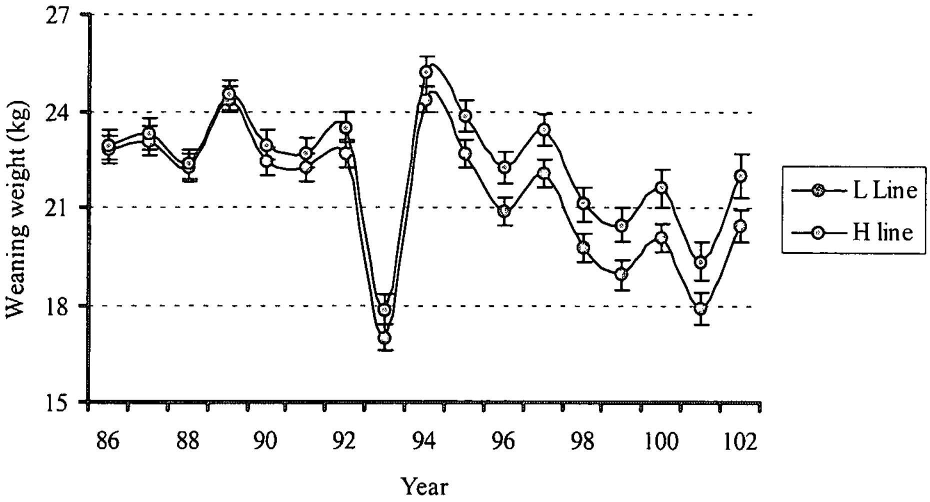


Fig. 2. Phenotypic trend for weaning weight in the H and L lines for a 17-year period from 1986 to 2002. Vertical bars around the means denote standard errors.

Random effects

The statistical model of choice included two or more random terms for all three traits (Table 2).

Table 2. Log likelihood ratios for birth weight, birth coat score and weaning weight in Merino lambs of the H and L lines under seven different models of analysis. The "best' models are in bold, italic figures.

Correlation	Birth weight	Birth coat score	Weaning weight
Fixed effects only	-580.592	-466.554	-5699.02
+ h^2	-388.743	-215.657	-5638.95
+ $h^2 + c^2$	-228.475	***-211.319***	-5605.51
+ $h^2 + m^2$	-203.669	-212.840	-5604.32
+ $h^2 + c^2 + m^2$	***-199.426***	-211.318	***-5600.59***
+ $h^2 + m^2 + r_{am}$	-202.319	-212.816	-5603.35
+ $h^2 + c^2 + m^2 + r_{am}$	-198.449	-211.270	-5599.40

Direct additive, maternal additive and maternal permanent environmental variances were included for birth weight and weaning weight, while only direct additive and maternal permanent environmental variances were included for birth coat score. Parameter estimates for birth weight were 0.12 for h^2, 0.23 for m^2 and 0.08 for c^2 (Table 3). Birth coat score was highly heritable (0.70), with a small c^2 component of 0.04. Direct heritability was estimated at 0.13 for weaning weight, with a m^2 estimate of 0.10 and a c^2 estimate of 0.08.

Table 3. Variance components and ratio estimates of the direct genetic (h^2), maternal genetic (m^2) and maternal permanent environmental (PE – c^2_{PE}) variance ratios (± *SE*) for the respective behavioural traits assessed in Merino lambs of the H and L lines

Component or ratio	Birth weight	Birth coat score	Weaning weight
Variance components			
Residual (σ^2_e)	0.2742	0.1530	9.7858
Direct additive (σ^2_a)	0.0582	0.4217	1.9006
Maternal additive (σ^2_m)	0.1112	-	1.4002
Maternal PE (σ^2_c)	0.0403	0.0269	1.1710
Total phenotype (σ^2_p)	0.4839	0.6016	14.2586
Variance ratios			
h^2	0.12 ± 0.03	0.70 ± 0.05	0.13 ± 0.04
m^2	0.23 ± 0.04	-	0.10 ± 0.04
c^2_{PE}	0.08 ± 0.03	0.04 ± 0.02	0.08 ± 0.03

- Effect not significant according to log likelihood ratio

Correlations between birth weight and birthcoat score were generally low, variable and smaller than double the corresponding standard errors (Table 4). Inspection of the correlations between weaning weight and birth coat score led to similar conclusions.

Birth weight and weaning weight were highly correlated on the direct and maternal genetic levels. Phenotypic and environmental correlations were lower, but still significant ($P < 0.05$).

Table 4. Direct additive (r_g), maternal additive (r_m), maternal permanent environmental (r_c), environmental (r_e) and phenotypic (r_p) correlations among traits recorded in H and L line lambs

Correlation	**Birth weight X birth coat score**	**Birth weight X weaning weight**	**Birth coat score X Weaning weight**
Direct additive (r_g)	-0.15 ± 0.14	0.63 ± 0.14	0.02± 0.14
Maternal additive (r_m)	-	0.66 ± 0.13	-
Maternal PE (r_c)	-0.11 ± 0.25	0.14 ± 0.26	-0.27 ± 0.27
Environmental (r_e)	0.01 ± 0.07	0.21 ± 0.03	-0.06 ± 0.07
Phenotypic (r_p)	-0.05 ± 0.03	0.32 ± 0.02	-0.04 ± 0.03

- Effect not significant according to log likelihood ratio

Genetic trends

Genetic trends derived from averaged annual breeding values for the H and L lines were divergent ($P < 0.05$) and symmetric (Fig. 3). The genetic trend in the H line was positive, and amounted to 0.23 % of the overall phenotypic mean annually (b ± SE = 0.057 ± 0.005; $R^2 = 0.73$). The corresponding downward trend in the L line amounted to 0.26 % of the overall phenotypic mean annually (b ± SE = -0.063 ± 0.009; $R^2 = 0.11$).

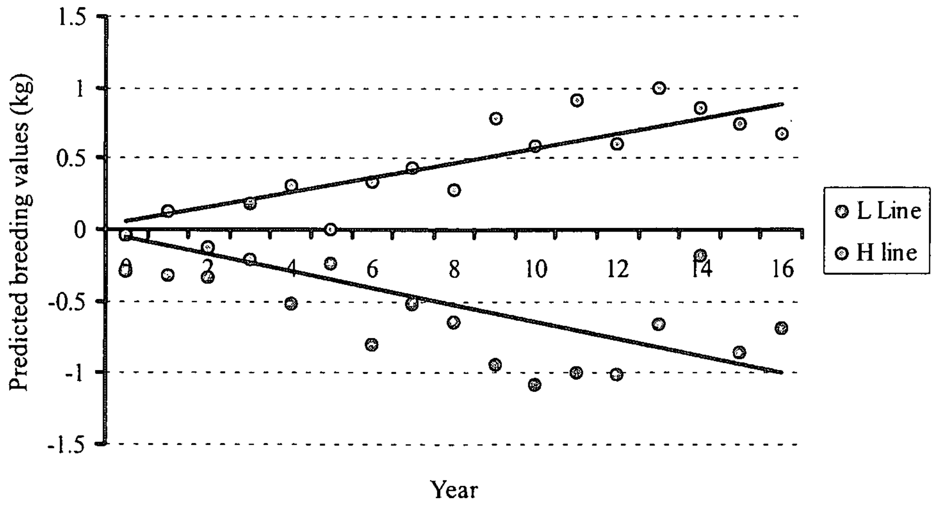


Fig. 3. Averaged direct additive breeding values for weaning weight in the H and L lines over a 17-year period. Both graphs were forced through the origin.

No significant maternal genetic trend was evident in the H line (Fig. 4). Maternal breeding values for weaning weight in the L line decreased annually at 0.19 % of the overall environmental mean for weaning weight (b ± SE = -0.046 ± 0.004; R^2 = 0.34). Trends for the respective selection lines were divergent ($P < 0.05$), but asymmetric in this instance.

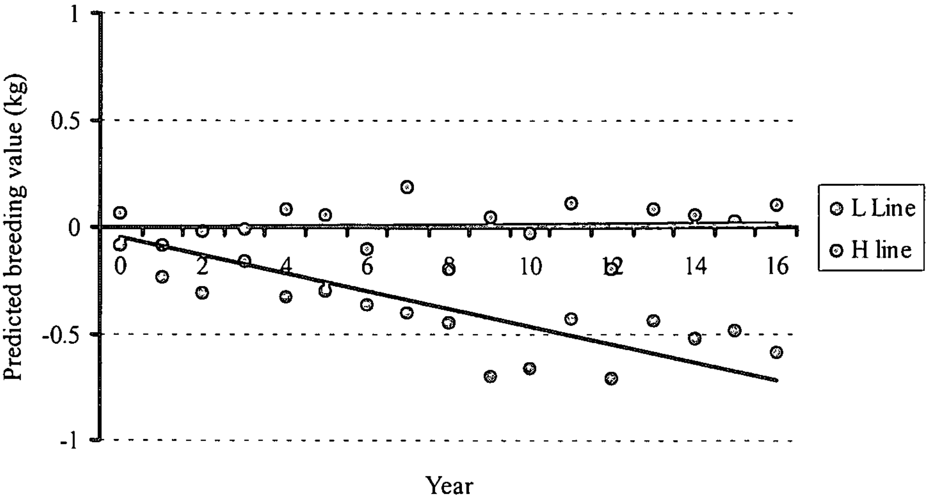


Fig. 4. Averaged maternal additive breeding values for weaning weight in the H and L lines over a 17-year period. Both graphs were forced through the origin.

Discussion

Fixed effects

Although selection line was fitted as a fixed effect in the analyses that were conducted, this effect is rather discussed with the random effects. This approach was chosen since it was reasoned that the observed line differences were in response to the selection pressure applied to the respective lines. The effects of gender, birth type and dam age on birth weight and weaning weight were consistent with those obtained from comparable data sets in the literature, and not worthy of discussion. It is noteworthy that birth weight in the experiment was generally lower initially, when the resource population was maintained at the Tygerhoek experimental farm (see Cloete and Scholtz, 1998 for general background). Generally higher birth weights were recorded in subsequent years, when the population was maintained at Elsenburg. This result is possibly related to the season of lambing used at the respective experimental sites (during autumn at Tygerhoek and during winter at Elsenburg). Winter lambing ewes were previously found to give birth to heavier lambs under Mediterranean conditions than autumn lambing ewes (Cloete *et al.*, 1994).

Birth coat score was independent of the fixed effects included in the analysis, with the exception of gender. Previous results indicated that birth coat score was not largely influenced by non-genetic sources of variation (Davis, 1987*b*; Ponzoni *et al.*, 1996). Ewes also generally had slightly coarser birth coats than rams in these studies, as was also found in the present study.

Random effects and genetic trends

Literature results from animal model analyses will generally be considered as far as genetic parameters for birth weight and for weaning weight are concerned. In the case of birth weight, genetic parameters obtained from a wide range of sheep breeds ranged from 0.04 to 0.42 for h^2, 0.09 to 0.65 for m^2 and from 0.08 to 0.37 for c^2 (see summary by Duguma *et al.*, 2002). Our estimates of 0.12 for h^2, 0.23 for m^2 and 0.08 for c^2 accords very well with the range of literature values cited above. Genetic parameters for birth weight are relatively scarce for Merino lambs. In this breed, previous estimates of h^2 ranged from 0.18 to 0.23 (Mortimer and Atkins, 1995; Cloete *et al.*, 2001; Duguma *et al.*, 2002). Corresponding estimates of m^2 ranged from 0.14 to 0.25, and those for c^2 from 0.08 to 0.12. Estimates from the present study accords with these findings. The exception was h^2, which tended to be slightly lower than the estimates cited.

Although H line lambs were phenotypically somewhat heavier ($P < 0.05$) at birth than L line contemporaries for a period during the mid-1990's (see also Cloete and Scholtz, 1998 in this regard), this effect was not consistent. No conclusive line differences were found at the beginning of the experiment and during the latter part of the experiment. Genetic trends derived from direct and maternal breeding values for birth weight similarly did not reflect marked correlated changes in birth weight to divergent selection for maternal multiple rearing ability. Unwanted changes in birth weight leading to either dystocia (as a result of heavier lambs), or poor lamb vigour and ill-thrift (typical of low live weight lambs) thus seems unlikely.

At 0.70, the obtained heritability estimate of birth coat score was very high. Literature results were in good agreement, although recent animal model estimates could not be found. Previous estimates ranged from 0.55 to 0.80 (Morley, 1955; Gregory, 1982; Davis, 1987*b*; Ponzoni *et al.*, 1996). It is evident that fast rates of genetic change in birth coat score are feasible, should it be desired. It was demonstrated in a climate chamber that lambs with hairy birth coats were able to conserve heat more readily than lambs with woolly birth coats (Alexander, 1964). Little evidence of improved survival in hairy lambs were obtained under paddock conditions (Davies, 1964; Mullaney, 1966; Ponzoni *et al.*, 1996). Based on results obtained in a particular year when the weather was particularly unfavourable (Mullaney, 1966), it was contended that an advantage in survival would only become noticeable under extremely adverse conditions. This contention was supported by results published subsequently (Purser and Karam, 1967; Obst and Evans, 1970). In the present study, lambing took place during winter. Cold spells with windy and rainy weather are common in the Mediterranean winter. It was demonstrated that lambs in the H line survived markedly better ($P < 0.05$) than their L line contemporaries during the periods from 1993 to 1997 (Cloete and Scholtz, 1998) and from 1998 to 2001 (Cloete *et al.*, 2002). The line difference in survival was particularly marked in multiple lambs (Cloete and Scholtz, 1998; Cloete *et al.*, 2002). Despite these differences, birth coat score were similar for the lines (see Table 1), suggesting no marked correlated change. The results from this study therefore supports literature findings that birth coat score are not highly related to lamb survival (Ponzoni *et al.*, 1996). Further studies on birth coat score showed that it was also of little consequence as far as hogget fleece traits (Olivier, 1996; Ponzoni *et al.*, 1996) or ewe reproduction (Ponzoni *et al.*, 1996) were concerned.

No line difference in weaning weight was observed in multiple lambs, while H line lambs were heavier ($P < 0.05$) at this stage than L line contemporaries. This interaction can be readily explained by the differential mortality rates in multiple lambs belonging to the respective lines (Cloete and Scholtz, 1998; Cloete *et al.*, 2002). Twin and triplet lambs in the H line were much more likely to be reared as multiples than those born in the L line.

Results summarised from the literature for weaning weight indicated h^2 estimates of 0.09 to 0.50, m^2 estimates of 0.02 to 0.48 and c^2 estimates of 0.06 to 0.20 (Duguma *et al.*, 2002). Respective estimates of 0.13, 0.10 and 0.08 in the present study are well within these ranges. Other studies on Merinos found estimates of h^2 ranging from 0.14 to 0.30, estimates of m^2 ranging from 0.05 to 0.23 and estimates of c^2 ranging from 0.02 to 0.10 (Swan and Hickson, 1994; Hickson *et al.*, 1995; Mortimer and Atkins, 1995; Snyman *et al.*, 1996; Cloete *et al.*, 2001; Duguma *et al.*, 2002). With the exception of h^2 (which was on the lower limit of these estimates) the present results closely resembled those cited above for Merinos.

Positive direct and maternal genetic correlations between birth weight and weaning weight are consistent with those reported by Duguma *et al.* (2002). Davis (1987*a*) correspondingly found a positive realised genetic correlation of 0.73 between birth weight and weaning weight. Correlations of birth coat score with birth weight and weaning weight were generally low, and not significant ($P > 0.05$). No comparable correlations were found in the literature.

Phenotypic means suggested that H line lambs were heavier at weaning than L line contemporaries at weaning towards the end of the experiment (Fig. 2). It was evident that genetic trends diverged for the lines when direct additive breeding values were derived (Fig. 3), suggesting than a correlated response in lamb weaning weight are likely when selection is based on ewe multiple rearing ability. This result is consistent with preliminary findings obtained earlier on the same resource population (Cloete and Olivier, 1998) as far as direct breeding values were concerned. It is also supported by findings in the Trangie weaning weight selection experiment. Selection for lamb weaning weight resulted in positive realised genetic correlations for components of reproduction (Davis, 1987*a*). These correlations were particularly high for lamb survival, ewe rearing ability and number of lambs weaned per ewe joined. These traits are closely related to the selection objective strived for in the present study. Genetic parameters derived for weaning weight, number of lambs weaned and total weight of lamb weaned in three South African Merino studs also supports the present results (Olivier *et al.*, 2001). When maternal breeding values were considered, it was evident that the maternal ability of L line animals for weaning weight declined with time. No conclusive trend was discernable in the H line. No comparable results on this topic were found in the literature at our disposal.

Conclusions

No marked correlated responses in birth weight and birth coat score resulting from divergent selection for multiple rearing ability were observed. Selection, however, resulted in a correlated change in lamb weaning weight, a trait which indicate the quality of the lamb(s) produced (Olivier, 1999). The study supports research findings that no antagonism exists between the ability of ewes to rear lambs and the quality of the lambs produced (Olivier *et al.*, 2001).

Acknowledgements

We wish to thank all those responsible for the maintenance and recording of the experimental animals (Miss E. du Toit at Tygerhoek as well as Mr J.E. Fourie and Miss A.J. Scholtz at Elsenburg). The maintenance of the animals was partially enabled by a grant from the SA Wool Industry.

References

Alexander, G., 1964. Lamb survival: physiological considerations. *Proceedings of the Australian Society for Animal Production* 5: 113 - 122.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2001. Environmental and genetic aspects of survival an early liveweight in Western Australian sheep. *South African Journal of Animal Science* 31: 123 - 129.

Cloete, S.W.P., Olivier, J.J., 1998. Direct and correlated responses to selection for multiple rearing ability in South African Merinos. *Proceedings of the Annual Congress of the South African Society for Animal Science* 36: 65 - 68.

Cloete, S.W.P., Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Scholtz, A.J., Cloete J.J.E., 2002. Mutual identification of ewes and lambs, as affected by divergent selection for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* (submitted).

Cloete, S.W.P., Scholtz, A.J., Franck, F., Durand, A., 1994. Diereproduksie- en weidingsparameters vir herfs- en winterlamseisoene in die Swartland. (In Afrikaans). *Elsenburg Journal* 1994: 1 - 6.

Cloete, S.W.P., Van Niekerk, F.E., Rust, J.M., 1998. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *Sheep and Goat Research Journal* 14: 11 - 12.

Davies, H.L., 1964. Lamb losses in south-western Australia. *Proceedings of the Australian Society for Animal Production* 5: 107 - 112.

Davis, G.P., 1987*a*. Direct and correlated responses to selection on weaning weight in Merinos. *Proceedings of the Australian Association for Animal Breeding and Genetics* 7: 83 - 86.

Davis, G.P., 1987*b*. Genetic relationships between lamb growth and lifetime productivity in Merino sheep. Ph.D. dissertation, University of New England, Australia.

Duguma, G.J., Schoeman, S.J., Cloete, S.W.P., Jordaan, G.F., 2002. Genetic parameter estimates of early growth traits in the Tygerhoek Merino flock. *South African Journal of Animal Science* 32: 66 - 75.

Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R., 1999. ASREML – Reference manual. NSW Agriculture Biometric Bulletin No. 3. NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia.

Gregory, I.P., 1982. Genetic studies of South Australian Merino sheep. III. Heritabilities of various wool and body traits. *Australian Journal of Agricultural Research* 33: 355 - 362.

Hickson, J.D., Swan, A.A., Kinghorn, B.P., Piper, L.R., 1995. Maternal effects at different ages in Merino sheep. *Proceedings of the Australian Association for Animal Breeding and Genetics* 11: 416 - 420.

Lewis, R.M., Beatson, P.R., 1999. Choosing maternal effect models to estimate (co)variances for live and fleece weight in New Zealand Coopworth sheep. *Livestock Production Science* 58: 137 - 150.

Meyer, K., 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative free algorithm. *Genetics, Selection and Evolution* 21: 317 - 340.

Morley, F.H.W., 1955. Selection for economic characters in Australian Merino sheep. V. Further estimates of phenotypic and genetic parameters. *Australian Journal of Agricultural Research* 6: 77 - 90.

Mortimer, S.I., Atkins, K.D., 1995. Maternal effects influence growth traits in Merino sheep. *Proceedings of the Australian Association for Animal Breeding and Genetics* 11: 421 - 424.

Mullaney, P.D., 1966. The relation of birth coat and lamb survival. *Australian Journal of Experimental Agriculture and Animal Husbandry* 6: 84 - 87.

Obst, J.M., Evans, J.V., 1970. Genotype-environment interactions in lamb survival with particular reference to birth coat and haemoglobin type. *Proceedings of the Australian Society for Animal Production* 8: 149 - 153.

Olivier, J.J., 1996. Bydrae van voorkomseienskappe ter bereiking van seleksiedoelwitte. . (In Afrikaans). In: Cloete, S.W.P & Coetzee, J. (Reds.). Seleksie-doelwitte vir Merinos, Aanbevelings voortspruited uit 'n simposium op initiatief van die Merino-Ontwikkelingskomitee van Streek I. pp. 43 - 55

Olivier, J.J., 1999. The South African Merino performance testing scheme. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 13: 119 - 124.

Olivier, W. J., Snyman, M. A., Olivier, J. J., Van Wyk, J. B., Erasmus, G. J., 2001. Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep. *South African Journal of Animal Science* 31: 115 – 121.

Ponzoni, R.W., Grimson, R.J., Jaensch, K.S., Smith, D.H., Hynd, P.I., 1996. Birth coat: is it worth taking it into consideration in Merino sheep genetic improvement programs? Demands of wool and wool growers beyond 2000. *SARDI Research Report Series*, No 11. pp. 44 - 60.

Purser, A.F., Karam, H.A., 1967. Lamb survival, growth and fleece production in relation to birth coat type among Welsh Mountain sheep. *Animal Production* 9: 75 - 85.

Snyman, M.A., Erasmus, G.J., van Wyk, J.B., 1995. Direct and maternal (co)variance components and heritability estimates for body weight at different ages and fleece traits in Afrino sheep. *Livestock Production Science* 44: 229 - 235.

Snyman, M.A., Olivier, J.J., Olivier, W.J., 1996. Variance components and genetic parameters for body weight and fleece traits of Merino sheep in an arid environment. *South African Journal of Animal Science* 26: 11 - 14.

Swan, A.A., Hickson, J.D., 1994. Maternal effects in Australian Merinos. *Proceedings of the 5th World Congress on Genetics Applied to Livestock Production* 18: 143 - 146.

Van der Merwe, C.A., 1976. 'n Studie van kuddestatistieke, teeltstruktuur, genetiese en fenotipiese aspekte van die Elsenburg Dormerkudde (In Afrikaans). Ph.D.-thesis, University of Stellenbosch, South-Africa.

CHAPTER 14

GENETIC AND PHENOTYPIC TRENDS AND PARAMETERS IN REPRODUCTION, GREASY FLEECE WEIGHT AND LIVE WEIGHT IN MERINO LINES DIVERGENTLY SELECTED FOR MULTIPLE REARING ABILITY

S.W.P. Cloete[1,2], A.R. Gilmour[3], J.J. Olivier[4], J.B. van Wyk[1]

[1]University of the Free State, PO Box 339,
Bloemfontein 9300, South Africa
[2]Elsenburg Agricultural Development Centre, Private Bag X1,
Elsenburg 7607, South Africa
[3]NSW Agriculture, Orange Agricultural Institute, Forest Road,
Orange 2800, NSW, Australia
[4]Irene Animal Improvement Institute, Private Bag X5013,
Stellenbosch 7599, South Africa

Submitted at:

Australian Journal of Experimental Agriculture

Genetic and phenotypic trends and parameters in reproduction, greasy fleece weight and live weight in Merino lines divergently selected for multiple rearing ability

S.W.P. Cloete [1,2], A.R. Gilmour[3], J.J.Olivier[4] and J.B. van Wyk[1]

[1]University of the Free State, PO Box 339, Bloemfontein 9300, South Africa
[2]Elsenburg Agricultural Centre, Private Bag X1, Elsenburg 7607, South Africa
[3]NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia
[4]ARC Animal Improvement Institute, Private Bag X5013, Stellenbosch 7599, South Africa

Abstract: Data were recorded for annual reproduction, ewe greasy fleece weight and pre-joining live weight of approximately 2900 lamb production records of 809 Merino ewes over the period from 1987 to 2002. The resource population has been divergently selected from the same base since 1986, either for (H line) or against (L line) maternal multiple rearing ability. Trends in production with an increase in age from 2 to 7+ years were consistent with corresponding trends in the literature. Phenotypic trends indicated divergence in reproduction (number of lambs born and weaned per ewe, weight of lamb weaned per ewe) between the H and L lines. The direct additive variance ratio ($h^2 \pm SE$) for day of lambing (relative to the date of the first birth in a season) was 0.08 ± 0.02. Estimates of h^2 for reproduction traits were 0.10 ± 0.02 for number of lambs born per ewe, 0.04 ± 0.02 for number of lambs weaned per ewe, 0.04 ± 0.02 for uncorrected weight of lamb weaned per ewe and 0.04 ± 0.02 for corrected (for gender and birth year) weight of lamb weaned per ewe. Corresponding h^2 estimates for annual production were 0.53 ± 0.06 for greasy fleece weight and 0.49 ± 0.06 for ewe live weight at joining. Service sire only exerted a significant ($P < 0.05$) effect on day of lambing, but it accounted for merely 2 % of the overall phenotypic variation. Ewe permanent environment variance ratios (c^2_{ewe}) for the reproduction traits were 0.07± 0.03 for number of lambs born per ewe, 0.11 ± 0.03 for number of lambs weaned per ewe, 0.11 ± 0.03 for uncorrected weight of lamb weaned per ewe and 0.12 ± 0.03 for corrected weight of lamb weaned per ewe. Corresponding c^2_{ewe} estimates for annual production traits were 0.16 ± 0.05 for greasy fleece weight and 0.25 ± 0.06 for ewe joining weight. Genetic and ewe permanent environmental correlations between measures of reproduction exceeded 0.7. Genetic correlations of reproduction traits with greasy fleece weight were low and generally negative. Genetic correlations of reproduction traits with ewe joining weight were positive and particularly high for weight of lamb weaned per ewe. Permanent environmental correlations of reproduction traits with greasy fleece weight and joining weight were generally negative. Genetic trends for the H and L lines (derived from averaged direct breeding values within birth years) were divergent ($P < 0.01$) for all reproduction traits. When expressed as percentage of the overall least squares means of the respective traits, breeding values in the H line increased annually with 1.3 % per year for lambs born per ewe, 1.5 % per year for lambs weaned per ewe and by 1.8 % per year for corrected weight of lamb weaned per ewe. Corresponding trends in the L line were respectively –0.6 %, –1.0 % and –1.3 % per year. In the case of annual ewe joining weight, breeding values in the H line tended to increase at a rate of 0.06 % of the overall mean per year. The concomitant genetic change in the L line amounted to –0.17 % per year. Substantial genetic progress in annual lamb output was attainable, despite relatively small h^2 estimates.

Keywords: Ewe productivity, lamb output, live weight, repeated records, weight of lamb weaned

Introduction

In sheep production systems, an increase in the efficacy of production per animal can be achieved by a combination of an enhanced net reproduction rate, a shorter production cycle, and optimum fibre production (Olivier, 1999). In the latter review, net reproduction was defined as total weight of lamb weaned per breeding ewe. This trait depends on the number (quantity) of lambs weaned, as well as the weight of the lamb(s), which reflects the quality of the lambs that were weaned.

Studies on lamb output of ewes, including total weight of lamb weaned per parity, are scarce in the literature. Most of the available heritability estimates for reproduction traits in general, and noted in the comprehensive review of Fogarty (1995) were derived from outdated paternal halfsib or parent offspring regression methods. Recent genetic correlations of total weight of lamb weaned with other traits of economic importance are also scarce in the scientific literature. Most estimates were obtained when this trait was expressed as overall weight of lamb weaned over a number of seasons, and related to live weight or wool traits obtained at hogget age (Snyman *et al.*, 1998*a*; Olivier *et al.*, 2001; Cloete *et al.*, 2002*c*). Information on such (co)variances is a prerequisite for making informed decisions about selection strategies. Realised responses on selection experiments with net reproduction (as defined above) as objective are scarce in sheep breeding, although responses similar to that achieved in normally distributed traits were observed in component traits (Purvis and Hillard, 1997). Genetic improvement of reproduction is challenging, as expression is sex-limited, computational difficulties owing to the discrete nature of data are encountered, while low levels of genetic variation are frequently observed (Purvis and Hillard, 1997). High coefficients of variation, however, allowed substantial gains based on simple phenotypic selection. Weight of lamb weaned was the objective strived for in the study of Ercanbrack and Knight (1998), where substantial genetic progress has been described. Number of lambs and weight of lamb weaned were also shown to be different in Merino lines divergently selected for ewe multiple rearing ability over a 7 to 12 year period (Cloete and Scholtz, 1998).

The objective of this study was to obtain parameter estimates for number of lambs born and weaned as well as weight of lamb weaned in a resource population that were divergently selected for maternal multiple rearing ability from the same base population (Cloete and Scholtz, 1998). The effect of correcting individual weaning weight for the effects of gender and year of birth prior to the calculation of weight of lamb weaned was studied simultaneously. Estimates of genetic, ewe permanent environmental, phenotypic and environmental correlations of lamb production with live weight at joining and annual ewe greasy fleece weight traits were also calculated. Genetic trends were obtained from the divergently selected population, to complement preliminary results published by Cloete and Olivier (1998).

Materials and Methods

Animals and location

Two lines of Merino sheep were divergently selected from the same base population since 1986, using maternal ranking values for lambs reared per joining (Turner, 1977). Details of the procedure for the selection of replacements can be found in the literature (Cloete and Scholtz, 1998). In short, ewe and ram progeny of ewes rearing more than 1 lamb per joining (*i.e.* reared twins at least once) were preferred as replacements in the High (H) line. Replacements in the Low (L) line were preferably descended from ewes rearing fewer than 1 lamb per joining (*i.e.* barren or lost all lambs born at least once). The H line was augmented by 28 ewes from a multiple ovulation and embryo transfer program, that were born during 1991 and 1992 (Cloete *et al.*, 1998*b*). Progeny of mature ewes screened into the respective lines from other lines were also included from the 1996 lambing season. The screening process was detailed by Cloete *et al.* (2002*e*).

Since their establishment, the two lines were maintained as a single flock. The flock was maintained at the Tygerhoek experimental farm at first (1986 to 1992). At the end of 1992 the animals were transferred to Elsenburg for studies on lambing behaviour (Cloete and Scholtz, 1998; Cloete *et al.*, 2002*e*). During this period the lines were also kept in a single flock, except during joining in single sire groups to 4-5 rams. Management of the experimental animals was fairly similar on both farms, except during the lambing season. At Tygerhoek, ewes were hand-mated in spring to lamb during autumn (March – April) of the following year. At Elsenburg, joining took place in summer, for lambing during the winter (June – July) of the same year. Dryland lucerne (*Medicago sativa*) and medic (*M. truncatula*) pastures were predominantly used at both localities. Small grain fodder crops (mostly oats) were occasionally grazed in winter, while small grain crop residues and oat standing hay were seasonally available during spring and early summer. At Elsenburg, irrigated kikuyu (*Pennisetium clandestinum*) paddocks were utilised during joining and lambing (Cloete and Scholtz, 1998). The shearing time also differed between locations. At Tygerhoek, ewes were shorn annually during August-September, prior to joining. At Elsenburg ewes were shorn prior to lambing each year, and ewes thus lambed with fewer than six weeks of wool growth.

Recordings

Weaning weight of individual lambs was recorded at an age of approximately 3.5 months, and corrected for age prior to analysis. Individual weaning weights were then corrected for the effects of gender and birth year, and used to calculate total weight of lamb weaned for a specific parity in individual ewes. Both corrected and uncorrected weaning weights were used to calculate total weight of lamb weaned per ewe per year. Complete reproduction records were available for individual parities. Data used in the analyses were the day of lambing within a lambing season (relative to the date of the first birth in that particular season), total number of lambs born and total number of lambs weaned. Day of lambing was only recorded for the 10 - year period from 1993 to 2002, but the other reproduction traits were recorded from 1987 to 2002. Number of lambs born, number of lambs weaned and total weight of lamb weaned were initially expressed on a per ewe joined basis. In later years stock theft and attacks by stray dogs became such a problem that these data were rather expressed relative to ewes present at lambing. Ewe live weight was recorded annually at joining, and greasy fleece weight was recorded annually at shearing. It was not attempted to adjust live weight and wool data for reproductive status. Reproduction in a given year would not directly affect the previous joining weight, while it is known that lactation has a major impact on wool weight (Charlick and Arnold, 1990). In pre-lamb shorn ewes, wool weight is thus more likely to be affected by reproduction in the previous season. Since wool growth was mostly measured on a year basis, data were not corrected for the actual number of days in the growth period. The fleece weights obtained for 1993 were lower because they related to a shortened production period arising from the switch from an August - September shearing to a May - June shearing. The traits that were assessed thus included: day of lambing, number of lambs born and weaned per ewe per parity, uncorrected and corrected total weight of lamb weaned per ewe per parity, ewe greasy fleece weight and ewe live weight at joining. The identity of the sire and dam of ewes were known individually, enabling the linkage of pedigree records back to previous generations.

Statistical analysis

The ASREML program (Gilmour *et al.*, 1999) was used for the estimation of the fixed effects, and also subsequently to derive variance components for the respective reproduction and production traits in univariate analyses. The analysis of discrete data such as number of lambs born and weaned with parametric methods used in the present study is not optimal, as was outlined by Purvis and Hillard (1997). The availability of suitable software, and the close approximation of outcomes from linear models to that derived from nonlinear methods has resulted in recommendations that the former methods could be employed until alternative software packages become readily available (Jorhensen, 1994; Brien *et al.*, 2002). Fixed effects that were considered included year of lambing (1987 - 2002), selection line (H and L) and ewe age (2 - 7+ years). Trends with regard to birth year and age of dam were modelled, using cubic splines (Verbyla *et al.*, 1999). Linear and non-linear components of the splines were interacted with selection line, to obtain indications of differences in these trends between lines. The first analyses involved fitting various combinations of fixed effects, random spline components and interactions between them to obtain an operational model. Effects found to be significant ($p<0.05$) in these preliminary analyses were retained in subsequent analyses. Random terms were then added to the operational model, resulting in the following genetic models for analyses (in matrix notation):

$$y = Xb + Z_1a + e \qquad (1)$$

$$y = Xb + Z_1a + Z_2c_{ewe} + e \qquad (2)$$

$$y = Xb + Z_1a + Z_3c_{sire} + e \qquad (3)$$

$$y = Xb + Z_1a + Z_2c_{ewe} + Z_3c_{sire} + e \qquad (4)$$

In these models, y was a vector of observations for ewe production or reproduction traits, b, a, c_{ewe} and c_{sire} were vectors of fixed effects, direct genetic effects, ewe permanent environmental effects and random service sire effects respectively, X, Z_1, Z_2, and Z_3 were the corresponding incidence matrices relating the respective effects to y, and e the vector of residuals.

It was assumed that:
$V(a) = A\sigma^2_a$; $V(c_{\mathrm{PE}}) = I\sigma^2_{ewe}$; $V(c_{sire}) = I\sigma^2_{sire}$; $V(e) = I\sigma^2_e$,
with A being the numerator relationship matrix, I an identity matrix; σ^2_a, σ^2_{ewe}, σ^2_{sire} and σ^2_e direct genetic variance, ewe permanent environmental variance, service sire permanent environmental variance and environmental (residual) variance respectively. All analyses included the full pedigree file, consisting of 4351 individuals, the progeny of 216 sires and 1107 dams.

Log likelihood tests were conducted to determine the most suitable model for each trait in uni-variate analyses. The random effects models that fitted the data for each trait best were identified, using the log likelihood ratios obtained from the respective analyses (Snyman *et al.*, 1996). Subsequently, 2-trait animal models were fitted. These analyses allowed the calculation of all relevant direct and ewe permanent environmental correlations between traits, together with their appropriate standard errors.

Direct and maternal breeding values for traits were obtained and averaged within birth years for ewes. Genetic trends were tested for divergence between the lines, using standard errors obtained for the regression coefficients. The breeding values used for this were obtained from analyses where selection line and its interactions with other traits were excluded from the operational model. The inclusion of selection line as fixed would reduce the breeding values for genetic differences between lines that accrued as a result of selection.

Results

Fixed effects

Three-factor interactions between selection line and linear or nonlinear spline components of lambing years and ewe age were not significant ($P > 0.05$) for any of the traits considered. Two-factor interactions involving lambing year and ewe age were significant in some instances. Since these findings were not pertinent to the objectives of the study, these results were not reported. Emphasis is placed on the effects of selection line, and interactions with linear or nonlinear spline components of lambing year and ewe age where appropriate.

Overall, H line ewes lambed 2.6 days earlier in the lambing season ($P < 0.01$) than L line contemporaries (Table 1). Selection line was not involved in significant ($P < 0.05$) interactions with lambing year or age for this trait. In general, overall reproduction in the H line was better ($P < 0.01$) than in the L line. The linear component of the spline for lambing year interacted with selection line for all the reproduction traits. This interaction is illustrated for number of lambs weaned per ewe per year in Fig. 1. It is clear that the difference between the selection lines increased ($P < 0.05$) with time. Year to year fluctuations resulted in a significant ($P < 0.05$) random nonlinear component in the spline for lambing year. Random deviations from linearity that could not be attributed to a smooth trend were also significant ($P < 0.05$). In the H line, lambs weaned per ewe fluctuated at levels exceeding 1 since 1993, while it declined to approximately 0.60 in the L line. The same basic trend was discernable in corrected weight of lamb weaned per breeding ewe (Fig. 2). In this case, weight of lamb weaned per ewe available oscillated around 25 kg since approximately 1994, while it declined to approximately 12 kg in the L line at the end of the experiment.

Table 1. Least squares means (± *SE*) for reproduction traits, greasy fleece weight and live weight in Merino ewes, as affected by year of lambing, selection line and ewe age. Selection line and year effects were estimated at an average ewe age.

Fixed effect	**Day of lambing**	**Number for lambs per ewe**		**Total weight weaned per ewe (kg)**		**Greasy fleece weight (kg)**	**Live weight at joining (kg)**
		Born	**Weaned**	**Uncorrected**	**Corrected** #		
Number of observations	1761	2955	2955	2955	2955	2872	2949
Overall mean	18.5 ± 0.9	1.41 ± 0.06	1.04 ± 0.05	21.0 ± 1.2	21.2 ± 0.9	5.32 ± 0.10	54.7 ± 1.3
Lambing year	**	**	**	**	**	**	**
Selection line	**	**	**	**	**	NS	NS
H line	17.2 ± 0.9	1.50 ± 0.06	1.16 ± 0.05	23.9 ± 1.2	24.2 ± 0.9	5.27 ± 0.11	54.8 ± 1.3
L line	19.8 ± 1.0	1.32 ± 0.07	0.91 ± 0.05	18.1 ± 1.3	18.2 ± 1.0	5.37 ± 0.11	54.7 ± 1.3
Age at lambing	*	**	**	**	**	*	**
2 years	20.2 ± 0.9	1.07 ± 0.06	0.75 ± 0.05	14.6 ± 1.2	14.9 ± 0.9	4.94 ± 0.10	39.8 ± 1.3
3 years	19.2 ± 0.9	1.30 ± 0.06	0.96 ± 0.05	19.3 ± 1.2	19.6 ± 0.9	5.27 ± 0.10	49.6 ± 1.3
4 years	18.5 ± 0.9	1.42 ± 0.06	1.04 ± 0.05	21.1 ± 1.2	21.3 ± 0.9	5.29 ± 0.10	55.7 ± 1.3
5 years	18.3 ± 0.9	1.40 ± 0.06	1.01 ± 0.05	20.5 ± 1.2	20.8 ± 0.9	5.11 ± 0.10	57.2 ± 1.3
6 years	18.7 ± 0.9	1.34 ± 0.06	0.91 ± 0.05	18.7 ± 1.2	18.9 ± 1.0	5.08 ± 0.10	56.0 ± 1.3
7+ years	19.3 ± 1.1	1.27 ± 0.08	0.73 ± 0.08	16.1 ± 1.6	16.2 ± 1.4	4.98 ± 0.10	50.3 ± 1.7

Total weight of lamb weaned per ewe per year corrected for gender and year of lambing

NS – Not significant ($P > 0.05$); * – Significant ($P < 0.05$) ** – Significant ($P < 0.01$)

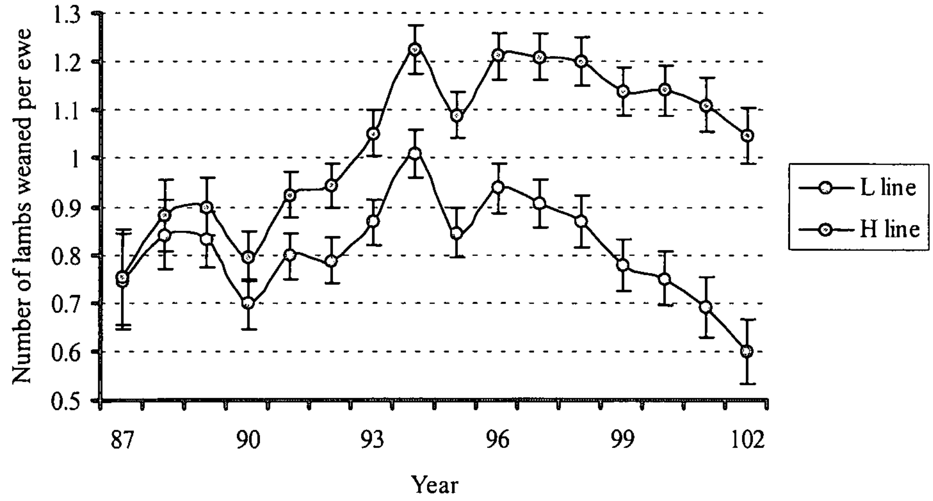


Fig. 1. Phenotypic trends depicting the annual performance of ewes in the H and L lines for number of lambs weaned per ewe. Vertical lines about the mean reflect standard errors.

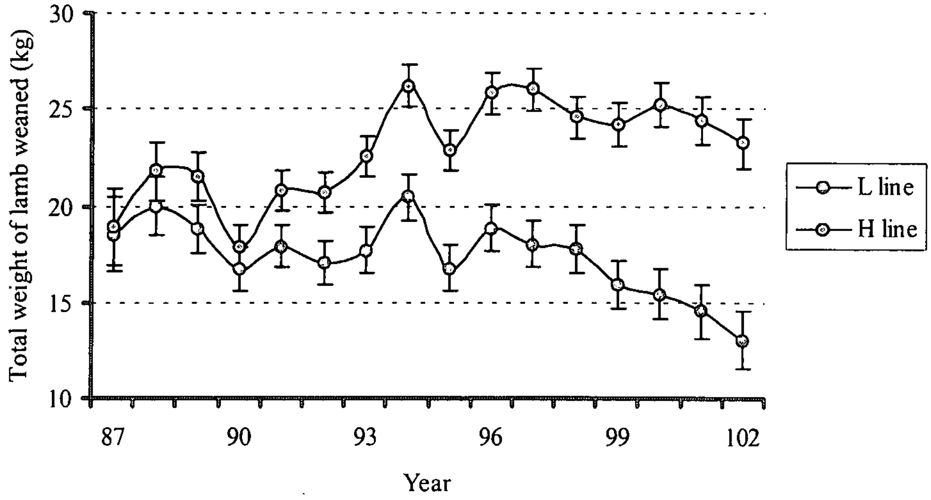


Fig. 2. Phenotypic trends depicting the annual performance of ewes in the H and L lines for corrected weight of lamb weaned per ewe. Vertical lines about the mean reflect standard errors.

Overall, no selection line differences were found for greasy fleece weight and live weight at joining. Greasy fleece weight of the ewes ranged from 5.5 kg to slightly above 6 kg prior to 1993, when the ewes were maintained at Tygerhoek. A marked decline ($P < 0.05$) in wool weight was observed in 1993, when the ewe flock was transferred to Elsenburg and wool growth was assessed over a shorter period. The wool production at Elsenburg were slightly lower in subsequent years, and ranged between 5 and 5.5 kg before declining to below 5 kg towards the end of the experiment. The linear component of the spline for birth year interacted ($P < 0.05$) with selection line for ewe live weight at joining (Fig. 3). Initially, H line ewes tended to be slightly heavier than L line contemporaries. Absolute means favoured the L line towards the end of the experiment. Initially live weight of ewes at joining was above 60 kg. Means for live weight at joining oscillated between 50 and 55 kg for the greatest part of the experiment, and declined to below 50 kg towards the end of the experiment.

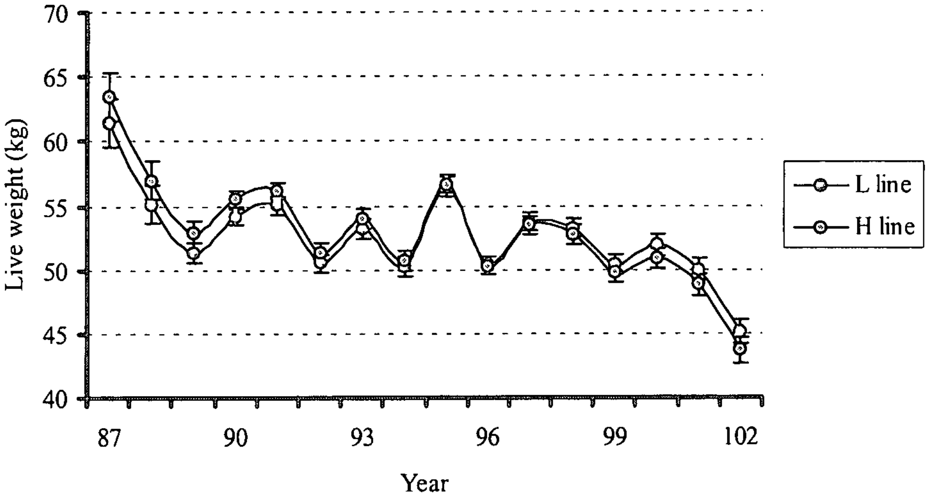


Fig 3. Phenotypic trends depicting the annual performance of ewes in the H and L lines for live weight at joining. Vertical lines about the mean reflect standard errors.

Day of lambing declined curvi-linearly with an increase in ewe age (Table 1), to reach a minimum at 5 years. Reproduction increased ($P < 0.05$) curvi-linearly with ewe age, reaching maxima at 4 to 5 years. A subsequent decline was discernable for all reproduction traits. Greasy fleece weight inclined ($P < 0.05$) with age, peaking at 3 to 4 years and declining subsequently. Selection line interacted ($P < 0.05$) with the nonlinear component of the spline for age as far as greasy fleece weight were concerned (Fig. 4). Within age groups, no significant ($P < 0.05$) difference was found between the selection lines for greasy fleece weight. Absolute means, however, favoured the L line in 3 to 6 year-old ewes. Live weight at joining increased curvi-linearly with age, to reach a maximum in 4 to 6 year-old ewes. From a maximum of approximately 55 kg, live weight at joining declined to approximately 50 kg in 7+ year-old ewes.

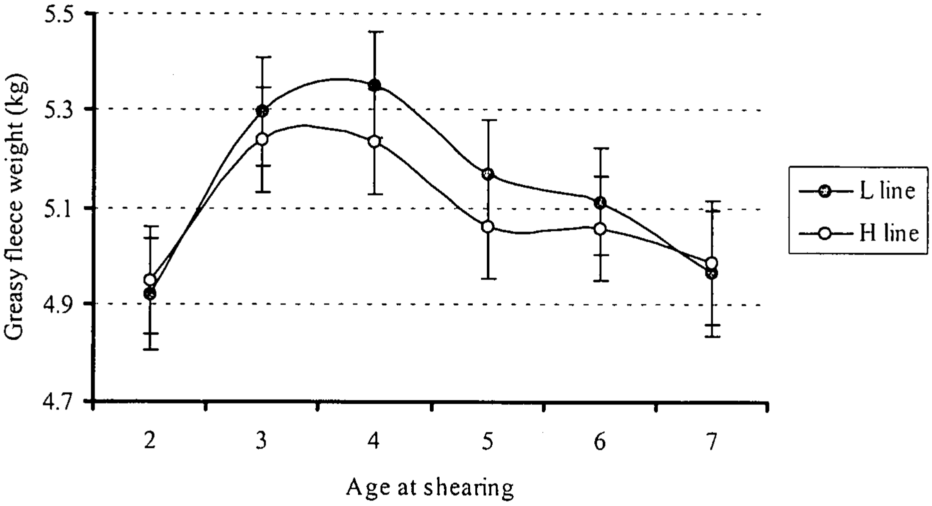


Fig. 4. Phenotypic trends depicting the influence of age at shearing on greasy fleece weight produced per year by ewes in the H and L lines. Vertical lines about the mean reflect standard errors.

Random effects

The inclusion of a random direct genetic component in the operational model resulted in an improved log likelihood ratio for all traits (Table 2). An additional random component of service sire was significant ($P < 0.05$) for day of lambing. Random ewe permanent environment variance components were significant in the other traits.

Typical ewes in the H line (above) and in the L Line (below)

Table 2. Log likelihood ratios for reproduction traits, greasy fleece weight and live weight in Merino ewes under different random effects models

Effects included	**Day of lambing**	**Number of lambs**		**Total weight of lamb weaned**		**Greasy fleece weight**	**Live weight at joining**
		Born	**Weaned**	**Uncorrected**	**Corrected #**		
Fixed effects	-4824.92	-141.553	-118.187	-9050.75	-9055.03	-1101.52	-6577.93
$+h^2$	-4814.52	-77.831	-80.663	-9008.96	-9011.01	-266.339	-5623.73
$+h^2 + c^2_{\mathrm{PE}}$	-4814.26	***-74.044***	***-70.994***	***-8999.39***	***-9001.59***	***-259.855***	***-5610.12***
$+h^2 + c^2_{ram}$	***-4811.73***	-77.715	-80.663	-9006.25	9009.20	-265.953	-5623.73
$+h^2 + c^2_{\mathrm{PE}} + c^2_{\mathrm{ram}}$	-4811.04	-73.926	-69.954	-8997.61	-8999.87	–	–

Total weight of lamb weaned per ewe per year corrected for gender and year of lambing

Table 3. Variance components and estimates of the direct genetic (h^2), ewe permanent environment (PE – c^2_{ewe}) and service sire permanent environmental (c^2_{sire}) variance ratios (± *SE)* for reproduction traits, greasy fleece weight and live weight at joining assessed in Merino ewes of the H and L lines

Random effects included	**Day of lambing**	**Number of lambs**		**Total weight of lamb weaned**		**Greasy fleece weight**	**Live weight at joining**
		Born	**Weaned**	**Uncorrected**	**Corrected[#]**		
Variance components							
Residual (σ^2_e)	78.3413	0.3238	0.3310	139.937	139.487	0.2489	7.6523
Direct additive (σ^2_a)	7.2839	0.0409	0.0145	6.909	7.150	0.4207	14.4905
Ewe PE (σ^2_{ewe})	–	0.0277	0.0430	18.663	19.920	0.1243	7.4341
Service sire PE (σ^2_{sire})	1.6713	–	–	–	–	–	–
Total phenotype (σ^2_p)	87.2965	0.3925	0.3885	165.509	166.557	0.7939	295769
Variance ratios							
h^2	0.08 ± 0.02	0.10 ± 0.02	0.04 ± 0.02	0.04 ± 0.02	0.04 ± 0.02	0.53 ± 0.06	0.49 ± 0.06
c^2_{ewe}	–	0.07 ± 0.03	0.11 ± 0.03	0.11 ± 0.03	0.12 ± 0.03	0.16 ± 0.05	0.25 ± 0.06
c^2_{sire}	0.02 ± 0.01	–	–	–	–	–	–

[#] Total weight of lamb weaned per ewe per year corrected for gender and year of lambing

Expressed relative to the overall phenotypic variance, h^2 and c^2_{ram} amounted to respectively 0.08 and 0.02 for day of lambing (Table 3). Estimates of h^2 amounted to 0.10 for number of lambs weaned per ewe, and to 0.04 for number of lambs weaned per ewe or weight of lamb weaned per ewe. Corresponding ewe permanent environment (c^2_{ewe}) estimates were 0.07 for number of lambs born per ewe and 0.11 to 0.12 for the other reproduction traits. Greasy fleece weight and live weight at joining were highly heritable at approximately 0.5. Corresponding c^2_{ewe} estimates were 0.16 for greasy fleece weight and 0.25 for live weight at joining. Although the inclusion of service sire only resulted in a tendency ($P < 0.10$) towards the improvement of log likelihood ratios for weight of lamb weaned per breeding ewe, it was decided to provide readers with the estimated variance ratios. Expressed relative to the overall phenotypic variance, service sire accounted for a proportion of 0.012 ± 0.007 for uncorrected weight of lamb weaned 0.011 ± 0.007 for corrected weight of lamb weaned per ewe.

Covariances

Genetic correlations of day of lambing with the other reproduction traits were generally high, but not significant (*i.e.* at a level of two times the corresponding standard error – Table 4). The corresponding phenotypic and environmental correlations were consistently below 0.1. The genetic and ewe permanent environmental correlations among reproduction traits were high and significant ($P < 0.05$). Phenotypic and environmental correlations of number of lambs born per ewe with number or weight of lambs weaned per ewe were in the 0.5 to 0.6 range. Correlations between number of lambs weaned per ewe and weight of lamb weaned per ewe were particularly high. All correlations between uncorrected and corrected weight of lamb weaned per ewe were either unity, or not significantly different from it.

Genetic, phenotypic and environmental correlations of the reproduction traits with greasy fleece weight were low, and generally negative in direction (Table 4). Ewe permanent environmental correlations of number or weight of lamb weaned per ewe with greasy fleece weight were high and negative. The reproduction traits were positively related to live weight at joining on a genetic level. The corresponding ewe permanent environmental correlations were relatively high, negative, and either significant, or approaching significance. Phenotypic and environmental correlations of the reproduction traits with live weight at joining were in the 0.06 to 0.12 range. Correlations of greasy fleece weight with live weight at joining were positive and particularly high on the ewe permanent environmental level.

Table 4. Genetic, ewe permanent environmental (PE), phenotypic and environmental correlations (± *SE*) among the reproduction traits, greasy fleece weight and live weight at joining in the H and L lines

Traits	**Genetic**	**Ewe PE**	**Phenotypic**	**Environmental**
Day of lambing x				
Number of lambs born	-0.29 ± 0.20	–	-0.08 ± 0.03	-0.06 ± 0.3
Number of lambs weaned	-0.64 ± 0.36	–	-0.08 ± 0.03	0.05 ± 0.3
Weight of lamb weaned	-0.40 ± 0.33	–	-0.01 ± 0.03	0.01 ± 0.03
Weight of lamb weaned [#]	-0.40 ± 0.32	–	0.02 ± 0.03	0.00 ± 0.03
Greasy fleece weight	0.06 ± 0.14	–	0.03 ± 0.03	0.03 ± 0.03
Live weight at joining	-0.03 ± 0.13	–	-0.03 ± 0.03	-0.06 ± 0.03
Number of lambs born x				
Number of lambs weaned	0.91 ± 0.13	0.87 ± 0.11	0.61 ± 0.01	0.57 ± 0.01
Weight of lamb weaned	0.73 ± 0.17	0.88 ± 0.13	0.54 ± 0.01	0.50 ± 0.02
Weight of lamb weaned [#]	0.77 ± 0.15	0.85 ± 0.13	0.55 ± 0.01	0.50 ± 0.02
Greasy fleece weight	-0.20 ± 0.15	-0.05 ± 0.25	-0.04 ± 0.02	0.03 ± 0.02
Live weight at joining	0.08 ± 0.15	0.12 ± 0.21	0.09 ± 0.02	0.12 ± 0.02
Number of lambs weaned x				
Weight of lamb weaned	0.87 ± 0.08	0.99 ± 0.01	0.94 ± 0.01	0.94 ± 0.01
Weight of lamb weaned [#]	0.91 ± 0.05	0.98 ± 0.01	0.95 ± 0.01	0.95 ± 0.01
Greasy fleece weight	-0.05 ± 0.22	-0.44 ± 0.19	-0.07 ± 0.02	-0.00 ± 0.02
Live weight at joining	0.36 ± 0.26	-0.27 ± 0.16	0.06 ± 0.02	0.12 ± 0.02
Weight of lamb weaned x				
Weight of lamb weaned [#]	1.00 ± 0.01	1.00 ± 0.01	0.99 ± 0.01	0.99 ± 0.01
Greasy fleece weight	-0.01 ± 0.18	-0.48 ± 0.22	-0.07 ± 0.02	-0.02 ± 0.02
Live weight at joining	0.73 ± 0.20	-0.38 ± 0.19	0.11 ± 0.02	0.12 ± 0.02
Weight of lamb weaned [#] x				
Greasy fleece weight	0.02±0.18	-0.52 ± 0.22	-0.07 ± 0.02	-0.01 ± 0.02
Live weight at joining	0.79 ± 0.21	-0.38 ± 0.18	0.11 ± 0.02	0.11 ± 0.02
Greasy fleece weight x				
Live weight at joining	0.39 ± 0.05	0.91 ± 0.20	0.45 ± 0.03	0.42 ± 0.02

[#] Total weight of lamb weaned per ewe per year corrected for gender and year of lambing

Genetic trends

Predicted breeding values that were averaged on birth year were used to depict genetic trends for traits where selection line interacted ($P < 0.05$) with the linear component of the spline for lambing year, to identify genetic trends. Genetic trends for the H and L lines were divergent ($P < 0.01$) for all reproduction traits (Table 5). Trends for corrected weight of lamb weaned per ewe are provided as illustration in Fig. 5. When expressed as percentage of the overall least squares means of the respective traits, breeding value in the H line increased annually with 1.3 % per year for lambs born per ewe, 1.5 % per year for lambs weaned per ewe and by 1.8 % per year for weight of lamb weaned per ewe. Corresponding trends in the L line were –0.6 %, –1.0 % and –1.3 % per annum respectively. When the respective regression coefficients in Table 5 were compared, it was clear that genetic change in the H line was faster ($P < 0.05$) than in the L line. Responses were thus slightly asymmetric for the selection lines.

Table 5. Details of linear regression equations depicting genetic change as reflected by the regression of averaged predicted breeding values on year of birth for ewe reproduction traits and live weight at joining. Regressions were forced through the origin in all instances.

Trait and Selection line	**Regression ($b \pm SE$)**	r	R^2
Lambs born per ewe joined			
H Line	$0.0185^{a} \pm 0.0004$	0.99	0.97
L Line	$-0.0096^{b} \pm 0.0012$	0.66	0.44
Lambs weaned per ewe joined			
H Line	$0.0158^{a} \pm 0.0006$	0.96	0.92
L Line	$-0.0105^{b} \pm 0.0007$	0.84	0.71
Weight of lamb weaned per ewe joined $^{\#}$			
H Line			
L Line	$0.392^{a} \pm 0.018$	0.93	0.87
Ewe joining weight	$-0.271^{b} \pm 0.018$	0.81	0.65
H Line			
L Line	$0.032^{a} \pm 0.015$	0.37	0.14
	$-0.094^{b} \pm 0.023$	0.53	0.28

$^{\#}$ Total weight of lamb weaned per ewe per year corrected for gender and year of lambing

^{a,b} Denote significant ($P<0.05$) divergence between lines for a specific trait

When genetic trends for ewe live weight at joining were assessed, the divergent trends were in an opposite direction than that reflected by the phenotypic trend in Fig. 4. Breeding values in the H line tended to increase at a rate of 0.06 % of the overall mean for ewe joining weight per year. The concomitant genetic change in the L line amounted to 0.17 % per year. The response was asymmetric once more, the downward trend in the L line being faster than the annual increase in the breeding values of the H line.

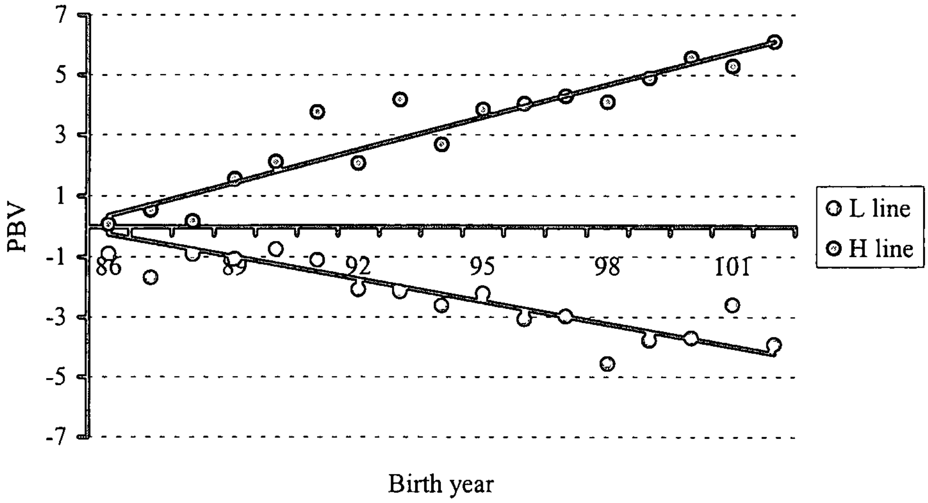


Fig. 5. Genetic trends depicting averaged predicted breeding values (PBV) within birth year for the H and L lines for corrected weight of lamb weaned per ewe in kg. Regressions were forced through the origin. Statistical information can be obtained from Table 5.

Discussion

Fixed effects

Selection line was fitted as fixed in the initial analyses. These results, as well as interactions of selection line with year of lambing, are more relevant to the discussion of responses to selection and are treated accordingly.

The present study accords with previous reports on the curvi-linear nature of age of ewe effects on reproduction (Olivier, 1982; Fourie *et al.*, 1983*a*; Lewer *et al.*, 1983; Karberg *et al.*, 1985; Cloete and Heydenrych, 1986), greasy fleece weight and ewe joining weight (Fourie *et al.*, 1983*b*; Lewer *et al.*, 1983). The effects of ewe age on these traits are well-established and further discussion would be superfluous. The interaction of selection line with the nonlinear component of the spline for ewe age was noted. The basic trends were similar to those derived for the same resource population over the period from 1993 to

2001 (Cloete *et al.*, 2002*a*), but the magnitude of the line differences were much smaller in the present study. It was reasoned that the stress associated with the increased reproduction rate in the H line contributed to the trends derived by Cloete *et al.*, (2002*a*). The same reasoning applies to the present study, although the magnitude of the interaction was much smaller. This is understandable, since the present study also involves records from the early years after the commencement of divergent selection, when the differences in reproduction between lines were much smaller (see Fig. 1, 2 and 5).

Random effects

Genetic parameters for reproduction traits in sheep derived from repeated-records models using an animal model is comparatively scarce in the literature. The h^2 estimate for number of lambs born in Table 3 (0.10) accorded with estimates in the literature (0.06 – Brash *et al.*, 1994*a*; 0.03 – Brash *et al.*, 1994*b*; 0.07 to 0.12 – Bromley *et al.*, 2000; 0.06 – Cloete *et al.*, 2002*d*). In the case of number of lambs weaned per ewe, h^2 was estimated at 0.04. Comparable estimates in the literature were 0.06 (Brash *et al.*, 1994*a*), 0.03 (Brash *et al.*, 1994*b*), 0.03 to 0.07 (Bromley *et al.*, 2000), 0.04 (Swan *et al.*, 2001) and 0.04 (Cloete *et al.*, 2002*d*). Our estimates for total weight of lamb weaned (0.04 in both instances) accorded with estimates ranging from 0.02 to 0.11 for four United States breeds (Bromley *et al.*, 2001), and 0.05 in a Western Australian Merino resource flock (Cloete *et al.*, 2002*d*). Estimates of c^2_{ewe} for the reproduction traits in the present study were 0.07 for number of lambs born per ewe, 0.11 for number of lambs weaned per ewe and 0.11 to 0.12 for weight of lamb weaned per ewe. Corresponding estimates reported by Bromley *et al.* (2000) for litter size at birth ranged from 0.01 to 0.04. For litter size at weaning, the corresponding range was between 0.02 and 0.07. Estimates of c^2_{ewe} for TWW in four United States breeds ranged from 0.08 to 0.10 (Bromley *et al.*, 2001). Swan *et al.* (2001) reported a c^2_{ewe} estimate of 0.09 for number of lambs weaned per ewe in Australian fine wool Merinos. Estimates for c^2_{ewe} derived by Cloete *et al.* (2002) for Western Australian Merinos were 0.11 for number of lambs born per ewe, 0.13 for number of lambs weaned per ewe and 0.13 for weight of lamb weaned per ewe. All these estimates were in good agreement with results from the present study.

Expressed relative to the overall phenotypic variance, the service sire variance (albeit being non significant) amounted to between 1 and 2 %. In the literature, it was shown that service sires had a small ($P < 0.05$) effect on the reproduction of the ewes to which they were mated (Burfening and Davis, 1996). This effect was shown to account for 0 to 3% of the variation in TWW in the study of Bromley *et al.* (2001). Corresponding estimates reported by Cloete *et al.* (2002*d*) for the number of lambs born and weaned as well as for weight of lamb weaned in Western Australian Merinos ranged from 3 to 4 %. The contribution of service sire to the additive genetic variance, breeding values and the ranking of individual female mates for reproduction were shown to be minimal (Burfening and Davis, 1996).

Correlations

The genetic and ewe permanent environmental correlations between the reproduction traits were high (Table 4). In the two measures of weight of lamb weaned per ewe (corrected or uncorrected for gender and birth year), genetic correlations were unity or not different ($P > 0.05$) from it. These traits were thus the same for all practical purposes. With regard to the other traits, Bromley *et al.* (2000) similarly reported genetic correlations ranging from 0.58 to 1.00 between litter size at birth and at weaning in four United States breeds. Genetic and c^2_{ewe} correlations of number of lambs weaned per ewe with fertility and fecundity were also high in the study of Swan *et al.* (2001) on Australian fine wool Merinos strains. In the study of Cloete *et al.* (2002*d*) on Western Australian Merinos, genetic correlations among number of lambs born, number of lambs weaned and weight of lamb weaned exceeded 0.84. In the case of ewe permanent environmental correlations, the estimates exceeded 0.89. When parameters were estimated for total reproduction over a number of lambing opportunities, similar conclusions were derived (Snyman *et al.*, 1997; Olivier *et al.*, 2001). These estimates thus appear to be fairly robust across strains and/or environments where sheep are kept.

Genetic correlations of reproduction traits with greasy fleece weight were low, variable and mostly negative (Table 4). No comparable estimates from repeated records models were found in the literature, but the average genetic correlations with greasy fleece weight derived by Fogarty (1995) from literature estimates amounted to –0.49 for lambs born per ewe and –0.10 for lambs weaned per ewe. In studies where hogget clean fleece weight were correlated with weight of lamb weaned over a number of opportunities, genetic correlations were generally positive (Snyman *et al.*, 1998*b*; Cloete *et al.*, 2002*c*). It is of interest to note that the ewe permanent environmental correlations of reproduction traits with greasy fleece weight were negative and substantial in magnitude. When the short-term (Corbett, 1979; Charlick and Arnold, 1990; Lee and Atkins, 1995) and long-term (Lee and Atkins, 1995) penalties of reproduction on fleece weight are considered, these results can hardly be regarded as surprising. Phenotypic correlations of reproduction traits with ewe greasy fleece weight were low and negative, and in general accordance with means derived by Fogarty (1995) from literature values.

Genetic correlations of the reproduction traits with ewe joining weight were positive and particularly high in the case of the two measures of weight of lamb weaned per ewe (Table 4). No comparable results from analyses involving repeated records models were found in the literature. When hogget live weight were correlated with weight of lamb weaned over a number of opportunities, correspondingly high genetic correlations were estimated (Snyman *et al.*, 1998*a*; Cloete *et al.*, 2002*c*). Phenotypic correlations were low, positive and generally significantly different from zero. Averaged estimates derived from the literature by Fogarty (1995) were similar in sign and magnitude.

Correlations involving greasy fleece weight and live weight at joining were positive and very high on the ewe permanent environmental level (Table 4). The positive genetic correlation of wool weight with live weight is well established in the literature (Cloete *et al.*, 1998*a*; 2002*b*). The higher than expected ewe permanent environmental correlation suggests than an ewe environment favouring wool production should also be conducive to the maintenance of heavy annual joining weights. The phenotypic correlation was consistent with averages of 0.37 to 0.38 derived by Fogarty (1995) from the literature.

Genetic and phenotypic trends

Phenotypic trends for reproduction were indicative of divergence between the respective selection lines (Fig. 1 and 2). These trends were confirmed by genetic divergence between the selection lines, as reflected by results depicted in Table 5 and Fig. 6. Genetic change per year amounted to between respectively 1.3 % and 1.8 % of the corresponding phenotypic means for number of lambs born and corrected weight of lamb weaned per ewe in the H line. Change in the downward direction were somewhat slower, ranging from –0.6 % per year to –1.3 % per year. These results are consistent with the review by Purvis and Hillard (1997), which contend that progress in the order of 1.3 % to 1.5 % of the phenotypic mean should be attainable in litter size of sheep. Preliminary estimates for number of lambs weaned per ewe in the same resource population indicated genetic trends amounting to 1.2 % per year, both in the upward and downward directions (Cloete and Olivier, 1998). Genetic trends in litter weight weaned per ewe amounted to between 1.0 and 3.4 % per year in four United States breeds studied by Ercanbrack and Knight (1998). In an Australian study, Atkins (1980) reported marked responses in lamb output resulting from selection against barrenness and rearing failure. Results from these studies are in good agreement with those obtained in the present study, and indicate that substantial genetic improvement is feasible when selection is based on a composite trait like total weight of lamb weaned per ewe. Against this background it was decided to include total weight of lamb weaned as a reproduction trait in the South African National Small Stock Improvement Scheme (Olivier, 1999). It is appropriate to briefly mention that responses were asymmetrical, genetic progress being faster in the upward direction than in the downward direction (Table 5). Possible reasons for this difference may be the fact that the H line were augmented by those ewes coming from the embryo transfer program, while selection progress in the downward direction may also be against natural selection, thus limiting progress. The reduced reproduction rate in the L line (see Fig 1 and 2) also resulted in smaller selection differentials in this line, thus limiting genetic change.

Phenotypic trends suggested that H line ewes became smaller with time, when compared to the L line contemporaries (Fig. 4). When genetic changes in joining weight were considered, this tendency was reversed, the H line becoming genetically heavier, and the L line becoming lighter (Table 5). This genetic change is understandable when genetic correlations of live weight with reproduction in sheep is considered (Snyman *et al.* 1998*a*; Olivier *et al.* 2001, Cloete *et al.* 2002*c*). In the study of Ercanbrack and Knight (1998), it was demonstrated that the correlated response in total weight of lamb weaned per ewe when selection was based on yearling body weight amounted to 67 % of that attainable through direct selection. The negative phenotypic trend is understandable when the demands of pregnancy and lactation on body reserves is considered (Corbett 1979; Lee and Atkins 1995). It is also reflected by the negative ewe permanent environmental correlations that were found in the present study.

Conclusions

This study found direct additive variance ratios that were of a small magnitude for lamb output, as reflected by number of lambs or weight of lamb weaned per ewe. Substantial genetic changes were, however, found despite the relatively small h^2 estimates derived. An improved reproductive efficiency is a prerequisite for economic success when meat production contributes markedly to the income from a sheep enterprise. The importance of genetic improvement of reproduction rate was thus stressed in the South African Small Stock Improvement Scheme (Olivier, 1999). Preliminary results suggested that this objective would be attainable without marked unwanted genetic correlated responses in the resource population used in the present investigation (Cloete and Olivier, 1998). Results from the present study led to similar conclusions.

Acknowledgements

We wish to thank all those responsible for the maintenance and recording of the experimental animals (Miss E. du Toit at Tygerhoek as well as Mr J.E. Fourie and Miss A.J. Scholtz at Elsenburg). The maintenance of the animals was partially enabled by a grant from the SA Wool Industry.

References

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of the Australian Society of Animal Production* 13: 174 - 176.

Brash, L.D., Fogarty, N.M., Gilmour, A.R., 1994*a*. Reproductive performance and genetic parameters for Australian Dorset sheep. *Australian Journal of Agricultural Research* 45: 427 - 441.

Brash, L.D., Fogarty, N.M., Gilmour, A.R., 1994*b*. Genetic parameters for Australian maternal and dual-purpose meatsheep breeds. II. Liveweight, wool and reproduction in Corriedale sheep. *Australian Journal of Agricultural Research* 45: 469 - 480.

Brien, F.D., Konstantinov, K.V., Greeff, J.C., 2002. Comparison of linear and threshold models for predicting direct and maternal genetic effects on number of lambs weaned in Western Australian Merinos. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production,* 18 - 23 August, Montpellier, France 32: 307 - 310.

Bromley, C.M., Snowder, G.D., Van Vleck, L.D., 2000. Genetic parameters among weight, prolificacy, and wool traits of Columbia, Polypay, Rambouillet, and Targhee sheep. *Journal of Animal Science* 78: 846 - 858.

Bromley, C.M., Van Vleck, L.D., Snowder, G.D., 2001. Genetic correlations for litter weight weaned with growth, prolificacy, and wool traits in Columbia, Polypay, Rambouillet, and Targhee sheep. *Journal of Animal Science* 79: 339 - 346.

Burfening, P.J., Davis, K.C., 1996. Effect of service sire on ewe reproductive rate and estimated breeding values for reproductive rate in Rambouillet sheep. *Sheep and Goat Research Journal* 12: 89 - 93.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J., 2002*a*. Responses of mature breeding ewes to selection for multiple rearing ability. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production,* 18 - 23 August, Montpellier, France 30: 689 - 692.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2002*b*. Direct and maternal genetic (co)variances for hogget live weight and fleece traits in Western Australian Merino sheep. *Australian Journal of Agricultural Research* 53: 271 - 279.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2002*c*. Heritability estimates and genetic and phenotypic correlations of lamb production parameters with hogget live weight and fleece traits in Western Australian Merino sheep. *Australian Journal of Agricultural Research* 53: 281 - 286.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2002*d*. Genetic and environmental variances in lamb production traits of Merino ewes in a Mediterranean environment. *Inaugural Wool Technology Conference*, Hamilton, Victoria, Australia 15 - 17 October 2001.

Cloete, S.W.P., Heydenrych, H.J., 1986. Factors affecting reproduction in Merino ewes of the Tygerhoek flock. *South African Journal of Animal Science* 16: 36 - 42.

Cloete, S.W.P., Olivier, J.J., 1998. Direct and correlated responses to selection for multiple rearing ability in South African Merinos. *Proceedings of the Annual Congress of the South African Society for Animal Science* 36: 65 - 68.

Cloete, S.W.P., Olivier, J.J., Snyman, M.A., du Toit, E., 1998*a*. Genetic parameters and trends in a selection experiment for increased clean fleece weight involving South African Merinos. *Australian Journal of Experimental Agriculture* 38: 427 - 432.

Cloete, S.W.P., Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Scholtz, A.J., Cloete, J.J.E., 2002*e*. Mutual identification of ewes and lambs, as affected by divergent selection for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture*, submitted.

Cloete, S.W.P., Van Niekerk, F.E., Rust, J.M., 1998*b*. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *Sheep and Goat Research Journal* 14: 11 - 12.

Corbett, J.L., 1979. Variation in wool growth with physiological state. In: Black, J.L. and Reis, P.J. (Eds.). 'Physiological limitations to wool growth'. University of New England Publishing Unit, Armidale, NSW, Australia. Pp. 79 - 98.

Ercanbrack, S.K., Knight, A.D., 1998. Responses to various selection protocols for lamb production in Rambioullet, Targhee, Columbia and Polypay sheep. *Journal of Animal Science* 76: 1311 - 1325.

Fogarty, N.M., 1995. Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction in sheep: a review. *Animal Breeding Abstracts* 63: 101 - 143.

Fourie, A.J., Heydenrych, H.J., 1983*a*. Phenotypic and genetic aspects of production in the Dohne Merino. III. The influence of age of the ewe on reproductive performance. *South African Journal of Animal Science* 13: 164 - 166.

Fourie, A.J., Heydenrych, H.J., 1983*b*. Phenotypic and genetic aspects of production in the Dohne Merino. IV. The influence of age of the ewe on production traits. *South African Journal of Animal Science* 13: 167 - 170.

Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R., 1999. ASREML – Reference manuel. NSW Agriculture Biometric Bulletin No. 3. NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia.

Jorgensen, J.N., 1994. Estimation of genetic parameters for litter size in sheep using a non-linear method. *Acta Agriculturae Scandinavica. A. Animal Science* 44: 8 - 11.

Karberg, F.O.W.C., Fourie, A.J., Barnard, H.H., 1985. Die reproduksievermoë van Dohnemerino-ooie in 'n versnelde teeltstelsel (in Afrikaans). *South African Journal of Animal Science* 15: 1 - 4.

Lee, G.J., Atkins, K.D., 1995. Consequences of reproduction on live weight, fat depth, wool growth, and intake of grazing Merino ewes in the short and long term. *Australian Journal of Experimental Agriculture* 35: 153 - 159.

Lewer, R.P., Rae, A.L., Wickham, G.A., 1983. Analysis of records of a Perendale flock III Estimates of environmental effects on productive traits of mature ewes. *New Zealand Journal of Agricultural Research* 26: 303 - 307.

Olivier, J.J., 1982. Reproduksie-eienskappe van Merinoskape in ekstensiewe gebiede (in Afrikaans). *South African Journal of Animal Science* 12: 379 - 382.

Olivier, J.J., 1999. The South African Merino performance testing scheme. In: Rising to the challenge – Breeding for the 21st Century Customer. Beef Industry and CRC for Premium Quality Wool Industry Symposia. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 13: 119 - 124.

Olivier, W.J., Snyman, M.A., Olivier, J.J., Van Wyk, J.B., Erasmus, G.J., 2001. Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep. *South African Journal of Animal Science* 31: 115 - 121.

Purvis, I.W., Hillard, M., 1997. Biology and genetics of reproduction. In: Piper, L. and Ruvinsky, A. (Eds.). 'The genetics of sheep.' CAB International, Wallingford, Oxon, United Kingdom. Pp. 375 - 394.

Snyman, M.A., Olivier, J.J., Olivier, W.J., 1996. Variance components and genetic parameters for body weight and fleece traits of Merino sheep in an arid environment. *South African Journal of Animal Science* 26: 11 - 14.

Snyman, M.A., Cloete, S.W.P., Olivier, J.J., 1998*a*. Genetic and phenotypic correlations of total weight of lamb weaned with body weight, clean fleece weight, and mean fibre diameter in three South African Merino flocks. *Livestock Production Science* 55: 157 - 162.

Snyman, M.A., Erasmus, G.J., Van Wyk, J.B., Olivier, J.J., 1998*b*. Genetic and phenotypic correlations among production and reproduction in Afrino sheep. *South African Journal of Animal Science* 28: 74 - 81.

Swan, A.A., Piper, L.R., Brewer, H.G., Purvis, I.W., 2001. Genetic variation in reproductive performance of fine wool Merinos. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 14: 417 - 420.

Turner, H.N., 1977. Australian sheep breeding research. *Animal Breeding Abstracts* 45: 9 - 31.

Verbyla, A.P., Cullis, B.R., Kenward, M.G., Welham, S.J., 1999. The analysis of designed experiments and longitudinal data using smoothing splines. *Journal of the Royal Statistical Society, Series C* 48: 269 - 311.

CHAPTER 15

GENETIC AND PHENOTYPIC PARAMETERS AND TRENDS FOR HOGGET LIVE WEIGHT AND WOOL TRAITS IN MERINO LINES DIVERGENTLY SELECTED FOR MULTIPLE REARING ABILITY

S.W.P. Cloete[1,2], J.J. Olivier[3], J.B. van Wyk[1], G.J. Erasmus[1] and S.J. Schoeman[4]

[1]University of the Free State, PO Box 339,
Bloemfontein 9300, South Africa
[2]Elsenburg Agricultural Development Centre, Private Bag X1,
Elsenburg 7607, South Africa
[3]Irene Animal Improvement Institute, Private Bag X5013,
Stellenbosch 7599, South Africa
[4]University of Stellenbosch, Private Bag X1,
Matieland 7602, South Africa

Submitted at:
South African Journal of Animal Science

Genetic and phenotypic parameters and trends for hogget live weight and wool traits in Merino lines divergently selected for multiple rearing ability

S.W.P. Cloete[1,2], J.J. Olivier[3], J.B. van Wyk[1], G.J. Erasmus[1] and S.J. Schoeman[4]

[1]University of the Free State, PO Box 339, Bloemfontein 9300, South Africa
[2]Elsenburg Agricultural Development Centre, Private Bag X1, Elsenburg 7607, South Africa
[3]Irene Animal Improvement Institute, Private Bag X5013, Stellenbosch 7599, South Africa
[4]University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

Abstract: Data were recorded for hogget live weight, qualitative and quantitative wool traits, total fold score and testis dimensions of approximately 2400 progeny over the period from 1986 to 2001. The resource population has been divergently selected from the same base since 1986, either for (H line) or against (L line) maternal multiple rearing ability. Environmental effects on the various production traits were consistent with comparable literature results. Least squares means for the respective production traits were largely independent of selection line. Estimates of direct heritability ($h^2 \pm SE$) amounted to 0.38±0.05 for live weight, 0.33 ± 0.5 for greasy fleece weight, 0.58 ± 0.04 for clean yield, 0.28 ± 0.05 for clean fleece weight, 0.31 ± 0.05 for staple length, 0.52 ± 0.04 for fibre diameter and 0.54 ± 0.04 for total fold score. Maternal genetic effects were significant for live weight, greasy fleece weight and clean fleece weight, amounting to 0.09 ± 0.03, 0.06 ± 0.02 and 0.08 ± 0.03 respectively. Estimates of h^2 were 0.36 ± 0.08 for scrotal circumference and 0.28 ± 0.08 for testis diameter. Corresponding h^2 estimates after adjustment for live weight were 0.38 ± 0.08 and 0.25 ± 0.07 respectively. Genetic correlations of live weight with fleece weight, staple length and fibre diameter were positive and moderate to high. The genetic correlation of live weight with total fold score was moderate and negative. Fleece weight was positively related to staple length, fibre diameter and total fold score. Clean yield and staple length was negatively related to total fold score. Genetic correlations with testis measurements were high and positive. The genetic correlation of scrotal circumference with testis diameter was unity. Genetic trends in the H and L line indicated divergence ($P < 0.05$) in the case of live weight, total fold score and scrotal circumference. Expressed as percentages of the overall means of the respective traits, annual genetic changes in the H line amounted to 0.32 % in the case of live weight, –1.3 % for total fold score and 0.06 % for scrotal circumference. Corresponding figure in the L line were –0.18 %, 1.2 % and –0.05 % respectively. The observed genetic divergence in scrotal circumference appeared to be mediated by the genetic changes in live weight, since it was absent in analyses where live weight was included as a covariate. No genetic divergence between lines was observed in any of the qualitative or quantitative wool traits.

Keywords: Fibre diameter, fleece weight, fold score, staple length, testis dimensions

Introduction

Renewed interest in the estimation of genetic parameters for all livestock species followed the advent of sophisticated computer software and hardware enabling analysts to partition genetic variances into direct additive effects, maternal additive effects, their covariance and maternal permanent environmental effects (Meyer, 1989). Several sets of estimates for traits of economic importance in the woolled sheep industry have thus been reported in the past decade (e.g. Olivier *et al.*, 1994; Ponzoni *et al.*, 1995; Swan *et al.*, 1995; Snyman *et al.*, 1996; Olivier *et al.*, 1998; Cloete *et al.*, 2002*c*). Significant maternal effects for wool traits have been reported on a number of occasions (Mortimer and Atkins, 1994; Hickson *et al.*, 1995; Snyman *et al.*, 1996; Cloete *et al.*, 1998*a*). Direct and maternal (co)variance components in South African Merino resource populations thus require further study to arrive at robust parameters for extension to the broader industry.

Marked changes in overall reproduction rate followed directed selection based on maternal multiple rearing ability (Cloete and Scholtz, 1998; Cloete *et al.*, 2002*b*). These genetic changes have a marked influence on the income from mutton and lamb in a woolled sheep enterprise. Mature breeding ewes of a line that was selected for an increased multiple rearing ability (H line) were shown to produce less greasy wool than their contemporaries in a line selected against multiple rearing ability (Cloete *et al.*, 2002*b*). Genetic correlations of weight of lamb weaned per breeding ewe with fibre diameter were furthermore found to be generally unfavourable, albeit not significantly so (Snyman *et al.*, 1998; Cloete *et al.*, 2002*d*). Income from the woolled sheep industry also depends on optimal fibre production, as determined by qualitative and quantitative wool traits (Olivier, 1999). The relative importance of wool and meat depends on the ratio between wool and meat prices at a specific point in time.

Testis measurements of rams were thought as being related genetically to the reproductive capacity of their female relatives (Land *et al.*, 1980). Further studies showed a genetic relationship of reproduction with testis size (Purvis *et al.*, 1988). In South Africa, it has recently been shown that the testis size of breeding rams was phenotypically related to the conception of the ewes they were mated to (Duguma *et al.*, 2002). Correlated responses in testis dimensions that resulted from divergent selection for ewe multiple rearing ability were assessed in this study.

This study thus reports genetic (co)variances for hogget traits in a South African Merino resource flock. Genetic and phenotypic trends that resulted from divergent selection for and against ewe multiple rearing ability were studied simultaneously.

Materials and Methods

Animals and location

Two lines of Merino sheep were divergently selected from the same base population since 1986, using maternal ranking values for lambs reared per joining (Turner, 1977). Details of the procedure for the selection of replacements can be found in the literature (Cloete and Scholtz, 1998). In short, ewe and ram progeny of ewes rearing more than one lamb per joining (*i.e.* reared twins at least once) were preferred as replacements in the High (H) line. Replacements were preferably descended from ewes rearing fewer than one lamb per joining (*i.e.* barren or lost all lambs born at least once) in the Low (L) line. The H line was augmented by 28 ewes from a multiple ovulation and embryo transfer program, that were born during 1991 and 1992 (Cloete *et al.*, 1998*b*). Progeny of mature ewes screened into the respective lines from other lines were also available since the 1996 lambing season. The screening process was detailed by Cloete *et al.* (2002*e*).

Since their establishment, the two lines were maintained as a single flock. The flock was maintained at the Tygerhoek experimental farm at first (1986 to 1992). At the end of 1992 the animals were transferred to Elsenburg for studies on lambing behaviour (Cloete and Scholtz 1998; Cloete *et al.*, 2002*e*). Management procedures and husbandry at the different localities were detailed elsewhere (Cloete *et al.*, 2002*b*), and will not be repeated here.

Recordings

Data that were recorded over a 16-year period from 1986 to 2001 included records of hogget live weight, greasy fleece weight, clean yield, clean fleece weight, staple length, fibre diameter and total fold score. These recordings were made on 2127 to 2470 individuals, born from the commencement of selection to the most recent progeny group. Environmental factors affecting the production traits included year of birth (1986 - 2001), gender (male or female), age of dam (2 to 7+ years) and birth type (singles or pooled multiples). Scrotal circumference and testis diameter were recorded in 1126 ram hoggets, following procedures that were described by Duguma *et al.* (2002). The identities of the sire and dam of all progeny were known. This information enabled linkage back to their line of origin.

Statistical analysis

The ASREML program (Gilmour *et al.*, 1999) was used for the estimation of the fixed effects, and also subsequently to derive variance components for the respective reproduction and production traits in univariate analyses. Fixed effects that were considered included year of birth (1986 - 2001), selection line (H or L), gender (male or female), birth type (single or multiple) and ewe age (2 - 7+ years). Trends with regard to birth year and age of dam were modelled, using cubic splines (Verbyla *et al.*, 1999). Linear and non-linear components of the splines were interacted with selection line, to obtain indications of differences between lines. The first analyses involved fitting various combinations of fixed effects, random spline components and interactions between them to obtain an operational model. Effects found to be significant ($P < 0.05$) in these preliminary analyses were retained in subsequent analyses. Random terms were then added to the operational model, resulting in the following genetic models for analyses (in matrix notation):

$$y = Xb + Z_1a + e \qquad (1)$$

$$y = Xb + Z_1a + Z_2c + e \qquad (2)$$

$$y = Xb + Z_1a + Z_3m + e \qquad (3)$$

[Covariance (a,m)=0]

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad (4)$$

[Covariance (a,m)=0]

$$y = Xb + Z_1a + Z_3m + e \qquad (5)$$

[Covariance $(a,m)=A\sigma_{am}$]

$$y = Xb + Z_1a + Z_3m + Z_2c + e \qquad (6)$$

[Covariance $(a,m)= A\sigma_{am}$]

In these analyses, y was a vector of observations for the respective hogget traits and b, a, m and c vectors of fixed effects, direct genetic variances, maternal genetic variances and maternal permanent environmental variances respectively. X, Z_1, Z_2 and Z_3 were the corresponding incidence matrices relating the respective effects to y, while e was the vector of residuals. A was the numerator relationship matrix, and σ_{am} the covariance between direct genetic and maternal genetic effects.

It was assumed that:

$V(a) = A\sigma^2_a$; $V(m) = A\sigma^2_m$; $V(c) = I\sigma^2_c$; $V(e) = I\sigma^2_e$,

with I being identity matrixes; σ^2_a, σ^2_m, σ^2_c and σ^2_e the direct genetic variance, maternal genetic variance and the maternal permanent environmental variance and environmental (residual) variance, respectively. These analyses yielded estimates of genetic and permanent environmental variances. Ratios for direct additive genetic, maternal genetic as well as maternal permanent environmental variances were computed from these estimates. These variances were expressed relative to the total phenotypic variance. Log likelihood tests were conducted to determine the most suitable model for each trait in uni-trait analyses (Snyman *et al.*, 1996). Subsequently, 2-trait animal models were fitted, allowing the calculation of all relevant direct and maternal correlations between traits, together with the appropriate standard errors. All analyses included the full pedigree file, consisting of 4351 individuals, the progeny of 216 sires and 1107 dams.

Direct breeding values for the relevant traits were obtained and averaged within birth years of progeny. Genetic trends were tested for divergence between the lines, using standard errors obtained for the regression coefficients. The breeding values used for these analyses were obtained from analyses where selection line and its interactions with other traits were excluded from the operational model. The inclusion of selection line as fixed would reduce the breeding values for genetic differences between lines that accrued as a result of selection.

Results

Fixed effects

Birth year effects on hogget performance are not tabulated, since year was involved in interactions ($P < 0.05$) with gender and/or selection line. Year effects were, however, substantial in magnitude (Table 1). No conclusive selection line differences were observed, except in the case of total fold score. Selection line was, however, involved in an interaction with the linear component of the spline for birth year in the case of total fold score (Fig. 1). Initially, no differences in total fold score were observed between the respective lines. Differences between the lines increased as the experiment progressed, the line difference being significant ($P < 0.05$) from 1992 onwards.

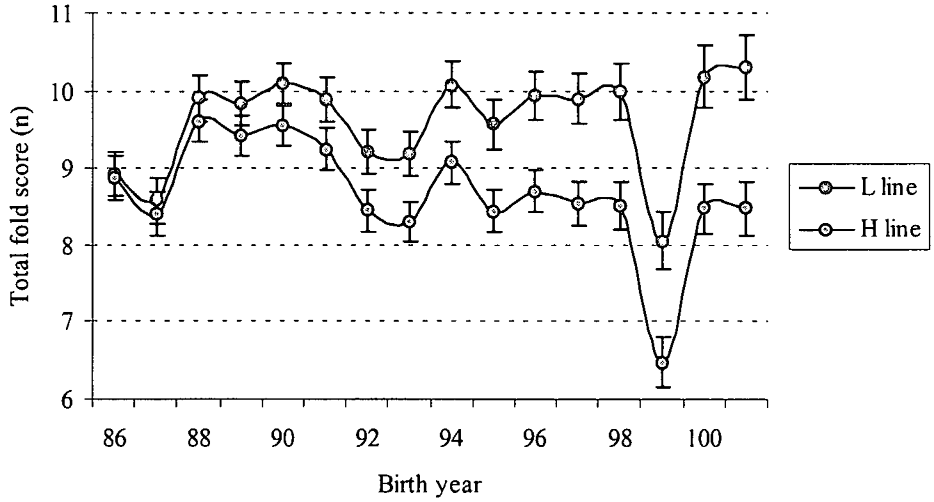


Fig. 1. Phenotypic trends depicting the annual fold score of progeny in the H and L lines. Vertical lines about the mean reflect standard errors.

Table 1. Least squares means (± *SE*) for hogget live weight and fleece in Merino progeny, as affected by year of lambing, selection line, birth type, gender and dam age. All effects were estimated at an average dam age.

Fixed effect	**Live weight (kg)**	**Greasy fleece weight (kg)**	**Clean yield (%)**	**Clean fleece weight (kg)**	**Staple length (mm)**	**Fibre diameter (µm)**	**Total fold score (n)**
Number of observations	2470	2321	2472	2320	2127	2473	2470
Overall mean	39.6 ± 1.5	4.03 ± 0.05	74.0 ± 0.7	2.94 ± 0.04	86.9 ± 1.6	19.6 ± 0.1	9.13 ± 0.24
Lambing year	**	**	**	**	**	*	*
Selection line	NS	NS	NS	NS	NS	NS	**
H line	40.2 ± 1.5	4.02 ± 0.06	74.3 ± 0.8	2.90 ± 0.4	87.8 ± 1.6	19.6 ± 0.11	8.66 ± 0.26
L line	39.0 ± 1.6	4.07 ± 0.07	73.7 ± 0.8	2.91 ± 0.4	86.6 ± 1.7	19.5 ± 0.11	9.60 ± 0.29
Birth type	NS	**	NS	**	NS	NS	**
Single	40.5 ± 1.5	4.21 ± 0.06	73.8 ± 0.7	3.01 ± 0.04	86.7 ± 1.6	19.5 ± 0.3	9.67 ± 0.24
Multiple	38.7 ± 1.5	3.88 ± 0.06	74.2 ± 0.8	2.80 ± 0.04	87.8 ± 1.6	19.7 ± 0.3	8.59 ± 0.24
Gender	**	NS	NS	*	0.10	**	NS
Ram	43.3 ± 1.5	4.01 ± 0.06	73.7 ± 0.8	2.86 ± 0.04	86.0 ± 1.6	19.1 ± 0.3	9.14 ± 0.26
Ewe	35.9 ± 1.5	4.08 ± 0.05	74.3 ± 0.08	2.95 ± 0.04	88.5 ± 1.6	20.0 ± 0.3	9.12 ± 0.26
Dam age at lambing	NS	NS	NS	*	NS	NS	**
2 years	38.5 ± 1.5	3.94 ± 0.06	74.2 ± 0.8	2.86 ± 0.04	87.8 ± 1.7	19.7 ± 0.3	8.72 ± 0.25
3 years	39.2 ± 1.5	4.00 ± 0.05	74.2 ± 0.8	2.92 ± 0.04	86.9±1.6	19.6 ± 0.3	8.99 ± 0.24
4 years	39.6 ± 1.5	4.04 ± 0.05	74.1 ± 0.8	2.95 ± 0.04	86.9 ± 1.6	19.6 ± 0.3	9.13 ± 0.24
5 years	39.6 ± 1.5	4.05 ± 0.05	74.0 ± 0.8	2.94 ± 0.04	86.9±1.6	19.6 ± 0.3	9.19 ± 0.24
6 years	39.1 ± 1.5	4.02 ± 0.05	73.7 ± 0.8	2.91 ± 0.04	86.7 ± 1.6	19.6 ± 0.3	9.23 ± 0.24
7+ years	38.2 ± 1.6	3.99 ± 0.07	74.0 ± 0.8	2.88 ± 0.06	88.2 ± 1.9	19.4 ± 0.3	9.22 ± 0.26

NS – Not significant (*P* > 0.05); * – Significant (*P* < 0.05) ** – Significant (*P* < 0.01)

Expressed relative to multiples, single hoggets had heavier fleeces, and were more developed as far as fold score was concerned ($P < 0.05$ – Table 1). Ram hoggets were heavier ($P < 0.01$) than ewes, and produced slightly less wool at a finer diameter ($P < 0.05$). Gender was involved in significant ($P < 0.05$) interactions with random deviations from a smooth trend for birth year in all traits. As an illustration, the interaction between gender and birth year for live weight is depicted in Fig. 2. Expressed relative to ewes, the superiority in live weight of rams ranged from 5.5 % in 1993 to 32.2 % in 1988. All the traits considered were independent of dam age, with the exception of clean fleece weight and total fold score (Table 1). Clean fleece weight showed a curvilinear response to dam age. In the case of total fold score, an incline was observed up to a dam age of 4 to 5 years. Total fold score subsequently remained stable.

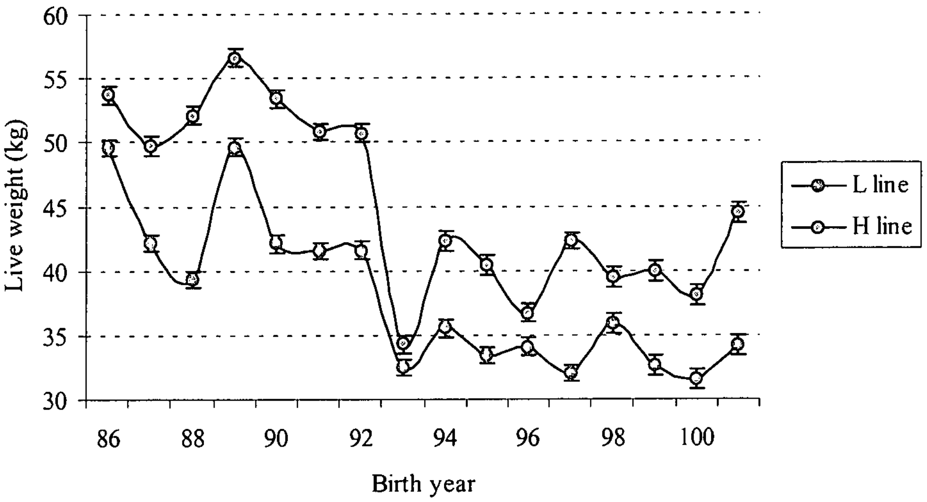


Fig. 2. Phenotypic trends depicting the interaction between gender and birth year for hogger live weight. Vertical lines about the mean reflect standard errors.

Testis measurements were relatively independent of the fixed effects analysed (Table 2). The exception was birth year, where the variation was reduced by the inclusion of ram live weight as a covariate. There was a tendency ($P < 0.10$) for selection line to interact with the linear component of the spline for birth year for scrotal circumference (Fig. 3). Initially, means for the H line were below those of the L line in absolute terms. Later on, significant ($P < 0.05$) differences in favour of the H line were found in most years. No such trend was observed in the analysis where live weight was included as a covariate.

Table 2. Least squares means (± *SE*) for testis traits in 1126 Merino ram progeny, as affected by year of lambing, selection line, birth type, gender and dam age. Means were predicted with and without the inclusion of line weight as a covariate. All effects were estimated at an average dam age.

Fixed effect	Not corrected for live weight		Corrected for live weight	
	Scrotal circumference (cm)	Testis diameter (mm)	Scrotal circumference (cm)	Testis diameter (mm)
Overall mean	29.9 ± 0.6	94.3 ± 2.7	30.9 ± 0.5	101.6 ± 1.4
Lambing year	**	**	*	*
Selection line	NS	NS	NS	NS
H line	30.6 ± 0.6	96.3 ± 2.8	31.3 ± 0.5	102.3 ± 1.4
L line	29.1 ± 0.6	92.3 ± 2.9	30.5 ± 0.5	101.0 ± 1.5
Birth type	NS	NS	NS	NS
Single	29.9 ± 0.6	94.4 ± 2.8	30.7 ± 0.5	101.0 ± 1.4
Multiple	29.8 ± 0.6	94.1 ± 2.7	31.1 ± 0.5	102.3 ± 1.4
Dam age at lambing	NS	NS	NS	NS
2 years	30.0 ± 0.6	94.3 ± 2.8	31.2 ± 0.5	101.8 ± 1.4
3 years	30.0 ± 0.6	94.3 ± 2.7	30.9 ± 0.5	101.7 ± 1.4
4 years	30.0 ± 0.6	94.3 ± 2.7	30.8 ± 0.5	101.6 ± 1.4
5 years	30.0 ± 0.6	94.3 ± 2.7	30.8 ± 0.5	101.6 ± 1.4
6 years	29.8 ± 0.6	94.2 ± 2.8	30.8 ± 0.5	101.5 ± 1.4
7+ years	29.5 ± 0.6	94.2 ± 2.8	30.9 ± 0.6	101.6 ± 1.4

NS – Not significant ($P > 0.05$); * – Significant ($P < 0.05$) ** – Significant ($P < 0.01$

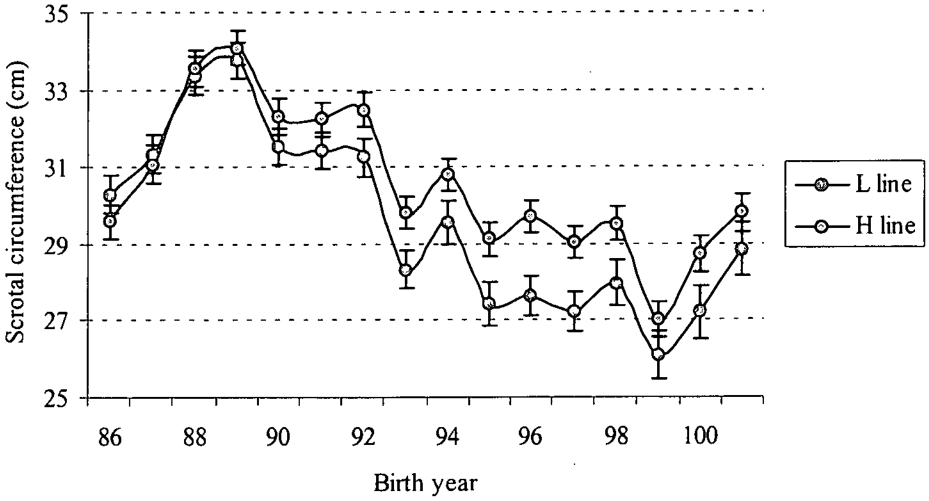


Fig. 2. Phenotypic trends depicting the annual performance of ram hoggets in the H and L lines for scrotal circumference. Vertical lines about the mean reflect standard errors.

Overall, increases in testis dimensions with an increase of 1 kg in live weight amounted to regression coefficients (± *SE*) of 0.27 ± 0.01 cm for scrotal circumference, and to 0.96 ± 0.04 mm for testis diameter.

Random effects

The addition of a random direct genetic component in the operational model resulted in an improved ($P < 0.05$) log likelihood ratio for all traits (Table 3). Maternal additive variances, as an additional random factor, led to a further improvement ($P < 0.05$) in the log likelihood ratios of live weight as well as greasy and clean fleece weight.

Estimates of h^2 were 0.38 for hogget live weight, 0.33 for greasy fleece weight, 0.58 for clean yield, 0.28 for clean fleece weight, 0.31 for staple length, 0.52 for fibre diameter and 0.54 for total fold score (Table 4). Corresponding m^2 estimates were below 0.1 in the traits where it was significant ($P < 0.05$).

Only direct additive genetic variances were significant ($P < 0.05$) in the case of scrotal circumference and diameter in rams (Table 5). The direct genetic correlation (± *SE*) of live weight with testis measurements were high (0.73 ± 0.09 for testis diameter and 0.72 ± 0.09 for scrotal circumference). Estimates of h^2 were thus derived with and without the inclusion of live weight as a covariate (Table 6). Variance components were somewhat lower in the analyses where live weight was included as a covariate, but the ratios were unchanged. Heritability estimates of scrotal circumference tended to be somewhat higher than those of testis diameter (0.36 and 0.38 *vs.* 0.28 and 0.25 respectively), but the differences were not significant ($P < 0.05$) when assessed with the derived standard errors.

Table 3. Log likelihood ratios for hogget live weight, wool traits and total fold score for Merino progeny of lines divergently selected for multiple rearing ability under different random effects models

Fixed effect	**Live weight (kg)**	**Greasy fleece weight (kg)**	**Clean yield (%)**	**Clean fleece weight (kg)**	**Staple length (mm)**	**Fibre diameter (μm)**	**Total fold score (n)**
Fixed effects only	-5203.53	-156.004	-4726.12	549.466	-5615.24	-1876.36	-3061.79
Fixed + h^2	-5098.40	-70.8592	***-4594.81***	611.473	***-5575.81***	***-1727.34***	***-2887.27***
Fixed + h^2 + c^2	-5090.47	-68.5757	-4594.81	614.266	-5575.81	-1726.50	-2886.32
Fixed + h^2 + m^2	***-5089.63***	***-67.7000***	-4594.81	***616.817***	-5575.86	-1726.17	-2887.13
Fixed + h^2 + m^2 + c^2	-5088.76	-67.6161	-4594.81	616.817	-5575.81	-1726.08	-2886.32
Fixed + h^2 + m^2 + r_{am}	-5087.79	-67.2041	N.C.	616.819	-5574.82	-1725.62	-2885.95
Fixed + h^2 + m^2 + c^2 + r_{am}	-5087.15	-67.1479	N.C.	616.819	5574.82	-1725.45	-2884.85

Table 4. Variance components for the residual, direct genetic, maternal genetic and total phenotypic variances as well as direct genetic (h^2) and maternal (m^2) variance ratios (± *SE*) for hogget live weight and fleece traits assessed in Merino progeny of the H and L lines

Random effects included	**Live weight (kg)**	**Greasy fleece weight (kg)**	**Clean yield (%)**	**Clean fleece weight (kg)**	**Staple length (mm)**	**Fibre diameter (m)**	**Total fold score (n)**
Variance components:							
Residual ($\sigma^2{}_e$)	13.2396	0.2491	7.5931	0.1425	69.8762	0.8012	2.0197
Direct additive ($\sigma^2{}_a$)	9.4432	0.1332	10.3249	0.0.0605	31.9527	0.8736	2.3592
Maternal additive ($\sigma^2{}_m$)	2.3594	0.0230	-	0.0168	-	-	-
Total phenotype ($\sigma^2{}_p$)	25.0422	0.4053	17.918	0.2199	1.8289	1.6749	4.3789
Variance ratios:							
h^2	0.38 ± 0.05	0.33 ± 0.05	0.58 ± 0.04	0.28 ± 0.05	0.31 ± 0.05	0.52 ± 0.04	0.54 ± 0.04
m^2	0.09 ± 0.03	0.06 ± 0.02	-	0.08 ± 0.03	-	-	-

Table 5. Log likelihood ratios for testis measurements of Merino ram progeny of lines divergently selected for multiple rearing ability under different random effect models. The "best" model is indicated in bold, italic type.

Model	Not corrected for live weight		Corrected for live weight	
	Scrotal circumference (cm)	Testis diameter (mm)	Scrotal circumference (cm)	Testis diameter (mm)
Fixed effects only	-1648.30	-3131.29	-1430.90	-2930.07
Fixed + h^2	***-1632.50***	***-3119.73***	-1410.29	-2918.41
Fixed + h^2 + c^2	-1631.45	-3118.56	-1410.29	-2918.33
Fixed + h^2 + m^2	-1631.39	-3118.70	-1410.29	-2118.41
Fixed + h^2 + m^2 + c^2	-1631.17	-3118.34	-1410.29	-2918.33
Fixed + h^2 + m^2 + r_{am}	-1631.36	-3117.73	-1410.29	-2917.20
Fixed + h^2 + m^2 + c^2 + r_{am}	-1631.12	-3117.31	-1410.29	-2916.90

Table 6. Variance components for the residual, direct genetic and total phenotypic variances as well as direct genetic (h^2) variance ratios (± *SE*) for testis measurements assessed in Merino ram hoggets of the H and L lines

Components or ratios	Not corrected for live weight		Corrected for live weight	
	Scrotal circumference (cm)	Testis diameter (mm)	Scrotal circumference (cm)	Testis diameter (mm)
Variance components:				
Residual (σ^2_e)	2.3798	26.1593	1.7137	16.2774
Direct additive (σ^2_a)	4.3019	66.3452	2.7809	47.6378
Total phenotype (σ^2_p)	6.6817	92.5045	4.4946	63.9152
Variance ratios				
h^2	0.36 ± 0.08	0.28 ± 0.07	0.38 ± 0.08	0.25 ± 0.07

Covariances

Genetic correlations of live weight with the other production traits were moderate to high, positive and significant (*i.e.* two times the corresponding standard error) in case of greasy fleece weight, clean fleece weight, staple length and fibre diameter (Table 7). A negative genetic correlation was obtained between live weight and total fold score. Maternal genetic correlations of live weight with greasy and clean fleece weights were high, as were the corresponding phenotypic and environmental correlations. Most of the other phenotypic and environmental correlations were below 0.2 (regardless of sign). The exception was the phenotypic correlations of live weight with staple length and fibre diameter, which were 0.23 and 0.22 respectively.

Table 7. Genetic, maternal genetic, phenotypic and environmental correlations (± *SE*) among hogget live weight and wool traits

Traits	**Direct genetic**	**Maternal genetic**	**Phenotypic**	**Environmental**
Live weight X				
Greasy fleece weight	0.29 ± 0.10	0.74 ± 0.16	0.39 ± 0.02	0.41 ± 0.02
Clean yield	0.13 ± 0.09	-	0.05 ± 0.03	-0.02 ± 0.05
Clean fleece weight	0.28 ± 0.11	0.76 ± 0.15	0.42 ± 0.02	0.45 ± 0.04
Staple length	0.43 ± 0.10	-	0.23 ± 0.02	0.12 ± 0.05
Fibre diameter	0.29 ± 0.09	-	0.22 ± 0.02	0.18 ± 0.05
Total fold score	-0.27 ± 0.09	-	-0.06 ± 0.03	0.13 ± 0.05
Greasy fleece weight X				
Clean yield	-0.32 ± 0.09	-	0.16 ± 0.03	0.06 ± 0.05
Clean fleece weight	0.89 ± 0.02	-	0.89 ± 0.01	0.90 ± 0.01
Staple length	0.19 ± 0.11	-	0.18 ± 0.02	0.19 ± 0.04
Fibre diameter	0.45 ± 0.08	-	0.28 ± 0.02	0.17 ± 0.04
Total fold score	0.41 ± 0.08	-	0.30 ± 0.02	0.24 ± 0.04
Clean yield X				
Clean fleece weight	0.19 ± 0.09	-	0.20 ± 0.02	0.24 ± 0.05
Staple length	0.20 ± 0.09	-	0.16 ± 0.03	0.14 ± 0.05
Fibre diameter	-0.04 ± 0.07	-	-0.06 ± 0.03	-0.08 ± 0.05
Total fold score	-0.35 ± 0.07	-	-0.24 ± 0.02	-0.10 ± 0.05
Clean fleece weight X				
Staple length	0.36 ± 0.12	-	0.26 ± 0.02	0.24 ± 0.04
Fibre diameter	0.46 ± 0.08	-	0.27 ± 0.02	0.16 ± 0.04
Total fold score	0.28 ± 0.09	-	0.21 ± 0.02	0.18 ± 0.05
Staple length X				
Fibre diameter	0.38 ± 0.09	-	0.22 ± 0.02	0.11 ± 0.05
Total fold score	-0.41 ± 0.08	-	-0.19 ± 0.02	-0.02 ± 0.05
Fibre diameter X				
Total fold score	-0.09 ± 0.07	-	-0.05 ± 0.03	-0.01 ± 0.05

The genetic correlation of greasy fleece weight with clean yield was negative (Table 7), with no conclusive environmental correlation between the traits. The analysis involving greasy and clean fleece weight proved difficult to converge, since the maternal genetic correlation went outside the parameter space (> 1). Eventually, based on the relative small variances for both traits (Table 4) and the inherent instability of the covariance component under such conditions, it was decided to leave the maternal genetic correlation out of the analysis. In the subsequent analysis, it was clear that greasy fleece weight and clean fleece weight were closely related, all correlations approaching 0.9. Genetic correlations of greasy fleece weight with fibre diameter were positive.

Phenotypic and environmental correlations were in the same direction, but of a smaller magnitude.

Genetic correlations of clean yield with clean fleece weight and staple length were positive, but low (Table 7). Phenotypic and environmental correlations were in the same direction and of the same magnitude. Clean yield was largely unrelated to fibre diameter. Genetic and phenotypic associations of clean yield with total fold score were negative and moderate. On a genetic level, clean fleece weight was positively related to staple length, fibre diameter and total fold score (Table 7). Corresponding phenotypic and environmental correlations were in the same direction, but smaller in magnitude. The genetic association of staple length with fibre diameter was positive (Table 7). Phenotypic and environmental correlations were similar in sign, but lower in magnitude. Staple length was negatively related to total fold score on a genetic level. The corresponding environmental correlation was negligible. Fibre diameter and total fold score were unrelated at a genetic and environmental level.

The genetic correlation of scrotal circumference with testis diameter was unity (1.00 ± 0.02). Phenotypic and environmental correlations were equally high (0.84 ± 0.01 and 0.75 ± 0.03 respectively).

Genetic trends

Predicted breeding values that were averaged on birth year were used to depict genetic trends for traits where evidence of divergence ($P < 0.05$) was observed between selection lines. No evidence of divergent genetic trends was observed for greasy fleece weight, clean yield, clean fleece weight and fibre diameter. When staple length was considered, there was a tendency ($P = 0.22$) for breeding values to increase in the H line, while no change was observed in the L line. No divergence ($P > 0.20$) between lines was, however, found.

In the case of hogget live weight, averaged breeding values increased ($P < 0.01$) at a rate of 0.32 % of the overall mean per annum in the H line (Table 8). Corresponding breeding values in the L line decreased at 0.18 % of the overall mean per annum. These genetic trends were divergent and slightly asymmetric ($P < 0.01$ – Fig. 4), faster response being obtained in the upward direction (H line). Genetic response in total fold score was clearly divergent ($P < 0.01$), and symmetric (Fig. 5). Averaged breeding values in the H line declined at 1.3 % of the overall mean per year, while the concomitant genetic increase in the L line amounted to 1.2 % per year (Table 8).

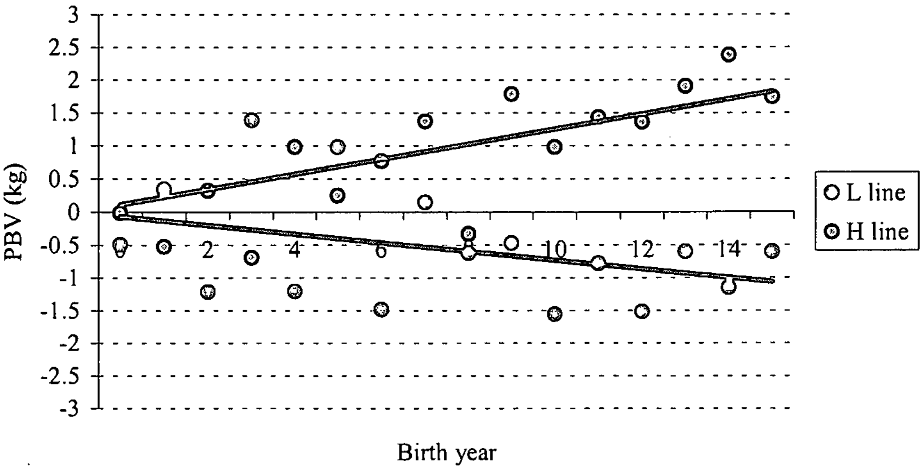


Fig. 4. Genetic trends depicting averaged predicted breeding values (PBV) within birth year for the H and L line hoggets for live weight. Regressions were forced through the origin. Statistical information can be obtained from Table 8.

Table 8. Details of linear regression equations depicting genetic change as reflected by the regression of averaged predicted breeding values on year of birth for hogget live weight, total fold score and scrotal circumference. Regressions were forced through the origin in all instances.

Trait and Selection line	**Regression (*b* ± *SE*)**	***R***	***R^2***
Live weight			
H Line	0.127 ± 0.016^a	0.79	0.62
L Line	-0.073 ± 0.023^b	0.38	0.15
Total fold score			
H Line	-0.119 ± 0.006^b	0.95	0.90
L Line	0.113 ± 0.010^a	0.69	0.47
Scrotal circumference			
H Line	0.019 ± 0.006^a	0.57	0.32
L Line	-0.015 ± 0.006^b	0.11	0.01

^{a,b} Denote significant ($P < 0.05$) divergence between lines for a specific trait Genetic divergence ($P < 0.05$)

Genetic response in total fold score was clearly divergent ($P < 0.01$), and symmetric (Fig. 5). Averaged breeding values in the H line declined at 1.3 % of the overall mean per year, while the concomitant genetic increase in the L line amounted to 1.2 % per year (Table 8).

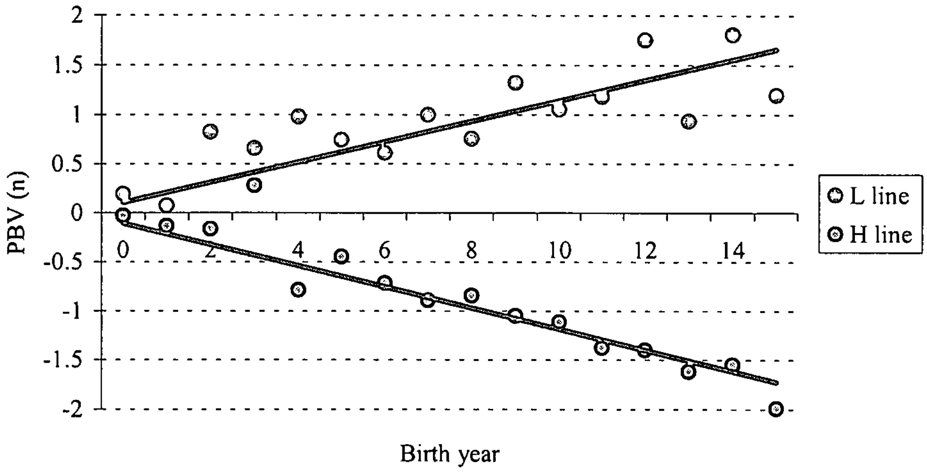


Fig. 5. Genetic trends depicting averaged predicted breeding values (PBV) within birth year for the H and L line hoggets for total fold score. Regressions were forced through the origin. Statistical information can be obtained from Table 8.

Divergence between the selection lines was also observed for scrotal circumference. Testis diameter was not considered, as it was genetically closely related to scrotal circumference. The annual increase ($P < 0.05$) in breeding values in the H line amounted to 0.06 % of the overall mean for the trait (Table 8). The corresponding decrease in breeding values for the L line was 0.05 % of the overall mean. These trends are depicted in Fig. 6. These genetic changes were evidently mediated by the divergence between lines for live weight (Fig. 4). No evidence of divergence was obtained when live weight was added as a covariate in the model used to analyse scrotal circumference.

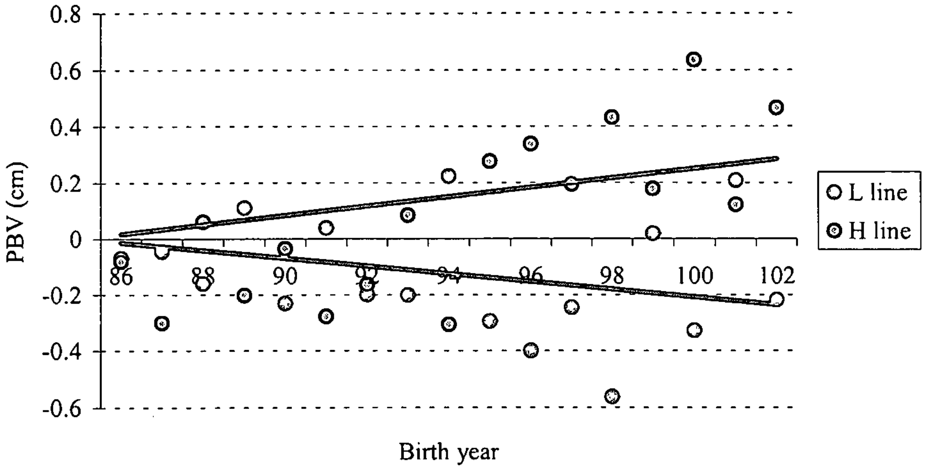


Fig. 6. Genetic trends depicting averaged predicted breeding values (PBV) within birth year for the H and L line ram hoggets for scrotal circumference. Regressions were forced through the origin. Statistical information can be obtained from Table 8.

Discussion

Fixed effects

Selection line was fitted as fixed in the initial analyses. These results, as well as interactions of selection line with year of lambing, are more relevant to the discussion of responses to selection and are treated accordingly. The effects of birth year, sex, age of dam, birth type, date of birth, and the interactions among them were consistent with what is generally expected from the literature. Detailed discussion is thus not warranted in this paper, and it is not presented.

Random effects

Genetic parameters for production traits in sheep have been thoroughly reviewed by Fogarty (1995). Apart from mentioning averaged parameters from the latter study, we will refrain from the citation of earlier paternal halfsib or parent-offspring heritability estimates, unless pertinent to this study. Averaged parameter estimates derived from Australian studies by Atkins (1997) will also be cited where appropriate. Literature estimates summarised by Cloete *et al.* (2002) will also be provided where applicable. Readers interested in more detailed information are referred to these references.

In general, h^2 ranged from 0.14 to 0.61, and m^2 from 0.01 to 0.15 in studies where it was reported (see list of literature estimates compiled by Cloete *et al.*, 2002*c*). Estimates of h^2 and m^2 for hogget live weight in the present study were respectively 0.38 and 0.09. Both these values are well within the range of estimates cited above. Fogarty (1995) reported a mean h^2 estimate of 0.57 for hogget live weight in woolled sheep in his review. Corresponding h^2 estimates reported by Lewer *et al.* (1994) for 14-month live weight ranged from 0.27 to 0.50.

Variance ratios depicting h^2 ranged from 0.20 to 0.62 in the case of greasy fleece weight and clean fleece weight (see Tables 4 and 5 of Cloete *et al.*, 2002*c*). Corresponding ranges for m^2 were from 0.02 to 0.17. The present h^2 estimates of 0.33 for greasy fleece weight and 0.28 for clean fleece weight are in good agreement with these estimates. Estimates of m^2 for greasy fleece weight and clean fleece weight were respectively 0.06 and 0.08, which fitted well into the ranges quoted above. Corresponding mean h^2 estimates from the review by Fogarty (1995) were 0.34 for greasy fleece weight and 0.37 for clean fleece weight. Atkins (1997) reported averaged h^2 estimates of 0.40 for hogget greasy fleece weight and 0.38 for hogget clean fleece weight, which were also in fair agreement with the present estimates. The present estimate for h^2 in clean yield was 0.58. This value is well within the range of estimates (0.34 to 0.72) cited from the literature (see Table 6 of Cloete *et al.*, 2002*c*). The averaged h^2 estimate given by Atkins (1997) for clean yield was 0.50. The h^2 of staple length was estimated at 0.31. The average corresponding h^2 based on literature estimates (Atkins, 1997) amounted to 0.41, while Cloete *et al.* (1998*a*) reported an estimate of 0.35. Literature estimates of the h^2 of fibre diameter ranged from 0.43 to 0.74 (see Table 7 of Cloete *et al.*, 2002*c*). At 0.52, the present estimate is consistent with this range of values. From a number of Australian studies, Atkins (1997) correspondingly derived an averaged h^2 estimate of 0.58 for fibre diameter. At 0.54, total fold score was highly heritable. A corresponding estimate reported in another South African Merino resource population amounted to 0.42 (Cloete *et al.*, 1998*a*).

Estimates of h^2 ranged from 0.36 to 0.38 for scrotal circumference, and from 0.25 to 0.28 for testis diameter, depending on adjustment for live weight. Duguma *et al.* (2002) reported estimates ranging from 0.29 to 0.40 for scrotal circumference and from 0.25 to 0.38 for testis diameter in another South African Merino resource population. In the latter study, scrotal circumference was shown to increase at 0.22 cm per kg of live weight, while testis diameter increased at 0.78 mm per kg live weight. Corresponding regressions in the present study amounted to respectively 0.27 cm per kg and 0.96 mm per kg.

Correlations

The genetic correlations of hogget live weight with fleece weight were positive (0.29 for greasy fleece weight and 0.28 for clean fleece weight). Corresponding genetic correlations reported in the literature for live weight with greasy fleece weight were a mean of 0.21 (Fogarty, 1995), 0.30-0.34 (Brash *et al.*, 1997) and 0.37 (Cloete *et al.*, 2002*c*). Estimates for live weight and clean fleece weight were a mean of 0.18 (Fogarty, 1995), 0.20-0.58 (Brash *et al.*, 1997), 0.27 (Purvis and Swan, 1997), 0.37 (Cloete *et al.*, 1998*a*) and 0.37 (Cloete *et al.*, 2002*c*). These estimates accorded with those obtained in the present study. The genetic relationship of hogget live weight with fibre diameter was positive (0.29), suggesting that selection for heavier sheep will probably result in a broader fibre diameter. Corresponding genetic correlations were found in the literature (a mean of 0.10 – Fogarty, 1995; 0.13-0.36 – Brash *et al.*, 1997; 0.18 – Purvis and Swan, 1997; 0.26 – Cloete *et al.*, 1998*a*; 0.17 – Cloete *et al.*, 2002*c*). On a genetic basis, hogget live weight was negatively related to total fold score (–0.27). Cloete *et al.* (1998*a*) previously reported a corresponding genetic correlation of –0.24. The environmental correlation of live weight with fold score was positive but relatively low. This correlation suggests that an increase in fold development was likely under good feeding conditions, as was reported by Herselman and King (1993).

Clean fleece weight and greasy fleece weight was closely related, as was also reported in the literature (Atkins, 1997; Brash *et al.*, 1997; Rose and Pepper, 1999; Cloete *et al.*, 2002*c*). The genetic correlation of greasy fleece weight with clean yield was negative (-

0.32 – Table 7). Literature estimates of this correlation corresponded with regard to sign and magnitude (-0.22 – Swan *et al.*, 1995; -0.23 – Brash *et al.*, 1997; -0.26 – Rose and Pepper, 1999). In the case of clean fleece weight, this correlation was positive (0.19). Literature estimates were similar in sign, but somewhat larger in magnitude (0.30 – Swan *et al.*, 1995; 0.40 – Atkins, 1997; 0.22 – Brash *et al.*, 1997; 0.38 – Cloete *et al.*, 1998*a*; 0.53 – Rose and Pepper, 1999; 0.31 – Cloete *et al.*, 2002*c*). Fleece weights were generally positively related to staple length (0.19 for greasy fleece weight and 0.36 for clean fleece weight). Corresponding correlations in the literature were 0.10 to 0.35 (Atkins, 1997) and 0.24 (Cloete *et al.*, 1998*a*). Selection for an increased fleece weight will thus result in a longer staple length, as was found by Cloete *et al.* (1998*a*).

Fleece weights were positively related to fibre diameter (0.45 for greasy fleece weight and 0.46 for clean fleece weight), suggesting that selection for fleece weight without cognisance of fibre diameter will lead to wool in breeding flocks becoming broader. Corresponding genetic correlations in the literature between clean fleece weight and fibre diameter were similar in sign and similar to somewhat smaller in magnitude (a mean estimate of 0.21 – Fogarty, 1995; 0.31 – Swan *et al.*, 1995; 0.15 to 0.20 – Atkins, 1997; 0.38 to 0.51 – Brash *et al.*, 1997; 0.14 – Purvis and Swan, 1997; 0.47 – Taylor *et al.*, 1997; 0.26 – Cloete *et al.*, 1998*a*; 0.25 – Taylor *et al.*, 1999; 0.14 – Rose and Pepper, 1999; 0.25 – Cloete *et al.*, 2002*c*). Total fold score was negatively related to clean yield (–0.35) and staple length (–0.41) on a genetic basis. The corresponding genetic correlations with both greasy fleece weight (0.41) and clean fleece weight (0.28) was positive. Atkins (1990) previously reported that fold development was more closely related to greasy fleece weight that to clean fleece weight. Corresponding genetic correlations with total fold score reported by Cloete *et al.* (1998*a*) amounted to 0.10 for clean fleece weight, –0.36 for clean yield and –0.50 for staple length.

The genetic correlation between testis measurements was unity, as also found by Duguma *et al.* (2002). Phenotypic and environmental correlations were equally high, at 0.84 and 0.75 respectively. Genetic correlations with hogget live weight were 0.73 for scrotal circumference and 0.72 for testis diameter. Corresponding correlations found by Duguma *et al.* (2002) amounted to 0.70 and 0.68, respectively.

Genetic and phenotypic trends

Phenotypic trends for hogget total fold score and scrotal circumference were indicative of divergent tendencies between the respective selection lines (Figure 1 and 2). Genetic trends indicated divergence ($P < 0.05$) in hogget live weight, total fold score and scrotal circumference. The genetic trends in live weight confirm previous observations in the same resource population with regard to live weight in mature breeding ewes (Cloete *et al.*, 2002*b*), as well as preliminary findings on hogget progeny (Cloete and Olivier, 1998). This trend is not unexpected, when the high genetic correlations between components of reproduction and ewe live weight is considered (Snyman *et al.*, 1997; 1998; Olivier *et al.*, 2001; Cloete *et al.*, 2002*d*). The trends with regard to total fold score are also consistent with preliminary findings (Cloete and Olivier, 1998). In the selection experiment of Atkins (1980), it has also been shown that divergent selection for fold development resulted in the reproduction of the folds plus line being impaired as a correlated response.

The genetic trends for the other traits of economic importance (fleece weight and fibre diameter) did not differ between lines. In this respect, generally positive genetic correlations were estimated between total weight of lamb weaned per ewe and ewe clean fleece weight (Snyman *et al.*, 1998; Cloete *et al.*, 2002*d*), although the majority of these genetic correlations did not reach a level of twice the corresponding standard error. The same basic results were obtained for the relationship of total weight of lamb weaned per ewe and fibre diameter. It should be stated that the preliminary study by Cloete and Olivier (1998) suggested possible divergent genetic trends in the resource population used in the present study. Based on these findings, the selection policy in the H line was adapted to only select a group of rams with an average fibre diameter equal or lower than the group mean for the ram hoggets available for selection. This check on fibre diameter probably contributed to the lack of a specific trend in the H line with regard to fibre diameter.

The genetic divergence between lines in scrotal circumference (see Figure 5) could be related to genetic changes of the respective lines in live weight, since no evidence of similar changes were derived from the analyses involving testis measurements corrected for live weight. This seems to be feasible if the high genetic correlations between live weight and testis measurements (present study; Duguma *et al.*, 2002) is considered. In the literature, it was demonstrated that the selection of rams on testis size corrected for live weight resulted in smaller breeding ewes (Haley *et al.*, 1990). When the reproduction of these ewes were adjusted for this reduction in live weight, it became clear that reproduction improved as a correlated response to selection for testis size, standardized for live weight.

Conclusions

Genetic parameters obtained from this study were consistent with published estimates. No detrimental correlated responses in other traits of economic importance could be found when divergent selection was based on ewe multiple rearing ability. The only genetic changes worth mentioning were H line animals that became heavier and plainer in fold development, whereas the L line animals became lighter, with more fold development. The South African Merino industry, in fact, favours heavier and plainer body types at this stage (Olivier, 1999), making these correlated changes desirable. No conclusive detrimental correlated genetic changes in qualitative or quantitative wool characteristics were found in either line.

Acknowledgements

We wish to thank all those responsible for the maintenance and recording of the experimental animals (Miss E. du Toit at Tygerhoek as well as Mr J.E. Fourie and Miss A.J. Scholtz at Elsenburg). The maintenance of the animals was partially enabled by a grant from the SA Wool Industry.

References

Atkins, K.D., 1980. Selection for skin folds and fertility. *Proceedings of the Australian Society of Animal Production* 13: 174 - 176.

Atkins, K.D., 1997. Genetic improvement of wool production. In: Piper, L.R., Ruvinsky, A. (Eds.). The genetics of sheep. CAB International, Wallingford UK. pp 471 - 504.

Brash, L.D., Taylor, P.J., Gilmour, A.R., 1997. Estimates of genetic parameters and environmental effcts for production traits in young Merino rams. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 12: 529 - 533.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J., 2002*a*. Responses of mature breeding ewes to selection for multiple rearing ability. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production* 30: 689 - 692. 18-23 August, Montpellier, France.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J., Van Wyk, J.B., 2002*b*. Genetic and phenotypic trends and parameters in reproduction, greasy fleece weight and live weight in Merino lines divergently selected for multiple rearing ability. *Australian Journal of Experimental Agriculture*, submitted.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2002*c*. Direct and maternal genetic (co)variances for hogget live weight and fleece traits in Western Australian Merino sheep. *Australian Journal of Agricultural Research* 53: 271 - 279.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2002*d*. Heritability estimates and genetic and phenotypic correlations of lamb production parameters with hogget live weight and fleece traits in Western Australian Merino sheep. *Australian Journal of Agricultural Research* 53: 281 - 286.

Cloete, S.W.P., Olivier, J.J., 1998. Direct and correlated responses to selection for multiple rearing ability in South African Merinos. *Proceedings of the Annual Congress of the South African Society for Animal Science* 36: 65 - 68.

Cloete, S.W.P., Olivier, J.J., Snyman, M.A., du Toit, E., 1998*a*. Genetic parameters and trends in a selection experiment for increased clean fleece weight involving South African Merinos. *Australian Journal of Experimental Agriculture* 38: 427 - 432.

Cloete, S.W.P., Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Scholtz, A.J., Cloete, J.J.E., 2002*e*. Mutual identification of ewes and lambs, as affected by divergent selection for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture*, submitted.

Cloete, S.W.P., Van Niekerk, F.E., Rust, J.M., 1998*b*. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *Sheep and Goat Research Journal* 14: 11 - 12.

Duguma, G., Cloete, S.W.P., Schoeman, S.J., Jordaan, G.F., 2002. Genetic parameters of testicular measurements in Merino rams and the influence of scrotal circumference on total flock fertility. *South African Journal of Animal Science* 32: 76 - 82.

Fogarty, N.M., 1995. Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction in sheep: a review. *Animal Breeding Abstracts* 63: 101 - 143.

Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R., 1999. ASREML – Reference manuel. *NSW Agriculture Biometric Bulletin* No. 3. NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia.

Haley, C.S., Lee, G.J., Ritchie, M., Land, R.P., 1990. Direct responses in males and correlated responses for reproduction in females to selection for testicular size adjusted for body weight in young male lambs. *Journal of Reproduction and Fertility* 89: 383.

Herselman, M.J., King, B.R., 1993. Effect of nutrition on wool production, body mass and pleat development in Merino rams. *Karoo Agric* 5(1): 3 - 7.

Hickson, J.D., Swan, A.A., Kinghorn, B.P., Piper, L.R., 1995. Maternal effects at different ages in Merino sheep. *Proceedings of the Australian Association of Animal Breeding and Genetics* 11: 416 - 420.

Land, R.B., 1973. The expression of female sex-limited characters in the male. *Nature, London* 241: 208 - 209.

Lewer, R.P., Woolaston, R.R., Howe, R.R., 1994. Studies on Western Australian Merino sheep. II Genetic and phenotypic parameter estimates for objectively measured traits on ram and ewe hoggets using different model types. *Australian Journal of Agricultural Research* 45: 829 - 840.

Meyer, K., 1989. Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative free algorithm. *Genetics, Selection and Evolution* 21: 317 - 340.

Mortimer, S.I., Atkins, K.D., 1994. Direct additive and maternal genetic effects on wool production in Merino sheep. *Proceedings of the 6th World Congress on Genetics Applied to Livestock Production* 18: 103 - 106.

Olivier, J.J., 1999. The South African Merino performance testing scheme. In: Rising to the challenge – Breeding for the 21st Century Customer. Beef Industry and CRC for Premium Quality Wool Industry Symposia. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 13:119 - 124.

Olivier, J.J., Erasmus, G.J., Van Wyk, J.B., Konstantinov, K.V., 1994. Direct and maternal variance component estimates for clean fleece weight, body weight and fibre diameter in the Grootfontein Merino stud. *South African Journal of Animal Science* 24: 122 - 124.

Olivier, W.J., Snyman, M.A., Olivier, J.J., Van Wyk, J.B., Erasmus, G.J., 2001. Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep. *South African Journal of Animal Science* 31: 115 - 121.

Ponzoni, R.W., Grinson, R.J., Jaensch, K.S., Smith, D.H., Gifford, D.R., Ancell, P.M.C., Walkley, J.R.W., Hynd, P.I., 1995. The Turretfield sheep breeding project: message on phenotypic and genetic parameters for South Australian Merino sheep. *Proceedings of the Australian Association for Animal Breeding and Genetics* 11: 303 - 313.

Purvis, I.W., Piper, L.R., Edey, T.N., Kilgour, R.J., 1988. The genetic relationship between ovulation rate and testicular diameter in a random breeding Merino flock. *Livestock Production Science* 18: 35 - 54.

Purvis, I.W., Swan, A.A., 1999. Can follicle density be used to enhance the rate of genetic improvement in Merino flocks? *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 12: 512 - 515.

Rose, M., Pepper, P.M., 1999. Genetic parameters for production traits in Queensland Merinos. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 13: 114 - 117.

Snyman, M.A., Olivier, J.J., Olivier, W.J., 1996. Variance components and genetic parameters for body weight and fleece traits of Merino sheep in an arid environment. *South African Journal of Animal Science* 26: 11 - 14.

Snyman, M.A., Cloete, S.W.P., Olivier, J.J., 1998*a*. Genetic and phenotypic correlations of total weight of lamb weaned with body weight, clean fleece weight, and mean fibre diameter in three South African Merino flocks. *Livestock Production Science* 55: 157 - 162.

Snyman, M.A., Erasmus, G.J., Van Wyk, J.B., Olivier, J.J., 1998*b*. Genetic and phenotypic correlations among production and reproduction in Afrino sheep. *South African Journal of Animal Science* 28: 74 - 81.

Swan, A.A., Lax, J., Purvis, I.W., 1995. Genetic variation in objectively measured wool traits in CSIRO'S fine wool flock. *Proceedings of the Australian Association for Animal Breeding and Genetics* 11: 516 - 520.

Taylor, P.J., Atkins, K.D., Gilmour, A.R., 1999. Genetic association between fibre curvature, staple crimp and wool production and quality of Merino sheep. *Proceedings of the Association for the Advancement of Animal breeding and Genetics* 13: 456 - 459.

Taylor, P.J., Gilmour, A.R., Crowe, D.W., Jackson, N., Atkins, K.D., 1997. Genetic parameters of objectively measured style traits in Merino fleeces. *Proceedings of the Association for the Advancement of Animal breeding and Genetics* 12: 149 - 152.

Turner, H.N., 1977. Australian sheep breeding research. *Animal Breeding Abstracts* 45: 9 - 31.

Verbyla, A.P., Cullis, B.R., Kenward, M.G., Welham, S.J., 1999. The analysis of designed experiments and longitudinal data using smoothing splines. *Journal of the Royal Statistical Society, Series C* 48: 269 - 311.

CHAPTER 16

AGE TRENDS IN ECONOMICALLY IMPORTANT TRAITS OF MERINO EWES SUBJECTED TO 10 YEARS OF DIVERGENT SELECTION FOR MULTIPLE REARING ABILITY

S.W.P. Cloete[1,2], A.R. Gilmour[3], J.J. Olivier[4], J.B. van Wyk[1]

[1]University of the Free State, PO Box 339,
Bloemfontein 9300, South Africa
[2]Elsenburg Agricultural Development Centre, Private Bag X1,
Elsenburg 7607, South Africa
[3]NSW Agriculture, Orange Agricultural Institute, Forest Road,
Orange 2800, NSW, Australia
[4]Irene Animal Improvement Institute, Private Bag X5013,
Stellenbosch 7599, South Africa

Submitted at:

South African Journal of Animal Science

Age trends in economically important traits of Merino ewes subjected to 10 years of divergent selection for multiple rearing ability

S.W.P. Cloete[1,2], A.R. Gilmour[3], J.J. Olivier[4] and J.B. van Wyk[1]

[1] University of the Free State, PO Box 339, Bloemfontein, 9300, South Africa
[2]Elsenburg Agricultural Centre, Private Bag X1, Elsenburg 7607, South Africa
[3]NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW Australia
[4]ARC:Animal Improvement Institute, Private Bag X5013, Stellenbosch 7599, South Africa

Abstract: Data were recorded for annual reproduction, wool traits and pre-joining live weight of between 992 (for staple strength) to approximately 1200 production records of Merino ewes over the period from 1997 to 2002. The resource population has been divergently selected from the same base since 1986, either for (H line) or against (L line) maternal multiple rearing ability. When expressed relative to mean L line performance, the advantage in reproduction for the H line amounted to 34 % for number of lambs born per ewe, 49 % for number of lambs weaned per ewe and 56 % for weight of lamb weaned per ewe ($P < 0.01$). Overall trends in reproduction with an increase in age from 2 to 7+ years were consistent with corresponding trends in the literature. The shape of these curves did not differ between selection lines, i.e. no significant interaction between selection line and ewe age was found. Maiden H line ewes were heavier ($P < 0.05$) than L line contemporaries. Ewe joining weight increased with age in both lines. Line differences were reduced to a tendency ($P < 0.10$) in 3 - year old ewes, and no subsequent line differences were found. The random non-linear component of the spline for ewe age also interacted ($P < 0.05$) with selection line for clean fleece weight. Conclusive advantages in favour of L line ewes were obtained at 3 to 6 years of age. In maiden ewes the line difference was restricted to a tendency ($P < 0.10$) in favour of the L line while no line difference occurred in 7-year old ewes. Ewes in the L line outperformed H line contemporaries for staple strength at 4 years of age, but no line difference were found at other ages. Coefficient of variation of fibre diameter and mean fibre diameter did not differ between lines ($P > 0.05$). Coefficient of variation of fibre diameter generally declined curvi-linearly with an increase in ewe age, while fibre diameter showed a near linear increase ($P < 0.05$). Estimates of h^2 for reproduction traits were 0.09 ± 0.05 for number of lambs born per ewe, 0.05 ± 0.05 for number of lambs weaned per ewe, and 0.05 ± 0.05 for weight of lamb weaned per ewe. Corresponding h^2 estimates for wool traits were 0.34 ± 0.08 for clean fleece weight, 0.05±0.05 for staple strength, 0.74 ± 0.02 for coefficient of variation and 0.76 ± 0.02 for fibre diameter. A h^2 estimate of 0.3 ± 0.09 was obtained for ewe live weight at joining. Ewe permanent environment (c^2_{ewe}) for the reproduction traits were 0.15 ± 0.05 for number of lambs born per ewe, 0.19 ± 0.05 for number of lambs weaned per ewe and 0.19 ± 0.05 for weight of lamb weaned per ewe. The corresponding c^2_{ewe} estimate for ewe joining weight was 0.40 ± 0.09, while those for annual wool production traits were 0.31 ± 0.08 for clean fleece weight and 0.12 ± 0.05 for staple strength. Coefficient of variation and mean fibre diameter were not influenced by the ewe permanent environment. Line differences in age trends for wool traits and ewe joining weight were attributed to the drainage by reproduction on the reserves of H line ewes.

Keywords: Age trends, lamb output, clean fleece weight, staple strength, ewe joining weight, smoothing splines

Introduction

Previous work at this institution indicated that divergent selection for ewe multiple rearing ability resulted in lines differing widely in lamb output (Cloete and Scholtz, 1998). Given that lamb and mutton are in demand by the South African consumer, this difference has considerable economic implications. Over the past decade, fluctuations in the ratio between wool and meat prices have resulted in the shifting of the emphasis between the two products during selection. This resulted in distinct changes in the South African Merino industry. The breeding strategy was adapted to enable an improved meat production capability (Olivier, 1999). It is well known that wool prices improved substantially over the last season, impacting on the income derived by farmers from that source. The implications of the strategy of selecting for an improved reproduction rate on other traits contributing to the lifetime income from ewes have, so far, not been studied in detail.

Against this background, we compared the performance of breeding ewes selected divergently for multiple rearing ability with regard to wool and live weight traits. In the previous study, it became clear that ewe permanent environmental correlations of reproduction with wool traits and live weight differed markedly from corresponding genetic correlations with regard to sign and magnitude (Cloete *et al.*, 2002*a*). The implications of a strategy for the improvement of reproduction on performance of ewes in the current flock thus needs to be studied further.

Material and methods

Two lines of Merino sheep were selected divergently from the same base population since 1986, using maternal ranking values for lambs reared per joining (Cloete and Scholtz, 1998). Ewe and ram replacements in the High (H) line were preferably the progeny of ewes rearing more than one lamb per joining (*i.e.* reared twins at least once). The progeny of ewes rearing fewer than one lamb per joining (*i.e.* barren or lost all lambs born at least once) were preferred as replacements in the Low (L) line. Depending on the average reproduction of the lines and the replacement needs, progeny of ewes that reared one lamb per joining were occasionally accepted in both lines. Selection decisions were mostly based on ≥ 3 maternal joinings, especially in the case of rams. Once selected, ewes normally remained in the breeding flock for five joinings. The H line was augmented by 28 ewe progeny born from an embryo transfer program during 1991 and 1992 (Cloete *et al.*, 1998). The mean performance of the ewes derived in this way was similar to that recorded in the H line, and they were treated as one group.

For the duration of the experiment (1997 to 2002, after at least 10 years of divergent selection), the two lines were maintained as a single flock, except during joining over a 6-week period in single sire groups to 4 - 5 rams during January - February each year. The lines were maintained on the Elsenburg experimental farm near Stellenbosch at this stage. Cloete and Scholtz (1998) and Cloete *et al.* (2002*a*) detailed the locality and the management practices implemented, as well as the recording of data in the flock. Reproduction traits under consideration included repeated records of number of lambs born per ewe, number of lambs weaned per ewe and total weight of lamb weaned per ewe (corrected for gender and birth year), as defined by Cloete *et al.* (2002*a*). Live weight at joining and annual greasy fleece weight were also recorded. A wool sample was taken at shearing from individual ewes, and analysed for clean yield, staple strength, coefficient of variation of fibre diameter as well as mean fibre diameter. Clean yield was used to calculate clean fleece weight.

ASREML (Gilmour *et al.*, 1999) was used to estimate variance components for the reproduction traits, clean fleece weight, staple strength, coefficient of variation, mean fibre diameter and live weight in single-trait, repeated records analyses. The analysis of discrete data such as number of lambs born and weaned with parametric methods used in the present study is not optimal, as was outlined by Purvis and Hillard (1997). The availability of suitable software, and the close approximation of outcomes from linear models to that derived from non-linear methods has resulted in recommendations that the former methods could be employed until alternative software packages become readily available (Jorhensen, 1994; Brien *et al.*, 2002). Direct additive genetic effects and permanent environmental ewe effects were computed where applicable, as determined by the derived log likelihood tests. The statistical modelling and assumptions were similar to that described by Cloete *et al.* (2002*a*). A random effect of service sire was initially included in the analyses for reproduction traits, but it was found not to affect ($P > 0.05$) log likelihood values, and was thus excluded from the final runs. A cubic spline (Verbyla *et al.*, 1999) was used to model changes in production with age. The interaction of selection line with the linear and curvilinear components of the spline was fitted initially, and retained in the final analyses where significant.

Results

All measures of overall reproduction over the 6-year study period were markedly higher ($P < 0.01$) in the H line than in the L line (Table 1).

Table 1. Least squares means (± *SE*) for reproduction traits and live weight at joining in 1199 records from ewes in the H and L lines, as affected by selection line and age. Means for selection line were predicted at and average ewe age.

Fixed effect	**Trait**			
	Number of Lambs born per ewe	**Number of Lambs weaned per ewe**	**Weight of lamb weaned per ewe (kg)**	**Live weight at joining (kg)**
Overall mean	1.23 ± 0.05	0.97 ± 0.04	20.6 ± 0.9	50.2 ± 0.6
Year	NS	NS	NS	**
Selection line	**	**	**	NS
H Line	1.41 ± 0.06	1.16 ± 0.05	25.1 ± 1.0	50.8 ± 0.7
L Line	1.05 ± 0.06	0.78 ± 0.06	16.1 ± 1.1	49.7 ± 0.7
Age at lambing	**	**	**	**
2 years	0.81 ± 0.05	0.65 ± 0.05	13.7 ± 1.0	40.0 ± 0.6
3 years	1.07 ± 0.05	0.86 ± 0.04	18.3 ± 0.9	47.0 ± 0.6
4 years	1.23 ± 0.05	0.97 ± 0.04	20.6 ± 0.9	50.3 ± 0.6
5 years	1.29 ± 0.05	0.98 ± 0.04	20.9 ± 0.9	51.9 ± 0.5
6 years	1.28 ± 0.05	0.90 ± 0.05	19.3 ± 0.9	53.3 ± 0.5
7+ years	1.26 ± 0.07	0.74 ± 0.07	15.4 ± 1.5	54.4 ± 0.7

NS Not significant ($P > 0.05$)

** Significant ($P < 0.01$)

Expressed relative to mean L line performance, the advantage in the H line amounted to 34 % for number of lambs born, 49 % for number of lambs weaned and 56 % for weight of lamb weaned. The linear and non-linear spline components of age at lambing did not interact with selection line for the reproduction traits ($P > 0.05$). Trends for total weight of lamb weaned are provided as illustration in Figure 1.

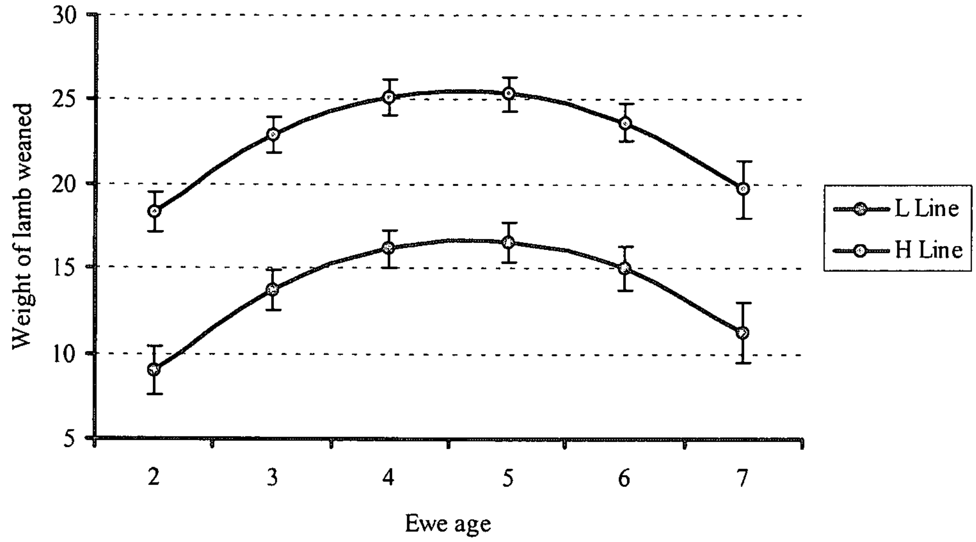


Fig. 1. Age trends in total weight of lamb weaned in H and L line ewes. Vertical bars about the means denote standard errors.

It is clear that the shape of the curves were similar for the two lines, but that the mean performance levels in the H line exceeded those in the L line. Number of lambs born and weaned per ewe, as well as total weight of lambs weaned per ewe increased ($P < 0.05$) with age to reach a maximum by 4 to 5 years (Table 1). A subsequent decline followed in number and total weight of lamb weaned per ewe, but not for number of lambs born per ewe.

Fig. 2. Age trends in ewe joining weight in H and L line ewes. Vertical bars about the means denote standard errors.

Selection line interacted ($P < 0.05$) with the linear component of the spline for ewe age in the case of live weight at joining. This interaction is depicted in Figure 2. Ewes in the H line were 5 % heavier ($P < 0.05$) than L line contemporaries at 2 years of age (41.0 ± 0.7 *vs*. 38.9 ± 0.8 kg respectively). Live weight increased ($P < 0.01$) with age in both lines, but the initial line difference was reduced to a tendency ($P < 0.10$) at 3 years of age. No line difference were found at later ages.

Overall means for clean fleece weight and staple strength suggested differences in favour of the L line for these traits (Table 2). The interpretation of results for these traits were, however, complicated by significant interactions of selection line with the curvilinear spline components for ewe age. Ewes in the L line had a higher ($P < 0.05$) clean fleece weight than H line contemporaries at 3 to 6 years of age. Ewes in the H line tended ($P < 0.10$) to have a lower clean wool production at 2-years of age than their L line contemporaries (3.45 ± 0.8 *vs*. 3.63 ± 1.0 kg respectively). In older ewes, very little evidence of an increase in clean fleece weight with age were observerved in the H line, while wool production increased ($P < 0.05$) to higher levels in 4-year old ewes belonging to the L line (Figure 3). A subsequent decline in fleece weight followed in L line, so that no line difference was observed in 7-year old ewes.

Table 2. Least squares means (± *SE*) for wool traits in 1199 records from ewes in the H and L lines (991 records in the case of staple strength), as affected by selection line and age. Means for selection line were predicted at and average ewe age.

Fixed effect	**Trait**			
	Clean fleece weight (kg)	**Staple strength (N/ktex)**	**Coefficient of variation (%)**	**Fibre diameter (μm)**
Overall mean	3.78 ± 0.06	43.6 ± 1.0	19.4 ± 0.3	22.5 ± 0.2
Year	**	**	**	*
Selection line	*	*	NS	NS
H Line	3.59 ± 0.08	40.9 ± 1.3	19.3 ± 0.3	22.6 ± 0.2
L Line	3.96 ± 0.09	46.4 ± 1.6	19.6 ± 0.4	22.4 ± 0.3
Age at lambing	**	**	*	**
2 years	3.54 ± 0.07	54.8 ± 1.1	20.3 ± 0.3	21.4 ± 0.2
3 years	3.72 ± 0.07	39.7 ± 1.0	19.7 ± 0.3	22.0 ± 0.2
4 years	3.78 ± 0.06	43.5 ± 1.1	19.4 ± 0.3	22.5 ± 0.2
5 years	3.74 ± 0.06	45.9 ± 1.1	19.4 ± 0.3	23.0 ± 0.2
6 years	3.67 ± 0.06	48.3 ± 1.2	19.4 ± 0.3	23.4 ± 0.2
7+ years	3.61 ± 0.08	53.8 ± 1.6	19.0 ± 0.3	23.8 ± 0.2

NS Not significant ($P > 0.05$)

* Significant ($P < 0.05$)

** Significant ($P < 0.01$)

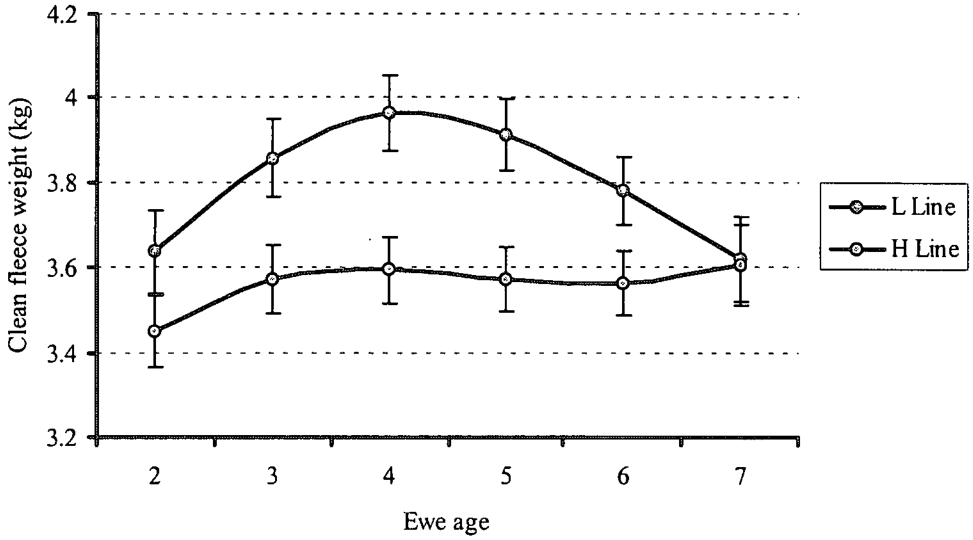


Fig. 3. Age trends in clean fleece weight in H and L line ewes. Vertical bars about the means denote standard errors.

Means for staple strength declined ($P < 0.05$) in both lines from 2 to 3 years of age (Figure 4). This decline was followed by a general increase in subsequent age groups (Table 2). The only age group where a 12 % advantage in favour of L line ewes could be discerned in staple strength, was in 4-year old ewes (40.8 ± 1.3 *vs.* 46.3 ± 1.6 N/ktex respectively).

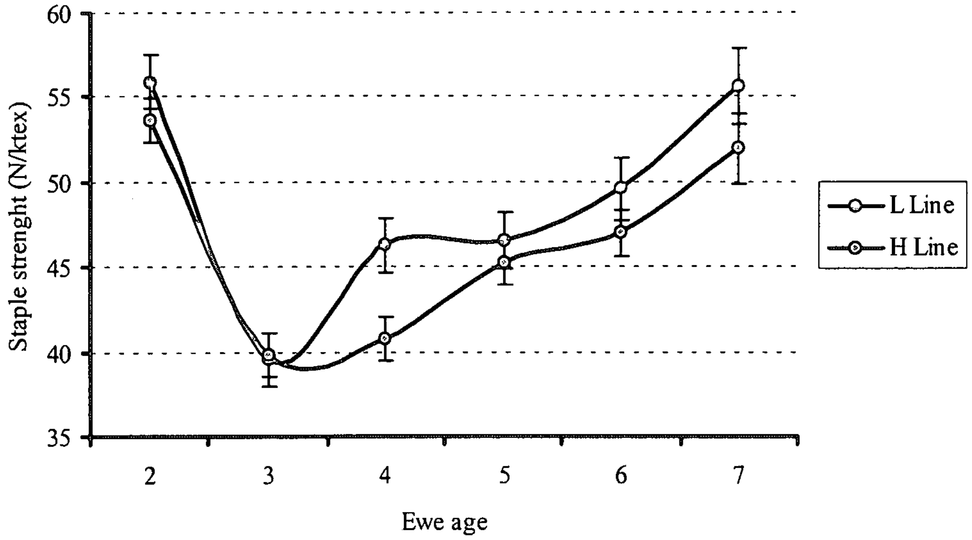


Fig. 4. Age trends in staple strength in H and L line ewes. Vertical bars about the means denote standard errors.

Selection line and ewe age were not involved in any interactions in the case of coefficient of variation and fibre diameter. Both traits were independent of selection line (Table 2). Coefficient of variation showed a declining tendency ($P < 0.05$) with age, and stabilized at approximately 19.4 % from 4 years of age onwards. Fibre diameter showed a near linear increase ($P < 0.05$) with age, to reach nearly 24 µm in 7-year old ewes.

Heritabilities obtained for the reproduction traits were consistently below 0.1 (Table 3). Ewe permanent environmental variance ratios were somewhat higher, approaching 0.2 for number and weight of lamb weaned per ewe. In the case of live weight at joining and clean fleece weight, h^2 estimates approached 0.4 while it exceeded 0.7 in analyses on coefficient of variation of fibre diameter and mean fibre diameter. Staple strength was lowly heritable, at 0.05. Estimates of c^2 were between 0.3 and 0.4 for ewe joining weight and clean fleece weight, and 0.12 for staple stength. Ewe permanent environmental effects were not significant for coefficient of variation of fibre diameter as well as mean fibre diameter.

Table 3. Variance components and ratios for traits of economic importance in mature breeding ewes in the H and L lines.

Trait	Variance components			Variance ratios	
	σ^2_a	σ^2_{pe}	σ^2_e	h^2	c^2_{pe}
Number of lambs born	0.0375	0.0667	0.3318	0.09 ± 0.05	0.15 ± 0.05
Number of lambs weaned	0.0201	0.0830	0.3243	0.05 ± 0.05	0.19 ± 0.05
Weight of lamb weaned (kg)	8.8327	32.992	130.63	0.05 ± 0.05	0.19 ± 0.05
Ewe joining weight (kg)	11.160	12.049	6.6957	0.37 ± 0.09	0.40 ± 0.09
Clean fleece weight (kg)	0.1388	0.1264	0.1394	0.34 ± 0.08	0.31 ± 0.08
Staple strength (N/ktex)	8.6737	19.670	139.61	0.05 ± 0.05	0.12 ± 0.05
Coefficient of variation (%)	4.1542	**n.a.**	1.4778	0.74 ± 0.02	**n.a.**
Fibre diameter (μm)	2.4194	**n.a.**	0.7694	0.76 ± 0.02	**n.a.**

σ^2_a – Direct additive variance; σ^2_{pe} – Ewe permanent environmental variance; σ^2_e – Environmental variance; h^2 – Heritability; c^2_{pe} – Ewe permanent environmental variance ratio; **n.a.** – Not applicable

Discussion

The general trends in ewe reproduction with an increase in age were consistent with those reported by Fourie and Heydenrych (1983*a*), Brash *et al.* (1994*a*) and Cloete *et al.* (2002*a*). The H line had an advantage ($P < 0.01$) relative to the L line with regard to lamb output, as was reported previously (Cloete and Scholtz, 1998; Cloete *et al.*, 2002*a*). Selection for total weight of lamb weaned in the United States led to similar benefits (Ercanbrack and Knight, 1998).

At 2 years of age, H line ewes were heavier ($P < 0.05$) than contemporaries in the L line. This line difference was consistent with genetic trends in the two lines, where H line progeny became heavier and plainer relative to the L line (Cloete and Olivier, 1998). It also accords with genetic correlations estimated earlier in the same resource population (Cloete *et al.*, 2002*a*). The difference, however, declined at later ages, and L line ewes were as heavy as H line contemporaries at 4 years of age and older. This result could be ascribed to the greater demands of a higher reproduction rate on the reserves of H line ewes. In the literature, lactating ewes were also shown to be leaner, and lower in live weight than non-lactating ewes (Lee and Atkins, 1995). It should also be seen in relation to the relatively high unfavourable ewe permanent environmental correlations between weight of lamb weaned and live weight at joining obtained earlier (Cloete *et al.*, 2002*a*). Age trends in ewe joining weight were consistent with those reported in the literature (Fourie and Heydenrych, 1983*b*).

Ewes in the L line had a higher ($P < 0.05$) clean fleece weight than H line contemporaries at ages from 3 to 6 years of age. The trend in clean fleece weight with age in the L line conformed to results in the literature (Fourie and Heydenrych, 1983*b*), while the H line ewes showed an atypical trend. This line difference could be attributed to the greater metabolic demands associated with an increased reproduction rate, since genetic trends for fleece weight in the two lines showed no evidence of a genetic divergence for clean fleece weight (Cloete and Olivier, 1998). The genetic correlation between greasy fleece weight and reproduction in the same resource population were correspondingly low in magnitude and variable in sign (Cloete *et al.*, 2002*a*). Ewe permanent environmental correlations of greasy fleece weight with reproduction were, on the other hand, relatively high and unfavourable. The impact of reproduction on fleece production has been quantified in the literature (Charlick and Arnold, 1990; Lee and Atkins, 1995; Hinch *et al.*, 1996). Compared to barren ewes, the penalty in fleece weight were 652 g in ewes rearing singles, and 846 g in ewes rearing twins (Charlick and Arnold, 1990). Comparable estimates in high fecundity Border Leicester X Merino ewes were 530 g for ewes bearing singles, 610 g for ewes bearing twins and 880 g for ewes bearing triplets (Hinch *et al.*, 1996). At this stage, the reason for the decline in clean fleece weight of L line ewes relative to H line ewes at ages older than 5 years is unclear.

Staple strength of L line ewes was superior ($P < 0.05$) to that of H line contemporaries at four years of age. Given that staple strength is known to be reduced by reproduction (Hinch *et al.*, 1996; Cloete *et al.*, 2000), this result was not entirely unexpected. The reason why it only involved 4 - year old ewes are, however, not clear. Staple strength was generally well above the value of 25 to 30 N/ktex which is generally considered as sound (Read, 1996; Scrivener and Vizard, 1997). In previous work at this institute, it was demonstrated that wool of ewes subjected to pre-lamb shearing was more sound ($P < 0.05$) than that of ewes shorn before joining, with fewer mid-staple breaks (Cloete *et al.*, 2000). The practice of pre-lamb shearing employed in the resource population used may thus well have contributed to the general soundness of the wool tested. The obtained age trends in staple strength could not be validated from the literature. Age did not have a uniform effect on staple strength in the study of Scrivener and Vizard (1997), but it was stated that the oldest age group had the highest staple strength in one year of a 2-year study. Is has also been shown that the staple strength of breeding ewes was reduced relative to 10- and 16-month old replacements (Greeff *et al.*, 1995). Maiden ewes correspondingly had a lower ($P < 0.01$) mean staple strength than adult ewes in the study of Hinch *et al.* (1996), when shorn late in October after lambing in July. In our study, with ewes being shorn prior to lambing, the low staple strength of ewes lambing at three years of age could possibly be related to a carry-over effect from the previous lambing as maidens (Figure 4).

Coefficient of variation of fibre diameter as well as fibre diameter was unaffected by selection line. In the sense that fibre diameter is one of the most important determinants of wool price (Purvis, 1995), this result is pleasing. It should, however, be kept in mind that higher reproducing ewes are known to produce finer fleeces than lower reproducing contemporaries (Cloete *et al.*, 2000). Genetic trends in the resource population used were inconclusive in this respect, although H line progeny tended to become stronger while L line progeny tended to become finer (Cloete and Olivier, 1998). The increase in fibre diameter with ewe age is consistent with trends reported in Australia (Atkins, 1990; Hickson *et al.*, 1995).

The h^2 estimate for number of lambs born per ewe in Table 3 accorded with estimates in the literature (0.06 – Brash *et al.*, 1994*a*; 0.03 – Brash *et al.*, 1994*b*; 0.07 to 0.12 – Bromley *et al.*, 2000; 0.06 to 0.10 – Cloete *et al.*, 2002*a*; 2002*c*). In the case of number of lambs weaned per ewe, h^2 was estimated at 0.05. Comparable estimates in the literature were 0.06 (Brash *et al.*, 1994*a*), 0.03 (Brash *et al.*, 1994*b*), 0.03 to 0.07 (Bromley *et al.*, 2000); 0.04 (Swan *et al.*, 2001) and 0.04 (Cloete *et al.*, 2002*a*; 2002*c*). The present h^2 estimate for total weight of lamb weaned per ewe (0.05) accorded with those of Bromley *et al.* (2001), ranging from 0.02 to 0.11. A previous estimate on a larger data set, but using the same resource population, amounted to 0.04 (Cloete *et al.*, 2002*a*). It was also closely associated with an estimate of 0.05 made in a Western Australian resource flock (Cloete *et al.*, 2002*c*). Estimates of c^2_{pe} for the reproduction traits in the present study exceeded 0.15 in all cases. Corresponding estimates reported by Bromley *et al.* (2000) were somewhat lower, at

0.01 to 0.07. Swan *et al.* (2001) reported a c^2_{pe} estimate of 0.09 for number of lambs weaned per ewe.

The h^2 estimate for live weight at joining was consistent with that of 0.46 reported by Swan *et al.* (2001). The latter study also reported a c^2_{pe} estimate of 0.13 for live weight, which was somewhat lower than that reported in this study. In a previous study on live weight at joining in the same resource population, but using the complete data set, h^2 was estimated at 0.49 and c^2_{pe} at 0.25 (Cloete *et al.*, 2002*a*). Estimates for the h^2 of fleece weight ranged from 0.47 to 0.55 in the studies of Bromley *et al.* (2000; 2001), which were slightly higher than our estimate of 0.31. In a previous study on greasy fleece weight in the same resource population, but using a larger data set, h^2 was estimated at 0.53 (Cloete *et al.*, 2002*a*). The present estimate of 0.31 is, however in good agreement with corresponding estimates reported for a number of studies on yearling and hogget sheep (see Cloete *et al.*, 2002*b* for summary). Bromley *et al.* (2000) reported c^2_{pe} estimates ranging from 0.08 to 0.17 for clean fleece weight in four breeds. The corresponding estimate from the present study was somewhat higher, at 0.31. This estimate is in good agreement with a previous estimate of 0.25 on the same resource population, but employing a larger data set (Cloete *et al.*, 2002*a*).

No estimates where the between ewe variance for staple strength in mature ewes was partitioned in genetic and ewe permanent environmental components were found in the literature. From the present data, repeatability (the sum of the former components) was estimated at 0.17 for staple strength. Greeff *et al.* (1995) estimated h^2 of staple strength at 0.25 in mature ewes at the great Southern Research Centre. From the information provided in the reference, this estimate seems to be the sum of genetic and ewe permanent environmental effects. It thus appears to be in correspondence with the present estimate. Estimates of h^2 for coefficient of variation and fibre diameter were well in excess of 0.70 in the present study. Comparable estimates on repeated records of ewes could not be found, but estimates of the same magnitude are commonly found in studies on yearling and hogget sheep (see Cloete *et al.*, 2002*b* for summary).

Conclusions

The estimation of genetic parameters was not considered as the primary objective of the study. It is nonetheless mentionable that estimates were in general agreement with those cited from the literature, despite the small size of the data set used. The study indicated that high levels of reproduction were attainable in pasture-fed sheep flocks selected for multiple rearing ability. On the down side, it was shown that H line ewes failed to carry their advantage in live weight through to an age where they would, generally, be cast for age. Clean wool production was also impaired in H line ewes aged between 3 and 6 years, which is generally regarded as the most productive years from a wool production perspective (Fourie and Heydenrych, 1983*b*). The penalties in live weight and wool traits in the current flock that could be associated with an increased reproduction should be balanced against the improvement in income derived from the production of lamb. The economic implications thereof would strongly depend on the ratio between the prices of wool and meat.

Acknowledgements

We wish to thank those responsible for the maintenance and recording of the experimental animals (J.E. Fourie, J.J.E. Cloete and Miss A.J. Scholtz). The maintenance of the animals was partially enabled by a grant from the SA Wool Industry.

References

Atkins, K.D., 1990. Incorporating parameters for lifetime productivity into breeding objectives for sheep. *Proceedings of the 4th World Congress on Genetics Applied to Livestock Production*, Edinburgh 15: 17 - 26.

Brash, L.D., Fogarty, N.M., Gilmour, A.R., 1994*a*. Reproductive performance and genetic parameters for Australian Dorset sheep. *Australian Journal of Agricultural Research* 45: 427 - 441.

Brash, L.D., Fogarty, N.M., Gilmour, A.R., 1994*b*. Genetic parameters for Australian maternal and dual-purpose meatsheep breeds. II. Liveweight, wool and reproduction in Corriedale sheep. *Australian Journal of Agricultural Research* 45: 469 - 480.

Brien, F.D., Konstantinov, K.V., Greeff, J.C., 2002. Comparison of linear and threshold models for predicting direct and maternal genetic effects on number of lambs weaned in Western Australian Merinos. *Proceedings of the 7th World Congress on Genetics Applied to Livestock Production,* 18 - 23 August, Montpellier, France. 32: 307 - 310.

Bromley, C.M., Snowder, G.D., Van Vleck, L.D., 2000. Genetic parameters among weight, prolificacy, and wool traits of Columbia, Polypay, Rambouillet, and Targhee sheep. *Journal of Animal Science* 78: 846 - 858.

Bromley, C.M., Van Vleck, L.D., Snowder, G.D., 2001. Genetic correlations for litter weight weaned with growth, prolificacy, and wool traits in Columbia, Polypay, Rambouillet, and Targhee sheep. *Journal of Animal Science* 79: 339 - 346.

Charlick, A.J., Arnold, G.W., 1990. Effect of bearing and rearing lambs on Merino wool production. *Australian Journal of Experimental Agriculture* 30: 591 - 594.

Cloete, S.W.P., Gilmour, A.R., Olivier, J.J., Van Wyk, J.B., 2002*a*. Genetic and phenotypic trends and parameters in reproduction, greasy fleece weight and live weight in Merino lines divergently selected for multiple rearing ability. *Australian Journal of Experimental Agriculture*, submitted.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2002*b*. Direct and maternal genetic (co)variances for hogget live weight and fleece traits in Western Australian Merino sheep. *Australian Journal of Agricultural Research* 53: 271 - 279.

Cloete, S.W.P., Greeff, J.C., Lewer, R.P., 2002*c*. Genetic and environmental variances in lamb production traits of Merino ewes in a Mediterranean environment. *Inaugural Wool Technology Conference*, Hamilton, Victoria, Australia 15 - 17 October 2001.

Cloete, S.W.P., Muller, C.J.C., Durand, A., 2000. The effects of shade and shearing date on the production of Merino sheep in the Swartland region of South Africa. *South African Journal of Animal Science* 30:164 - 171.

Cloete, S.W.P., Olivier, J.J., 1998. Direct and correlated responses to selection for multiple rearing ability in South African Merinos. *Proceedings of the Annual Congress of the South African Society for Animal Science* 36: 65 - 68.

Cloete, S.W.P. and Scholtz, A.J., 1998. Lamb survival in relation to lambing and neonatal behaviour in medium wool Merino lines divergently selected for ewe multiple rearing ability. *Australian Journal of Experimental Agriculture* 38: 801 - 811.

Cloete, S.W.P., Van Niekerk, F.E. and Rust, J.M., 1998. Application of embryo transfer for the improvement of multiple rearing ability in medium wool Merino ewes. *International Sheep and Goat Research Journal* 14:11 - 12.

Ercanbrack, S.K., Knight, A.D., 1998. Responses to various selection protocols for lamb production in Rambioullet, Targhee, Columbia and Polypay sheep. *Journal of Animal Science* 76: 1311 - 1325.

Fourie, A.J., Heydenrych, H.J., 1983*a*. Phenotypic and genetic aspects of production in the Dohne Merino. III. The influence of age of the ewe on reproductive performance. *South African Journal of Animal Science* 13: 164 - 166.

Fourie, A.J., Heydenrych, H.J., 1983*b*. Phenotypic and genetic aspects of production in the Dohne Merino. IV. The influence of age of the ewe on production traits. *South African Journal of Animal Science* 13: 167 - 170.

Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R. 1999. ASREML – Reference manuel. NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800, NSW, Australia. *NSW Agriculture Biometric Bulletin* No. 3.

Greeff, J.C., Lewer, R.P., Ponzoni, R.W., Purvis, I.W., 1995. Staple strength: progress towards elucidating its place in Merino breeding. *Proceedings of the Australian Association for Animal Breeding and Genetics* 11: 595 - 601.

Hickson, J.D., Kinghorn. B.P., Piper, L.R., Swan, A.A., 1995. Micron blowout – using available genetic variation. *Proceedings of the Australian Association of Animal breeding and Genetics* 11: 529 - 533.

Hinch, G.N., Lynch, J.J., Nolan, J.V., Leng, R.A., Bindon, B.M., Piper, L.R., 1996. Supplementation of high fecundity Border Leicester X Merinos ewes with a high protein feed: its effect on lamb survival. *Australian Journal of Experimental Agriculture* 36: 129 - 136.

Jorgensen, J.N., 1994. Estimation of genetic parameters for litter size in sheep using a non-linear method. *Acta Agriculturae Scandinavica. A. Animal Science* 44: 8 - 11.

Lee, G.J., Atkins, K.D., 1995. Consequences of reproduction on live weight, fat depth, wool growth, and intake of grazing Merino ewes in the short and long term. *Australian Journal of Experimental Agriculture* 35: 153 - 159.

Olivier, J.J., 1999. The South African Merino performance testing scheme. In: Rising to the challenge – Breeding for the 21st Century Customer. Beef Industry and CRC for Premium Quality Wool Industry Symposia. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 13:119 - 124.

Purvis, I.W., 1995. Strategies for improving wool quality and productivity in fine and superfine woolled Merino flocks. *Proceedings of the Australian Association of Animal breeding and Genetics* 11: 510 - 515.

Purvis, I.W., Hillard, M., 1997. Biology and genetics of reproduction. In: Piper, L. and Ruvinsky, A., (Eds.). 'The genetics of sheep'. CAB International, Wallingford, Oxon, United Kingdom. Pp 375 - 394.

Read, S., 1996. Consumer demands of wool beyond 2000. Demands of wool and wool growers beyond 2000. *SARDI Research report series*, No 11. pp. 5 - 13.

Scrivener, C.J., Vizard, A.L., 1997. The relationship between reproductive performance, time of lambing and the staple strength of wool from Merino ewes. *Wool Technology and Sheep Breeding* 45: 120 - 128.

Swan, A.A., Piper, L.R., Brewer, H.G., Purvis, I.W., 2001. Genetic variation in reproductive performance of fine wool Merinos. *Proceedings of the Association for the Advancement of Animal Breeding and Genetics* 14: 417 - 420.

Verbyla, A.P., Cullis, B.R., Kenward, M.G., Welham, S.J., 1999. The analysis of designed experiments and longitudinal data using smoothing splines. *Journal of the Royal Statistical Society, Series C* 48: 269 - 311.

Chapter 17

General Conclusions

Individual chapters included in this dissertation already carry abstracts. This chapter therefore attempts to summarize the objectives, and the outcomes generated. The recommendations made by Haughey (1989) forms the basis of discussion.

Levels and causes of reproduction failure in commercial sheep flocks

It was found that levels of reproduction failure were high to very high in the high potential district of Bredasdorp (see Chapter 2). It seems reasonable to assume that reproduction failure will also be high in other parts of the country. Similar conclusions were derived at in the experimental flocks that contributed data to Chapter 2. Both studies seemed to indicate that rearing failure was repeatable, and that selection progress (at least in the current flock) is likely. Causes of mortality could not be assessed on a broader basis in all major sheep producing areas, as recommended by Haughey (1989). Results obtained from experimental flocks and provided in Chapters 4 and 10 were, however, consistent with the contentions made by Haughey (1989) that parturient deaths as well as starvation, mismothering and exposure contributed largely to overall lamb deaths, and consequently rearing failure.

The study of rearing failure in relation to maternal pelvic size

Radiographic pelvimetry methods were adapted for South African sheep breeds for this part of the study (Cloete and Haughey, 1990). It was demonstrated that repeated rearing failure of ewes were phenotypically related to one or more pelvic dimensions in the majority of flocks considered (Chapter 3). The exception in this regard was the Elsenburg Dormer flock, where no relationship was evident (Chapters 3 and 6). The relationships between pelvic dimensions, length of parturition and rearing failure was, however, not strong enough to allow accurate predictions on an individual basis in flocks where it existed. A personal disappointment was the fact that sufficient data for the assessment of possible changes in the pelvic dimensions of the H and L lines were not available. The commercial x-ray unit that allowed us to do the studies reported in Chapters 3 and 6 broke down during 1997/98, and ewes born from 1994 onwards in the H and L lines could thus not be assessed. In this respect, it has been shown that the pelvic dimensions of the Trangie Fertility flock (selected against barrenness and rearing failure) were larger than those of an unselected control flock (Kilgour and Haughey, 1993).

Breeding studies to investigate the improvement of rearing ability

Progress in this field was reported in Part 3 of this dissertation. Because this work formed the bulk of the study, it is possible to be very elaborate on the results that were obtained. It would, however, suffice to say that genetic progress comparable to that achieved in other production traits were realised for weight of lamb weaned per ewe (Chapter 14). Selection for the ability of ewes to rear multiples resulted in behavioural adaptations that would be conducive to lamb survival (Chapters 8 to 11). These results were confirmed by genetic and phenotypic divergence in behavioural traits that were derived both for ewes and for lambs (Chapters 9 and 12).

Responses in behaviour were achieved with minimal unfavourable genetic changes in other traits of economic importance, both in lamb weaning weight (Chapter 13), and in the hogget performance of replacements from the respective lines (Chapter 15). The higher reproduction rate achieved by mature H line breeding ewes resulted in live weight and wool traits being compromised to an extent (Chapter 16). This result was not entirely unexpected, since the impact of the bearing and rearing of lambs on the live weight and fleece production of ewes is well known (Lee and Atkins, 1995).

Given the relative performance of the H and L line, readers may wonder about the possibility of inbreeding depression being involved in the line differences that were reported in Chapters 13 to 15. The average inbreeding coefficients of the H and the L lines are thus presented in Figure 1. Inbreeding increased with time, as is expected in any population of finite size. Inbreeding in the H and L lines was, however, similar by the end of the experimental period. The average inbreeding coefficients in both lines were below 2.5 % at this stage. The maximum individual inbreeding coefficients in both lines over the period from 1994 onwards oscillated between 5 and 15 % within birth years. In view of this information, it appears to be highly unlikely that inbreeding played a role in the outcome of the experiment.

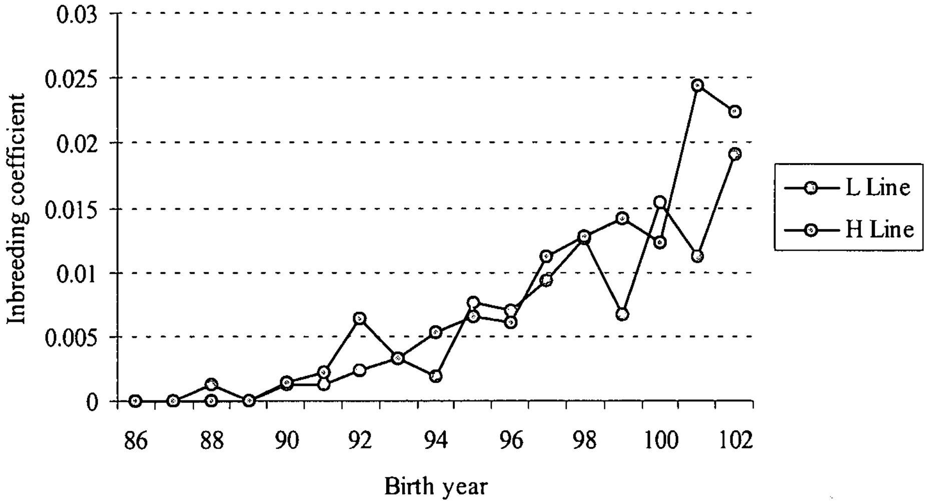


Fig. 1. Mean inbreeding coefficients of lambs born in the H and L lines during the experimental period.

Lambing management

This topic was not studied explicitly in designed experiments during the course of the study. It was, however, clear that known management factors considered in the study reported in Chapter 2 could not conclusively be related to reproductive failure. The exception was size of the breeding flock. This result could possibly be related to the findings pertaining to the impact density of lambed ewes had on the frequency of separation of ewes from one or more lambs (Chapter 4). Separation of ewes from one or more lambs was also related to the period ewes spent on or near the birth site (Chapters 4 and 8). These results led to general recommendations that ewes should not be lambed in large mobs, that lambing ewes should not be concentrated in small paddocks, and that the general nature of lambing paddocks should not impair the bonding process between ewe and lamb. The latter process could be facilitated by not forcing ewes to leave the birth site soon after birth in search of food or water. Paddocks with sparse vegetation, supplying inadequate quantities of nutrients, and with large distances to watering points would be counterproductive in this respect. Ewes would need to leave the birth site soon under such conditions, to look for food and/or water.

Behavioural studies

This topic was the other major focus area during the study. It was soon evident that breeds (Chapters 5, 6 and 7) and lines (Chapters 8 to 11) differed with regard to aspects of behaviour. In the literature, such differences are often seen as indicative of genetic variation (Hinch, 1997). The nature and quantity of data recorded in this study allowed the estimation of genetic (co)variances for behavioural traits. It was possible to confirm that some aspects of behaviour were indeed heritable (Chapters 7 and 12). It also appeared to be related to lamb survival on a genetic basis, as reflected by the differences in predicted breeding values of lambs that survived compared to those that died (Chapter 7). The genetic trends reflecting correlated responses to selection for ewe multiple rearing ability (Chapter 12) serve as further confirmation of this suggestion.

Implications

Finally, it is attempted to relate the improved performance due to selection in production to possible economic benefits for sheep producers. For this purpose, data from the experiment were derived and subjected to simulations using current economic data, and economic data for the same period during 1998. The data were obtained from the same source in the popular South African agricultural press during November of the respective years (Landbouweekblad, 1998*a*,*b*; 2002*a*,*b*). The SM200 simulation model were used for the simulation studies (Herselman, 2002). The basis of the simulation was three hypothetical sheep flocks generated from data presented in this dissertation. Data typical of average L line performance was entered for the first flock, while data derived from the H line was entered for the third flock. The second flock served as a control, and production in this case was taken as the mean of that achieved by the first and third flocks. This outlay implies that responses in production were symmetric in the two experimental flocks. The observant reader will know that this was not the case, since asymmetry was found in quite a number of genetic trends reported in Chapters 13, 14 and 15. The purpose of the simulation study was to establish a principle rather than to generate actual income figures. It was thus decided to assume symmetric responses in the H and L lines, for the sake of the argument.

Mean production figures for the respective ewe flocks are provided in Table 1. Most figures were either drawn from or derived from data presented in Chapters 13 to 16, while some were obtained from the original databases. Slaughter data were derived from the study of Cloete (2001).

Table 1. Production parameters for the respective sheep flocks used in the simulations

Production parameter	Line		
	L line	Control	H line
Reproduction, growth and survival:			
Joining age (months)	18	18	18
Lambs born/ewe joined (%)	105	123	141
Birth weight (kg)	4.1	4.0	3.9
Deaths to weaning (%)	32.0	27.1	22.2
Weaning weight (kg)	19.6	20.5	21.3
Deaths to two-tooth age (%)	7.8	6.4	5.0
Live weight at two-tooth (kg)	34.9	36.6	38.2
Joining weight of mature ewes (kg)	49.7	50.3	50.8
Slaughter traits:			
Slaughter age of young sheep (months)	18	18	18
Slaughter weight (kg)	39.1	40.9	42.6
Dressing (%)	37.4	38.1	38.8
Slaughter weight of mature ewes (kg)	49.7	50.3	50.8
Dressing (%)	38.2	38.9	39.6
Wool traits (mature ewes):			
Greasy fleece weight (kg)	5.17	4.97	4.77
Clean yield (%)	76.1	76.0	75.9
Fibre diameter (μm)	22.4	22.5	22.6
Wool traits (two-tooth hoggets):			
Greasy fleece weight (kg)	3.03	3.05	3.07
Clean yield (%)	77.5	77.2	76.9
Fibre diameter (μm)	18.9	19.15	19.4

A breeding unit consisting of a total number of 1000 control ewes formed the basis of the simulation. Using the production figures provided above, it was derived that a total of 1141 L line ewes or 877 H line ewes could be maintained on the same basic resource. It was recommended that the increased flock requirements following upon improvements in reproduction should be considered in simulations (White, 1984). The wool and meat prices used in the simulation are provided in Table 2 (source: Landbouweekblad, 1998*a*,*b*; 2002*a*,*b*).

Table 2. Wool and meat prices (in South African Rand) used in the simulations for 2000 and 2002

Product and age group	Year	
	1998	2002
Meat (R):		
Grade B	11.74	19.36
Grade C	10.03	16.61
Wool (R):		
19 µm	24.29	54.83
22 µm	16.78	49.32

Only product income was considered in the simulation, since the major outcomes of this study were not concerned with the input side. It could be stated that the respective lines were traditionally maintained as a single flock. It was reasoned that the flocks would not differ completely with regard to input requirements. No attempt was made to adjust product prices for the effects of inflation that affected the product price structure between 1998 and 2002. The outcome of the simulations is provided in Table 3.

Table 3. Monetary income derived from the selling of meat and wool in the simulation study. Deviations are expressed relative to the control line, with the control line taken as 100.

Year and source of income	Line		
	L line	Control	H line
Number of breeding ewes maintained	1141	1000	877
1998:			
Wool income (R 1000)	161 (103)	157	152 (97)
Meat income (R 1000)	146 (82)	178	211 (119)
Total income of unit (R 1000)	307 (92)	335	363 (108)
2002:			
Wool income (R 1000)	444 (103)	429	414 (97)
Meat income (R 1000)	234 (82)	285	337 (118)
Total income of unit (R 1000)	678 (95)	714	751 (105)

The scenarios that were simulated were deliberately chosen to reflect differences in the ratio between wool and meat prices that occurred over the past 5 years. This ratio grew wider from about 2:1 during 1998 to approximately 3:1 during 2002. It is evident that the relative proportion of the income derived from the sale of meat is consistently higher in the H line, where higher reproduction is maintained. Under conditions when the wool:meat price ratio is fairly narrow (say 2:1) the monetary yield of flock based on such ewes are approximately 16 % higher in comparison with lower reproducing ewes. At wider wool:meat price ratios (as was recorded in 2002) the relative advantage of the improvement in reproduction diminishes markedly. The monetary yield of a flock based on ewes similar to the H line would only exceed a flock based on L line ewes by 10 % under these conditions. The contribution of wool to the total income of the enterprise increases correspondingly.

The situation where ewe flocks were standardized on 1000 breeding ewes of each of the hypothetical lines was also simulated. This approach is motivated by the propensity of primary producers to maintain a ewe flock of a given size on a specific resource area, irrespective of the level of production achieved. The outcome of these runs is provided in Table 4.

Table 4. Monetary income derived from the selling of meat and wool in the second simulation study, where the size of the breeding flock were standardized on 1000 ewes. Deviations are expressed relative to the control line, with the control line taken as 100.

Year and source of income	Line		
	L line	Control	H line
Number of breeding ewes maintained	1000	1000	1000
1998:			
Wool income (R 1000)	132 (92)	143	154 (108)
Meat income (R 1000)	131 (76)	172	223 (130)
Total income of unit (R 1000)	263 (83)	315	377 (120)
2002:			
Wool income (R 1000)	363 (93)	391	420 (107)
Meat income (R 1000)	206 (75)	274	355 (130)
Total income of unit (R 1000)	569 (86)	665	775 (117)

The improved meat production capacity of H line ewes relative to the L line is evident when ewe flock sizes were standardized (Table 4). This led to considerable total income margins relative to the other lines, particularly during 1998 when the narrower wool:meat price ratio applied.

In conclusion, it is evident that marked differences in reproduction could be attained in pasture-fed sheep through selection (Chapter 14). This genetic change was achieved with a minimal impact on other economically important traits of two-tooth replacements (Chapter 15). When assessed on a standardized ewe flock, these gains resulted in marked improvements derived from product income, as was depicted in Table 4. The correlated changes in the H line (heavier and plainer) would in general accord with the current breeding objectives strived for in the broader Merino industry. The penalty in wool weight and quality as well as in live weight of mature breeding ewes that was associated with the increased reproduction was relatively small (Chapter 16), while fewer such ewes could be maintained on a given resource (see Table 3). The combination of the latter factors could become extremely important under conditions where the ratio between wool and meat prices is wide.

References

Cloete, J.J.E., 2002. Carcass traits in relation to genotype in sheep. M.Sc. (Agric.) thesis, University of Stellenbosch.

Cloete, S.W.P., Haughey, K.G., 1990. Radiographic pelvimetry for the estimation of pelvic dimensions in live Merino, Dormer and SA Mutton Merino ewes. *Journal of the South African Veterinary Association* 61: 55 - 58.

Haughey, K.G., 1989. Studies on causes of perinatal lamb mortality in the Western Cape and pelvic dimensions of ewes relative to their lifetime rearing performance. Report on activities during a visiting research fellowship 1987-1988, Department of Agriculture and Water Supply, Private Bag, Elsenburg.

Herselman, M.J., 2002. The role of simulation models in agricultural extension. *Proceedings of the 1st Joint Congress of the Grassland Society of Southern Africa and the South African Society for Animal Science*, 13-16 May 2002, Cristiana Aventura, pp 46a-46c.

Hinch, G.N., 1997. Genetics of behaviour. In: Piper, L., Ruvinsky, A., (Eds.). The genetics of sheep. pp. 353 - 374. CAB International, Wallingford, Oxon, United Kingdom.

Kilgour, R.J., Haughey, K.G., 1993. Pelvic size in Merino ewes selected for lambrearing ability is greater than that of unselected Merino ewes. *Animal Reproduction Science* 31: 237 - 242.

Landbouweekblad, 1998*a*. Wolpryse styg weer. Landbouweekblad, 8 November 1998, 70.

Landbouweekblad, 1998*b*. Marktendense. Landbouweekblad, 8 November 1998, 79.

Landbouweekblad, 2002*a*. Wolpryse effens hoër. Landbouweekblad, 15 November 2002, 94.

Landbouweekblad, 1998*b*. Marktendense. Landbouweekblad, 15 November 2002, 105.

Lee, G.J., Atkins, K.D., 1995 Consequences of reproduction on live weight, fat depth, wool growth, and intake of grazing Merino ewes in the short and long term. *Australian Journal of Experimental Agriculture* 35, 153-159.

White, D.H., 1984. Economic values of changing reproductive rate. In: Lindsay, D.R., Pearce, D.T. (Eds.), Reproduction in Sheep. Australian Academy of Science in Conjunction with Australian Wool Corporation, Canberra, Australia, pp. 371 - 377.

Abstract:

The dissertation is based on a number of separate trials conducted since 1989. The central theme is ewe rearing ability and lamb survival, and the study includes 15 papers prepared over an 11-year period from 1992 to 2002. These papers are all linked by their emphasis on sheep production as influenced by lambing and neonatal behaviour and its interface with breeding and management. The papers demonstrate the various phases the study went through, and how it eventually transpired into an account of genetic change in lamb output achievable through rigorous selection. The individual papers already contain abstracts. This summary is intended to provide readers with a broad overview of the most important outcomes of the study. The study was organised in three parts, as follows:

Part 1: Background

Initially, two papers provided the background for the investigations into lamb survival and ewe rearing ability. The first paper dealt with the average reproductive performance of sheep in the Southern Cape, and with levels of reproductive wastage in a number of flocks. It demonstrated that approximately one in four breeding ewes did not care for at least one lamb at lamb marking. Losses were more or less evenly distributed between barrenness and rearing failure. It was impossible to identify managerial practices conclusively associated with a good reproductive performance. Evidence was provided that an improvement in the reproduction of the current flock can be achieved by a simple method of selection that can be practiced by commercial farmers with minimal record keeping.

The second paper considered rearing ability in four experimental flocks of the Merino, SA Mutton Merino and Dormer breeds. A minority of ewes was shown to contribute markedly to the observed levels of rearing failure. Animals classified as being "good" or "poor" mothers on their lamb rearing history were shown to differ in one or more pelvic dimensions in two Merino flocks and the SA Mutton Merino flocks. Ewes classified as "good" had larger dimensions. Rearing ability was also demonstrated to be repeatable in the Tygerhoek Merino flock, where sufficient data were available.

Part 2: The dynamics of behaviour in lambing flocks

This part of the dissertation included four papers. The first paper detailed aspects of parturition and separation from one or more lamb in Dormer and SA Mutton Merino ewes. Length of parturition was found to be dependent on breed, with Dormer ewes having shorter parturitions than SA Mutton Merinos. They also were less likely to be assisted and Dormer lambs were less likely to die during or shortly after parturition. Across years, length of parturition was also repeatable in ewes. Early movement (within two hours) of ewes from the lambing site and high concentrations of lambed ewes in the same paddock were found to result in higher levels of separation from one or more lambs, resulting in lamb mortality.

The second paper detailed neonatal progress in lambs and related it to birth weight and lamb survival. Survival was affected by neonatal progress as well as by live weight gain from birth to 3 days in lambs. No breed differences were found for the interval from birth to standing or from standing to apparently suckling in Dormer and SA Mutton Merino lambs. It was, however, found that the traits were moderately heritable, using paternal halfsib methods on a relatively small data set.

The mechanisms of difficult births were subsequently investigated in Dormer and SA Mutton Merino ewes, since the two breeds were markedly different in this respect. The etiology of difficult births in the breeds was found to differ vastly. Dystocia and feto-pelvic disproportions commonly led to prolonged parturitions and assistance in SA Mutton Merinos. Uterine inertia were more likely to be observed in Dormers. The ability of factors associated with birth difficulties (pelvic dimensions, litter size and weight, ewe live weight and conformation) to predict length of parturition within breeds was, however, limited.

In the final paper of this part of the dissertation, it was possible to partition the genetic variances for behaviour traits observed during lambing in Dormer and SA Mutton Merino ewes. Maternal additive variance ratios for length of parturition were moderate and significant in both breeds. Neonatal progress (time intervals from birth to standing and from standing to apparently suckling) was lowly heritable in both breeds. The interval from standing to suckling was also influenced by the maternal permanent environmental variance in SA Mutton Merinos. Direct and maternal breeding values for behavioural traits differed significantly between lambs that survived and those that died in most cases. This result suggested a genetic association of lamb mortality with lambing and neonatal behaviour.

Part 3: Responses to selection for ewe multiple rearing ability

This part of the dissertation was based on observed responses in two Merino lines that were divergently selected for ewe multiple rearing ability since 1986. The line selected in an upward direction for multiple rearing ability is referred to as the High (H) line. The line selected downwards is referred to as the Low (L) line. This part of the study consists of nine papers.

In the first paper, separation of ewes from one or more lambs was studied in the Merino lines referred to above. Ewes in the H line were more likely to be separated from one or more lambs because of interference, and they tended to be more interested in other parturient ewes. Ewes in the L line tended to be more likely to desert their lamb(s). Ewes that left their birth sites within two hours of birth were more likely to be separated from one or more offspring.

The ability of ewes and lambs from the H and L lines to recognize each other were investigated next. Ewes in the H line were able to find their lambs sooner after the lamb being tethered 20 m away, compared to their L line contemporaries. They were also able to establish contact with all litter members in multiples sooner after finding a tethered lamb. Lambs in the H line tended to be more likely to bleat and tug on the tethering rope when tethered. They also followed their dams more closely when chased away with their dams at three days of age. The paper allowed the estimation of preliminary genetic parameters for mutual recognition of one another by ewes and lambs, although it was not the primary objective. Significant maternal genetic variances were found for most of the traits.

The following paper demonstrated a better lamb survival in H line lambs, despite a higher multiple birth rate. Line differences were reported, mostly involving behavioural adaptations conducive to lamb survival in the H line. Ewes in the H line generally experienced shorter births, and H line lambs were less likely to succumb during or soon after parturition. Ewes in the H line showed better cooperation with the first suckling attempts of their lambs, and H line lambs apparently suckled sooner after standing than L line contemporaries. This line difference remained after correction for the better cooperation of H line ewes. A marked advantage in terms of weight of lamb weaned per breeding ewe in the H line was demonstrated for the five years of this study, when compared to the L line.

It was found that a substantial proportion of births will not be supervised if the supervision of Merino ewes in South Africa was confined to daylight hours in intensive systems. A larger than expected frequency of very short intervals between subsequent onsets of parturition was observed. If the contention that births would trigger each other could be substantiated, it could be of benefit to quantify the mechanism involved. Knowledge of this would facilitate the synchronisation of natural births in pasture lambing flocks, where it is impractical to alter the distribution of births by nutrition. Relatively few line differences were found in this paper. The distribution of birth sites within paddocks could not be related to selection line. Ewes in the H line ewes were more likely to groom their lambs shortly after birth, while L line ewes commenced grazing sooner after birth. These behavioural adaptations in the H line would generally facilitate lamb survival.

Behavioural data from the H and L lines were recorded over a 10-year period and subjected to a genetic analysis. The line differences obtained earlier could be confirmed in this study. Genetic parameters estimated from the data indicated that behaviour traits in lambs and ewes were lowly to moderately heritable. In lambs, a significant heritability estimate was derived for the interval from birth to standing. Maternal heritability estimates were significant for length of parturition and for the interval from birth to standing. Maternal permanent environmental variances were significant for maternal cooperation and the interval from standing to apparently suckling. When behavioural traits were assessed in ewes, length of parturition, maternal behaviour score and the period that ewes remained on or near the birth site were found to be moderately heritable. Genetic divergence was found for the H line compared to the L line. The derived genetic trends indicated changes conducive to lamb survival in the H line.

Direct additive, maternal additive and maternal permanent environmental variance ratios were subsequently derived for lamb birth weight, birth coat score and lamb weaning weight. Birth coat score was highly heritable and not influenced maternally. Genetic and phenotypic trends indicated divergence between the H and L lines for weaning weight over the period of assessment. Genetic divergence was particularly strong in the case of direct breeding values for weaning weight. Birth weight and birth coat score were independent of selection line.

Genetic parameters were estimated for annual reproduction traits, ewe greasy fleece weight and ewe body weight at joining, using a repeatability model. Heritability estimates for reproduction traits were low, consistently below 10 % of the overall phenotypic variance. Ewe permanent environmental variances were higher, between 7 and 12 %. Genetic correlations of reproduction traits with ewe joining weight were favourable and very high in the case of weight of lamb weaned per ewe. Corresponding genetic correlations with ewe greasy fleece weight were low and variable. Ewe permanent environmental correlations of reproduction traits with ewe joining weight and greasy fleece weight were unfavourable and high in some instances. Phenotypic trends indicated divergence in the expected direction between the H and L lines in the reproduction traits considered. These tendencies were confirmed by genetic trends based on averaged predicted breeding values within birth years. The results confirmed that genetic progress at a rate of 1-2 % per year was attainable in reproduction traits, despite low additive variance ratios.

Genetic parameters were estimated for hogget wool and live weight traits, as well as for testis measurements. Adequate genetic variation for exploitation in a well-structured breeding program was estimated in all traits. Genetic trends indicated change towards heavier and plainer sheep in the H line, while L line contemporaries became smaller and more developed. Genetic trends for testis circumference suggested divergence in the expected direction between lines. This result was, however, associated with the genetic change in live weight, since no line difference was found in testis circumference corrected for live weight. Genetic trends for clean fleece weight and fibre diameter indicated no divergence between lines.

Age influences on reproduction, wool traits and live weight were assessed in H and L line ewes subjected to at least 10 years of divergent selection. Genetic parameters derived from this data set were generally consistent with previous estimates, despite the usage of a much smaller data set. The H and L lines differed markedly for reproduction, but no differences in the shape of age trends were found between lines. Compared to average L line performance, the superiority of H line ewes amounted to 56 % in the case of weight of lamb weaned per ewe. Ewes in the H line were heavier than L line contemporaries at two-tooth age, but the line difference disappeared at later ages. Wool production of L line ewes were heavier than those of their H line contemporaries, particularly in the middle age groups (3 to 6 years), where the highest fleece weights are expected. Fibre diameter increased with ewe age, with no apparent line difference. It was contended that the stress of increased reproduction resulted in the different age trends for the respective selection lines for live weight and greasy fleece weight.

In the final instance, this dissertation provides a framework for the genetic improvement of lamb output in pasture-fed sheep by selection for reproductivity. Unwanted correlated genetic changes were minimal, although the stress associated with an increased reproduction impaired live weight and wool traits in mature animals to an extent. The interface between behaviour, lamb survival and ewe rearing ability were clarified for a number of South African sheep breeds, leading to a better understanding of the dynamics involved. These results contributed to the formulation of adapted husbandry and breeding practices, in the context of overall flock productivity. Results pertaining to behaviour appeared to be fairly robust across studies involving different resource populations, and should be appropriate for extension to the broader industry.

Opsomming:

Die proefskrif is gebaseer op 'n aantal afsonderlike studies wat sedert 1989 uitgevoer is. Die onderwerp wat ondersoek is, is die grootmaakvermoë van ooie en oorlewing van lammers. Die studie sluit 15 artikels wat oor 'n 11-jaartydperk van 1992 tot 2002 geskryf is, in. Die artikels handel almal oor skaapproduksie, die invloed van gedrag tydens lam en die neonatale fase daarop, sowel as die wisselwerking daarvan met aangepaste teelt- en bestuurspraktyke. Die artikels dui op die fases waardeur die studie gegaan het, en hoe daar gevorder is om genetiese vordering in lamopbrengs aan te toon. Die ingeslote artikels sluit reeds Engelse opsommings in. Hierdie opsomming verskaf dus slegs 'n breë oorsig aangaande die belangrikste bevindings van die studie. Die navorsing word in drie dele opgedeel, as volg:

Deel 1: Agtergrond

Twee artikels het aanvanklik agtergrond verskaf vir die ondersoek van lamoorlewing en ooigrootmaakvermoë. Die eerste artikel het oor die gemiddelde reproduksie en vlakke van produksieverliese van skaapkuddes in die Suid-Kaap gehandel. Tydens merktyd is gevind dat ongeveer een uit elke vier teeltooie nie een of meer lammers versorg het nie. Verliese is ongeveer gelyk verdeel tussen onvrugbaarheid en grootmaakmislukkings. Dit was onmoontlik om bestuursfaktore wat onomstootlik aan 'n goeie reproduksietempo verwant was te identifiseer. Die artikel het aangedui dat 'n verbetering in die reproduksie van die huidige kudde bewerkstellig kan word deur 'n eenvoudige stelsel van seleksie wat met minimale rekordhouding deur kommersiële produsente toegepas kan word.

The tweede artikel het die grootmaakvermoë van ooie in vier eksperimentele kuddes (Merino, SA Vleismerino en Dormer) ondersoek. 'n Minderheid ooie het grootliks bygedra tot die totale grootmaakmislukking wat waargeneem is. Ooie wat op grond van hulle produksiegeskiedenis as "goed" of "swak" geklassifiseer is, het by die Merino of SA Vleismerinokuddes ten opsigte van een of meer pelvisafmetings verskil. Ooie wat as goed geklassifiseer is, het groter pelvisafmetings gehad. Grootmaakvermoë was herhaalbaar in die Tygerhoek Merinokudde, waar voldoende waarnemings vir herhaalbaarheidsberamings beskikbaar was.

Deel 2: Die dinamika van gedrag in lammerkuddes

Hierdie gedeelte van die proefskrif het vier artikels beslaan. Die eerste hiervan het aspekte van die geboorteproses, sowel as die skeiding van ooie van een of meer lammers by SA Vleismerinos en Dormers ingesluit. Duur van geboorte was verwant aan ras, met Dormers wat gouer geboorte gegee het as SA Vleismerinos. Dormers is ook minder gehelp om te lam, en hulle lammers was minder geneig om gedurende of kort na geboorte te vrek as by SA Vleismerinos. Duur van geboorte by ooie was verder herhaalbaar oor jare. Ooie wat vroeg van hulle lamplekke padgegee het, en hoë konsentrasies lammerooie in 'n kamp het skeiding van een of meer lammers in die hand gewerk.

Neonatale gedrag in lammers is in 'n tweede artikel ondersoek, en in verband gebring met geboortegewig en oorlewing. Oorlewing was fenotipies verwant aan neonatale vordering, sowel as aan gewigstoename van geboorte tot 3 dae. Dormers en SA Vleismerinos het nie verskil ten opsigte van die tydperke van geboorte tot staan, of vanaf staan tot oënskynlik suip nie. Die eienskappe was egter matig oorerflik, soos bepaal met 'n halfsibmodel op 'n betreklike klein datastel.

Die prosesse betrokke by moeilike geboortes is vervolgens by Dormers en SA Vleismerinos ondersoek. Die oorsake van moeilike geboortes het aanmerklik tussen die rasse verskil. By SA Vleismerinos was distokia en feto-pelvis wanverhoudings meerendeels by verlengde geboortes en hulp tydens geboorte betrokke. Baarmoedertraagheid het meer algemeen by Dormers voorgekom. Alhoewel verskeie faktore met duur van geboorte in verband gebring is (o.a. pelvisafmetings, werpselgrootte en –gewig, ooi liggaamsgewig en –bouvorm), was dit onmoontlik om duur van geboorte met 'n groot mate van sekerheid te voorspel.

In die laaste artikel van hierdie gedeelte, was dit moontlik om genetiese variansies vir lamgedrag (wat tydens intensiewe waarnemingsperiodes by Dormers en SA Vleismerinos bekom is) te beraam. Maternale genetiese variansie verhoudings vir duur van geboorte was matig en betekenisvol in beide rasse. Neonatale vordering (die tydperke vanaf geboorte tot staan en vanaf staan tot oënskynlik suip) was laag oorerflik in beide rasse. Die tydperk vanaf staan tot oënskynlik suip is ook deur 'n maternale permanente omgewingseffek beïnvloed in SA Vleismerinos. Direkte en maternale teeltwaardes vir gedragseienskappe het meestal betekenisvol verskil tussen lammers wat oorleef het, en die wat gevrek het. Hierdie resultaat het op 'n genetiese verwantskap van lamvrektes met lam- en neonatale gedrag gedui.

Deel 3: Response op seleksie vir die vermoë van ooie om meerlinge groot te maak

Die deel van die proefskrif is gebaseer op waargenome response in twee Merinolyne wat uiteenlopend vir maternale grootmaakvermoë geselekteer is. Daar word na die lyn wat vir die vermoë om meerlinge groot te maak geselekteer is, verwys as die Hoë (H) lyn. Die lyn wat afwaarts geselekteer is, staan ooreenstemmend bekend as die Lae (L) lyn. Die gedeelte van die proefskrif het nege artikels beslaan.

In die eerste artikel is skeiding van ooie van een of meer lammers in die lyne wat bo vermeld is, ondersoek. Ooie in die H-lyn was meer geneig om weens inmenging van een of meer lammers geskei te word, en was meer geïnteresseerd in ooie wat in die proses van lam was. Ooie in die L-lyn was meer geneig om hulle lammers te verlaat. Skeiding van ooie van een of meer lammers was verwant aan die tydperk wat ooie op die lamplek deurgebring het. Ooie wat hulle lamplekke binne twee ure verlaat het, was meer geneig om van een of meer lammers geskei te word as die wat langer gebly het.

Die vermoë van ooie en lammers om mekaar wedersyds te herken, is vervolgens ondersoek. Ooie in die H-lyn het hulle lammers gouer as L-lyntydgenote gevind nadat hulle 20 m weg vasgemaak is. Hulle was ook in staat om by meerlinge gouer kontak met alle lammers te bewerkstellig nadat 'n vasgemaakte lam gekry is. Lammers in die H-lyn het geneig om meer te blêr en aan die tou te rem wanneer hulle vasgemaak is. Hulle het ook hulle moeders nader gevolg as hulle op drie dae aangejaag is. Die artikel het die beraming van voorlopige genetiese parameters vir die wedersydse herkenning van ooie en lammers toegelaat. Betekenisvolle maternale genetiese variansies is vir die meeste van die eienskappe verkry.

Die volgende artikels het 'n beter lamoorlewing in die H-lyn verkry, ten spyte van 'n hoër meerlinggeboortetempo. Lynverskille is gevind, in die meeste gevalle vir gedragseienskappe wat lamoorlewing in die hand sal werk ten gunste van die H-lyn. Ooie in die H-lyn het in die algemeen korter gevat om te lam, terwyl H-lyn lammers minder geneig was om tydens of net na geboorte te vrek as L-lyntydgenote. Ooie in die H-lyn het beter samewerking met die eerste suippogings van hulle lammers getoon, en H-lynlammers het gouer na staan oënskynlik gesuip as L-lyntydgenote. Die lynverskil is steeds waargeneem nadat die beter samewerking van H-lynooie met hulle lammers se eerste suippogings in ag geneem is. 'n Aansienlike voordeel in terme van gewig lam gespeen per teeltooi is oor die vyf jaar van die studie aangetoon, in vergelyking met die prestasie in die L-lyn.

Indien toesig slegs tydens dagligure aan lammerooie verskaf word, sal 'n aansienlike proporsie van ooie in Suid-Afrikaanse intensiewe lamstelsels sonder toesig lam. 'n Hoër as verwagte frekwensie van baie kort intervalle tussen opeenvolgende geboortes is waargeneem. Indien die aanname dat geboortes mekaar 'n aanvang laat neem bevestig kan word, sou dit van waarde wees om die meganisme wat daaraan gekoppel is beter te verstaan. Die kennis kan ingespan word om natuurlike geboortes van weidende ooie te sinchroniseer, onder omstandighede waar dit onmoontlik is om die verspreiding van geboortes met voeding te manipuleer. Relatief min lynverskille is in die studie gevind. Die verspreiding van lamplekke in die kampe kon nie aan 'n lyn toegeskryf word nie. Ooie in die H-lyn het meer geneig om hulle lammers skoon te maak kort na geboorte, terwyl hulle L-lyn tydgenote korter na geboorte begin het om te wei. Die gedragsaanpassings in die H-lyn sal ook lamoorlewing in die hand werk.

Gedragsdata van die H- en L-lyne is oor 'n periode van 10 jaar aangeteken, en aan 'n genetiese analise onderwerp. Die lynverskille wat vroeër verkry is, is deur die analise bevestig. Genetiese parameters wat beraam is, het aangetoon dat gedragseienskappe in lammers en ooie laag tot matig oorerflik was. In lammers is ‘n betekenisvolle direkte oorerflikheidsberaming gevind vir die tydperk van geboorte tot staan. Maternale oorerflikhede was betekenisvol vir duur van geboorte, en die tydperk van geboorte tot staan. Maternale permanente omgewingsvariansies was betekenisvol vir maternale samewerking met die lam se eerste suippogings, en vir die tydperk vanaf staan tot oënskynlike suip. Met die analise van gedragseienskappe by ooie het dit geblyk dat duur van geboorte, maternale samewerkingspunt en die tydperk wat ooie op of naby aan hulle lamplekke deurgebring het, matig oorerflik was. Genetiese tendense vir die H- en L-lyne was uiteenlopend. Die verhaalde genetiese tendense in die H-lyn was aanduidend van veranderinge wat lamoorlewing in die hand sal werk.

Direkte en maternale genetiese, sowel as maternale permanente omgewingseffekte is vervolgens vir geboortegewig, geboortehaar en speengewig beraam. Geboortehaarpunt was hoog oorerflik en onafhanklik van maternale invloede. Genetiese en fenotipiese waardes het gedui op uiteenlopende tendense vir speengewig in die H- en L-lyne. Uiteenlopende genetiese verskille was veral opmerklik by direkte teeltwaardes vir speengewig. Geboortegewig en geboortehaarpunt was grootliks onafhanklik van seleksielyn.

Genetiese parameters is met ‘n herhaalbaarheidsmodel beraam vir jaarlikse reproduksie-eienskappe, rouvaggewig en liggaaamsgewig van ooie. Die oorerflikheid van reproduksie-eienskappe was laag, naamlik onder 10 % van die fenotipiese variansie. Permanente omgewingsvariansies van die ooie was hoër, tussen 7 en 13 %. Genetiese korrelasies van reproduksie-eienskappe met paargewig was gunstig en baie hoog in die geval van gewig lam gespeen per ooi. Ooreenstemmende korrelasies met rouvaggewig was laag en veranderlik. Permanente omgewingskorrelasies van reproduksie-eienskappe met paargewig en rouvaggewig was ongunstig en hoog in sommige gevalle. Uiteenlopende fenotipiese tendense in die verwagte rigting is vir reproduksie-eienskappe tussen die H- en L-lyne verkry. Die neigings is bevestig deur verkreë genetiese tendense gebaseer op gemiddelde teeltwaardes binne geboortejare. Die resultate het bevestig dat genetiese vordering in die orde van 1-2 % per jaar haalbaar is in reproduksie, ten spyte van relatief lae oorerflikhede.

Genetiese parameters is beraam vir tweetand wol- en liggaamsgewigeienskappe, sowel as vir testisafmetings. Voldoende genetiese variasie vir benutting in goedgestruktureerde teeltprogramme is vir al die eienskappe verkry. Genetiese tendense het op 'n verandering na groter en gladder skape in die H-lyn gedui, terwyl L-lyn tydgenote kleiner en meer ontwikkeld geword het. Uiteenlopende genetiese tendense tussen lyne is vir testisdeursnee verkry. Die tendense was in die verwagte rigting. Die resultaat het met die genetiese tendense in liggaamsgewig verband gehou, siende dat geen lynverskil vir testisgrootte wat vir liggaamsgewig gekorrigeer is, verkry is nie. Genetiese tendense vir skoonvaggewig en veseldikte het op geen noemenswaardige verskille tussen lyne gedui nie.

Die invloed van ouderdom op reproduksie, woleienskappe en paargewig is ondersoek in H- en L-lynooie wat vir ten minste 10 jaar aan uiteenlopende seleksie onderwerp is. Genetiese parameters uit die ontleding was in algemene ooreenstemming met vorige beramings, al is 'n kleiner datastel gebruik. Die H- en L-lyne het aanmerklik in reproduksie verskil, maar geen verskille het in die vorm van ouderdomstendense vir die lyne voorgekom nie. Uitgedruk relatief to prestasie in die L-lyn, het die verskil tussen die lyne vir gewig lam gespeen per ooi tot 56 % beloop. Ooie in die H-lyn was swaarder as L-lyntydgenote by tweetandouderdom, maar die lynverskil het by ouer ouderdomsgroepe verdwyn. Ooie in die L-lyne het hoër skoonvaggewigte gehandhaaf as H-lyntydgenote, veral by die middelste ouderdomsgroepe (3 tot 6 jaar), die ouderdomsgroepe waar die hoogste wolopbrengs verwag word. Veseldikte het toegeneem met ouderdom, met geen opmerklike lynverskille. Dit is gestel dat die stres van dragtigheid en laktasie tot die lynverskille ten opsigte van paargewig en skoonvaggewig gelei het.

Ten slotte het die proefskrif 'n raamwerk vir die genetiese verbetering van lamopbrengs by skape op weidings deur seleksie vir produktiwiteit verskaf. Ongunstige gekorreleerde response was gering, maar die stres van dragtigheid en laktasie het die liggaamsgewig en woleienskappe van volwasse teeltooie tot 'n mate benadeel. Die wisselwerking tussen gedrag, lamoorlewing en ooigrootmaakvermoë is duideliker gemaak vir 'n aantal Suid-Afrikaanse skaaprasse. Dit het gelei to 'n beter begrip vir die dinamiese prosesse betrokke. Die resultate het tot die formulering van aangepaste bestuurs- en teeltstelsels gelei, veral in die konteks van kuddeproduktiwiteit. Resultate uit die studie was redelik robuus wat verskillende hulpbronkuddes betref, en behoort in die breër bedryf toepaslik te wees.