Direct and correlated responses to selection for total weight of lamb weaned in Merino sheep

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Abstract

This study was conducted to evaluate direct and correlated selection responses to selection for total weight of lamb weaned per ewe joined (TWW), number of lambs born (NLB), number of lambs weaned (NLW) and weaning weight (WW). Data from the Grootfontein Merino stud and the Carnarvon Merino flock were used. Estimated heritabilities for TWW, NLB, NLW and WW were 0.19, 0.23, 0.17 and 0.21 for the Grootfontein Merino stud and 0.21, 0.19, 0.16 and 0.30 for the Carnarvon Merino flock. High genetic correlations (0.89-0.98) were obtained between reproduction traits in both flocks, while the genetic correlations between WW and TWW, NLB and NLW were moderate to high (0.32-0.78). Phenotypic correlations between WW and reproduction traits were low (0.04-0.19) and phenotypic correlations between reproduction traits were high (0.71-0.96). In the Grootfontein Merino stud, approximately the same selection response (gain per generation) for TWW could be expected from direct selection (9.03 kg) as from indirect selection for NLB (9.20 kg). In the Carnarvon Merino flock, the highest selection response for TWW (6.37 kg) would be achieved by direct selection for TWW. The estimated selection responses indicate that direct selection for TWW would be the most suitable selection criterion for improving reproductive performance in flocks with a high reproduction rate where an increase in the number of lambs would be undesirable.

Key words: Merino, sheep, genetics, reproduction, breeding
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Introduction

Reproduction and survival rate are the most important factors determining the efficiency of lamb production (Large, 1970; Snyman *et al.*, 1997). Falconer & Mackay (1996) showed that several components influence ewe productivity and that each of these components can be used as a selection criterion, as each has a direct impact on total ewe productivity. In areas where lambing percentages are already high, an increase in the number of lambs born may be undesirable, as it may lead to the production of less and/or poorer quality wool by ewes (Kennedy, 1967; Shelton & Menzies, 1968), or the production of weaned lambs of inferior quality. Some of the factors determining total weight of lamb weaned per ewe are ovulation rate, mothering ability and milk production of the ewe, as well as growth rate and viability of the lamb (Falconer & Mackay, 1996). Genetic improvement of reproductive performance could be achieved either by direct selection for a composite trait (total weight of lamb weaned) or by indirect selection for one of the component traits. It is important to determine whether direct selection for total weight of lamb weaned per ewe joined is more efficient than selection for number of lambs born, number of lambs weaned or weaning weight. Knowledge of the nature of genetic and phenotypic correlations is important for multiple trait evaluation (Hazel, 1943; Henderson & Quaas, 1976) and to predict correlated responses to selection (Falconer & Mackay, 1996). The objective of this study was to evaluate direct and correlated selection responses per generation of various reproduction traits in order to identify the most suitable criteria for improving lifetime reproductive efficiency in Merino sheep.

Material and methods

Data from the Grootfontein Merino stud (1968-1996) and the Carnarvon Merino flock (1964-1983) were used. Detailed descriptions of the management and selection procedures followed in these flocks have been reported for the Grootfontein Merino stud by Olivier (1989) and for the Carnarvon Merino flock by Erasmus *et al.* (1990). The Grootfontein Merino stud is kept at the Grootfontein Agricultural Development Institute near Middelburg (31°28' S, 25°1' E) in the Northeastern Karoo region of South Africa. The site is situated in the False Upper Karoo (Acocks, 1988) and has an annual rainfall of 360 mm. The animals are kept under favourable nutritional conditions that include irrigated pastures and supplementary feeding. The Carnarvon Merino flock was kept on natural pastures at an experimental station near Carnarvon (30°59' S, 20°9' E) in the Northwestern Karoo region. The vegetation consists of mixed grass and karoo shrub and is described as arid karoo. The average rainfall is 209 mm and occurs mainly during autumn. The estimated grazing capacity is 5.5 ha per small stock unit. The Grootfontein ewes were hand-mated from 1956 to 1986 and artificially inseminated from 1987 to 1996. Teaser rams were used to identify ewes in estrus and these ewes were then inseminated twice within 12 hours. No hormonal treatment was used with artificial insemination. The Carnavon ewes were hand-mated.

Traits analysed in this study included the number of lambs born (NLB) or weaned (NLW) and the total weight of lamb weaned (TWW) per ewe joined over three lambing opportunities at 2, 3 and 4 years of age as well as the weaning weight of individual lambs (WW). The first three lambing opportunities of a ewe were used as an indication of lifetime reproduction, and only data from ewes with three consecutive lambing opportunities were used in the analysis. The traits NLB and NLW were treated as being continuous, as these traits are a combination of three separate lambing opportunities, which increases the number of categories. Total weight of lamb weaned per ewe mated for each lambing opportunity was calculated as described by Snyman *et al.* (1997). For this calculation, weaning weights were adjusted to 120 d for both flocks, followed by least-squares adjustments for sex of lamb. No adjustments were made for birth status. The total weight of lamb weaned for each ewe for each lambing opportunity (TWW/EJ) was calculated by summation of the adjusted weaning weights of all the lambs weaned by the ewe in a specific lambing season. TWW over three consecutive lambing opportunities was calculated by summation of TWW/EJ for the first, second and third lambing opportunities.

The DFREML programme of Meyer (1989,1991 & 1993) was used to estimate (co)variance components for the various traits. The most suitable model for each trait was identified on the basis of log likelihood ratios. The heritabilities for TWW, NLB and NLW were obtained by fitting the following single trait animal model:

$$y = Xb + Z_1a + e$$

The following model was fitted for WW:

$$y = Xb + Z_1a + Z_2m + Z_3c + e$$
$$\text{with } cov(a,m) = A\sigma_{am}$$

where y is a vector of observed traits of animals, b, a, m and c are vectors of fixed effects, direct additive genetic effects, maternal additive genetic effects and maternal permanent environmental effects respectively, and X, Z_1, Z_2 and Z_3 are the corresponding incidence matrices relating to y, e is the vector of residuals, A is the numerator relationship matrix, and σ_{am} is the covariance between direct additive genetic and maternal additive genetic effects.

Year-season of birth of the ewe was included as a fixed effect for TWW, NLB and NLW and in the case of WW, year-season, sex, rearing status and age of dam were included as fixed effects and age at weaning as a linear covariable. Total heritabilities for WW were used in all calculations for selection responses (Willham, 1972). Bivariate animal models, including only additive genetic effects, were fitted for the estimation of genetic and phenotypic correlations between traits. The same fixed effects, with the exception of sex, were included. Sex was excluded for WW in the bivariate analysis because only the WW of the ewes with reproduction records were included. The standard errors for genetic correlations were calculated as described by Falconer & Mackay (1996). The direct selection response for each trait was calculated using the formula:

$$R = ih^2\ddot{a}_P$$

where R is the direct selection response, i is the selection intensity, h^2 is the heritability and $\ddot{a}_P$ is the phenotypic standard deviation of the trait.

It was assumed that 5% of males and 50% of females were selected. The selection intensities for the males and females were taken from the Appendix Table A of Falconer & Mackay (1996). The selection intensities used were calculated as the unweighted means of the selection intensities of males and females. Correlated selection response was calculated using the formula:

$$CR_Y = ih_Xh_Yr_A\ddot{a}_{PY}$$

where CR_Y is the correlated response in Y when selection is based on X, i is the selection intensity, h_X is the square-root of the heritability of X, h_Y is the square-root of the heritability of Y, r_A is the genetic correlation between X and Y and $ä_{PY}$ is the phenotypic standard deviation of Y.

Results and discussion

The means for TWW and WW (90.84 kg and 27.74 kg respectively) were substantially higher for the Grootfontein Merino stud than for the Carnarvon Merino flock (Table 1) as were the means for NLB and NLW. The large difference between the two flocks for TWW and WW is ascribed to the more favourable conditions under which the Grootfontein Merino stud was kept. The conditions at Carnarvon also resulted in failure of a large number of ewes to wean a lamb during their first parity and in lower weaning weights. The high c.v. for reproduction traits is expected, as the data contained records from ewes which failed to wean a lamb over the three lambing opportunities as well as from ewes that weaned up to eight lambs.

Table 1 Number of ewe records, mean, standard deviation (s.d.) and coefficient of variation (c.v.) for various traits in the Grootfontein Merino stud and the Carnarvon Merino flock

Trait	No. records	Mean	s.d.	c.v. (%)
Grootfontein Merino Stud				
WW[a] (kg)	7035	27.7	5.4	19.5
WW[b] (kg)	1712	26.6	5.5	20.5
TWW[ab] (kg)	1777	90.8	36.2	39.8
NLB[ab]	1777	4.0	1.3	31.8
NLW[ab]	1777	3.3	1.3	39.8
Carnarvon Merino Flock				
WW[a] (kg)	8480	20.8	4.3	20.7
WW[b] (kg)	1960	20.5	2.8	18.6
TWW[ab] (kg)	1971	37.6	21.8	57.8
NLB[ab]	1971	2.2	1.0	45.1
NLW[ab]	1971	1.9	1.0	55.2

[a] Univariate analysis - for the total data set
[b] Bivariate analysis - only data of ewes with three lambing opportunities

The heritability for WW in the Carnavon Merino flock was higher than the corresponding value for the Grootfontein Merino stud (Table 2). While the heritabilities for TWW and NLW in both the flocks were approximately the same, the heritability for NLB was slightly higher for the Grootfontein Merino stud than for the Carnavon Merino flock. Heritability estimates for WW derived from animal models (AM) range from 0.09 (Burfening & Kress, 1993) to 0.45 (Brash *et al.*, 1994d), and were reviewed by Fogarty (1995) and Snyman *et al.* (1995). Heritability estimates for TWW, NLB and NLW are summarised in Table 3. The heritability estimates obtained in this study for TWW, NLB and NLW agree well with estimates obtained by Snyman *et al.* (1997) and Snyman *et al.* (1998), but were slightly higher than other estimates (Table 3). The estimates obtained in this study for WW are within the range reported in the literature.

Phenotypic correlations between WW and the other traits and genetic correlations between WW and NLB or NLW were moderate in both the flocks (Table 2). This was expected, as these traits do not have a large influence on the expression of WW. On the other hand, the genetic correlations between WW and TWW were 0.65 and 0.78 in the Grootfontein Merino stud and Carnavon Merino flocks respectively. This is due to the fact WW forms an integral part of the equation used for calculation of TWW.

Genetic and phenotypic correlations between TWW, NLB and NLW ranged from high to very high in both flocks. This was expected, as these traits are closely related with one another. Although estimates of genetic and phenotypic correlations (Table 4) vary substantially, the estimates derived from this study are within the reported range of correlations.

Table 2 Heritability estimates (on the diagonal) for various traits and genetic (above the diagonal) and phenotypic (below the diagonal) correlations between traits in the Grootfontein Merino stud and the Carnarvon Merino flock

	WW	TWW	NLB	NLW
Grootfontein Merino Stud				
WW	**0.21**	0.65	0.32	0.34
	(0.04)	(0.15)	(0.16)	(0.16)
TWW	0.08	**0.19**	0.91	0.97
	(0.03)	**(0.05)**	(0.03)	(0.01)
NLB	0.06	0.71	**0.23**	0.97
	(0.03)	(0.01)	**(0.05)**	(0.01)
NLW	0.04	0.95	0.77	**0.17**
	(0.03)	(0.01)	(0.01)	**(0.05)**
Carnarvon Merino Flock				
WW	**0.30**[a]	0.78	0.45	0.57
	(0.05)	(0.08)	(0.12)	(0.12)
TWW	0.19	**0.21**	0.89	0.98
	(0.02)	**(0.04)**	(0.04)	(0.01)
NLB	0.14	0.82	**0.19**	0.93
	(0.02)	(0.01)	**(0.04)**	(0.02)
NLW	0.14	0.96	0.84	**0.16**
	(0.02)	(0.01)	(0.01)	**(0.04)**

[a] – Total heritability

Table 3 Summary of published heritability estimates obtained with animal models for NLB, NLW and TWW

NLB[a]	NLW[b]	TWW[c]	Breed	Reference
0.12	0.04		Rambouillet	Burfening *et al.*, 1993
0.00			Border Leicester	Brash *et al.*, 1994a
0.06	0.04		Dorset	Brash *et al.*, 1994b
0.03	0.03		Corriedale	Brash *et al.*, 1994c
0.09	0.04	0.06	Hyfer	Fogarty *et al.*, 1994
		0.17	Afrino	Snyman, *et al.*, 1997
0.26	0.17		Afrino	Snyman, *et al.*, 1998
		0.22	Merino	Snyman, *et al.*, 1997
		0.13	Merino	Snyman, *et al.*, 1997

[a] - Number of lambs born; [b] - Number of lambs weaned; [c] - Total weight of lamb weaned

Table 4 Summary of published genetic and phenotypic correlations between WW, NLB, NLW and TWW

Trait 1	Trait 2	Genetic correlation	Phenotypic correlation	Breed	Reference
a	b	-0.61	0.05	Romney	Baker et al., 1982 [sm]
a	b	0.32	0.13	Romney	Ch'ang &Rae, 1972 [sm]
a	b	0.25	0.05	Merino	Davis, 1987 [sm]
a	b	-0.01	0.04	Afrino	Snyman et al., 1998 [am]
a	c	0.34	0.09	Merino	Davis, 1987 [sm]
a	c	0.11	0.03	Afrino	Snyman et al., 1998 [am]
a	d	0.75	0.15	Afrino	Snyman et al., 1998 [am]
b	c	0.91	0.73	Merino	Davis, 1987 [sm]
b	c	0.42	0.64	Various	Fogarty et al., 1985 [sm]
b	c	0.99	0.87	Afrino	Snyman et al., 1998 [qm]
b	d	0.50	0.58	Various	Fogarty et al., 1985 [sm]
b	d	0.83	0.79	Afrino	Snyman et al., 1998 [am]
c	d	0.97	0.95	Various	Fogarty et al., 1985 [sm]
c	d	0.88	0.92	Galway	More O'Farrell, 1976 [sm]
c	d	0.84	0.92	Afrino	Snyman et al., 1998 [am]

a - Weaning weight; b - Number of lambs born; c - Number of lambs weaned; d- Total weight of lamb weaned; am - Animal model; sm - Sire model

The selection responses for WW and TWW were expressed as the average gain (kg) per generation and for NLB and NLW as the average gain in the number of lambs born or weaned per generation. In the Grootfontein Merino stud the expected direct selection responses for WW, TWW, NLB and NLW were 1.16 kg, 9.03 kg, 0.41 lambs and 0.31 lambs respectively, while in Carnavon Merino flock, the respective responses were 1.36 kg, 6.37 kg, 0.27 lambs and 0.24 lambs (Table 5). The correlated selection responses per generation to selection based on TWW in the Grootfontein Merino stud were 0.70 kg, 0.33 lambs and 0.33 lambs for WW, NLB and NLW respectively and in the Carnavon Merino flock the correlated responses were 0.89 kg, 0.25 lambs and 0.26 lambs respectively. The increase in TWW, which can be obtained through direct or indirect selection, was higher in the Grootfontein Merino stud than in the Carnavon Merino flock. (Table 5). However, the gain in the Carnavon Merino flock was of greater magnitude when the increase was expressed as a percentage of mean TWW. This is attributed to the lower reproduction rate of the Carnavon Merino flock and implies that the impact of selection for TWW in the Carnavon Merino flock would have been greater than in the Grootfontein Merino stud if reproduction rate was higher. This also applies to direct and indirect selection for NLB and NLW. The selection response for WW expressed as a percentage of the mean when selection was based on WW or TWW was higher in the Carnavon Merino flock than in the Grootfontein Merino stud. The selection response was higher in the Grootfontein Merino stud when selection was based on NLB or NLW.

Table 5 Direct (on the diagonal) and correlated selection responses (off the diagonal) per generation for various traits in the Grootfontein Merino stud and the Carnarvon Merino flock

	Response (kg or number of lambs)				Response (percentage of the mean)			
	WW kg	TWW kg	NLB	NLW	WW %	TWW %	NLB %	NLW %
Grootfontein Merino Stud								
WW	**1.16**	6.01	0.12	0.12	**4.18**	6.63	2.95	3.51
TWW	0.70	**9.03**	0.33	0.33	2.52	**9.97**	8.21	9.91
NLB	0.38	9.20	**0.41**	0.36	1.37	10.16	**10.20**	10.81
NLW	0.36	8.50	0.34	**0.32**	1.30	9.38	8.45	**9.61**
Carnarvon Merino Flock								
WW	**1.36**	5.92	0.07	0.04	**6.55**	15.72	3.15	2.13
TWW	0.89	**6.37**	0.25	0.26	4.34	**16.91**	11.26	13.83
NLB	0.21	5.38	**0.27**	0.24	1.02	14.28	**12.16**	12.77
NLW	0.14	5.47	0.23	**0.24**	0.68	14.52	10.36	**12.77**

Selection based on WW alone would lead to a 50% higher selection response for WW compared to selection based on TWW (Table 6). In the Grootfontein Merino stud the response of TWW would be 34% lower when selection was based on WW, while in the Carnavon Merino flock it would only be 7% lower. In both flocks the responses of NLB and NLW would be more than 63% lower for selection based on WW compared to selection based on TWW. The large difference between the responses in TWW is because of the higher heritability of WW in the Carnavon Merino flock. In other words, WW could be improved to a greater extent in the Carnavon Merino flock than in the Grootfontein Merino stud. In the Grootfontein Merino stud, the response of WW to indirect selection based on either NLB or NLW would be half that of selection for TWW, and a third that of selection for WW. In the Carnavon Merino flock the selection response of WW to selection based on NLB or NLW would be 75% lower than that of selection based on TWW.

Selection based on NLB in the Grootfontein Merino stud would lead to a slightly higher response in TWW compared to direct selection for TWW. However, this slightly better response was not mediated through the improvement of TWW, but rather through an increase of almost 25% in NLB. The selection response of TWW to selection based on NLW in the Grootfontein Merino stud would be 6% lower than the response to direct selection for TWW. The selection responses for NLB and NLW in the Grootfontein Merino stud to selection based on NLB were more than 9% higher than the response to selection based on TWW. Selection responses of NLB and NLW in the Grootfontein Merino stud were equal for selection based on NLW or TWW. In the Carnavon Merino flock the selection response of TWW would have been 15% lower for selection based on NLB or NLW compared to direct selection for TWW. The response of NLB to selection based on NLB would be 8% higher than to selection based on TWW, while the response of NLW to selection based on NLB or NLW and the response of NLB to selection based on NLW would be 8% lower than selection based on TWW.

Table 6 Responses of selection based on WW, NLB or NLW expressed as percentages of the response to selection based solely on TWW in the Grootfontein Merino stud and the Carnarvon Merino flock

Trait under selection	WW[a] %	TWW[b] %	NLB[c] %	NLW[d] %
Grootfontein Merino Stud				
TWW	100.0	100.0	100.0	100.0
WW	165.7	66.6	36.4	36.4
NLB	54.3	101.9	124.3	109.1
NLW	51.4	94.1	103.0	97.0
Carnarvon Merino Flock				
TWW	100.0	100.0	100.0	100.0
WW	152.8	92.9	28.0	15.4
NLB	23.6	84.5	108.0	92.3
NLW	15.7	85.9	92.0	92.3

[a] - Weaning weight; [b] - Total weight of lamb weaned; [c] - Number of lambs born;
[d] - Number of lambs weaned

Selection based on TWW and NLB in the Grootfontein Merino stud and on TWW and WW in Carnavon Merino flock would theoretically result in the best selection responses in TWW (Table 6). The genetic and phenotypic correlations between TWW and WW in the Carnavon Merino flock indicate that the highest producers in TWW for the current flock would not necessarily be selected if selection were solely based on WW. In large areas of South Africa sheep are run under harsh conditions and in some of these flocks the lambing percentages are already high. In such flocks, selection for increased reproductive performance should also include TWW and not be based solely on NLB or NLW.

Conclusion

The most important result of this study is that reproductive performance, defined as total weight of lamb weaned per ewe joined, can be improved genetically through either direct or indirect selection. The estimated selection responses indicate that direct selection for TWW would be the most suitable selection criterion to improve reproductive performance without increasing the number of lambs born. This is an important consideration in flocks where the lambing and weaning percentages are already high and an increase in the number of lambs is undesirable. In the past WW was not regarded as an important selection criterion, especially for Merino sheep in South Africa, and was therefore not recorded for most flocks. It is evident that WW should be recorded, as it is necessary for the calculation of total weight of lamb weaned, which is the trait that has the largest influence on the income of a farming enterprise.

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