Genetic parameters for early growth traits in a Merino lambs estimated using multitrait analysis

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Abstract

Genetic parameter estimates for birth weight, weaning weight and pre-weaning average daily gain were assessed for Merino lambs maintained at the Tygerhoek Experimental Farm. Random effects fitted were direct and maternal additive genetic effects, and maternal permanent environmental effect. Direct heritability (h^2) estimates of 0.21, 0.40 and 0.40 and maternal heritability (m^2) estimates of 0.27, 0.02 and 0.01 were obtained for body weight at birth, weaning and preweaning average daily gain, respectively. The corresponding maternal permanent environmental effects (h^2) were 0.05, 0.02 and 0.01. The genetic correlation estimates between direct and maternal effects were -0.02, -0.10 and -0.16 for birth weight, weaning weight and pre-weaning average daily gain, respectively. Direct genetic correlation estimates between birth and weaning weights and between birth weight and pre-weaning average daily gain were of low to moderate magnitude and positive. However, the direct genetic correlation between weaning weight and pre-weaning average daily gain was almost unity. Maternal genetic correlation estimates among the traits were high and positive. It is concluded that the traits can be improved if selection could be based on either of the traits studied.
Keywords: Early growth; genetic parameter; Merino lamb

Introduction

In mammals, growth is influenced by the genes of the individual for growth, by the environment provided by the dam and other environmental effects (Lewis & Beatson, 1999; Albuquerque & Meyer, 2001). In young animals, the milk supply of the dam (Bradford, 1972; Meyer, 1992; Lewis & Beatson, 1999)

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and the maternal care she provides largely contribute to their growth (Bradford, 1972; Lewis & Beatson, 1999). The dam's genes for these traits affect the environment experienced by the offspring through milk production and mothering ability (Bourdon, 2000). Maternal effects may be expected to be more important in sheep than in cattle because of the greater relative variation in litter size in sheep and the competition between lambs for their mother's milk supply. It incorporates both similarities between twins and similarities between lambs born to the same ewe in different years (Snyman *et al.*, 1995). The dam, therefore, contributes to the phenotypic value of her offspring, not only by a sample half of her genes, but also through her genes responsible for the expression of her maternal performance.

The confounding of the maternal effect of the dam and her genetic contribution to the phenotypic value of her offspring and the possibility of a negative genetic correlation between the direct and maternal effect are the two most important problems in selection programmes (Willham, 1980). Thus, in order to decide upon a feasible selection strategy, estimation of the genetic parameters and the correlations between direct and maternal additive genetic effects are necessary. The recent statistical and computational developments have made routine analysis to estimate these parameters by Restricted Maximum Likelihood (REML), fitting an animal model, conceptually straightforward and technically feasible. Further, a multitrait genetic evaluation by best linear unbiased prediction (BLUP) fitting an animal model requires partitioning of the phenotypic variances and covariances into their direct genetic, maternal genetic, maternal permanent environmental and residual components (Meyer, 1993).

The objective of this study was to assess genetic parameters for birth weight, weaning weight and average daily gain to weaning in the Tygerhoek Merino flock using multitrait analysis.

Materials and Methods

Data used in this study were obtained from the Merino flock maintained at the Tygerhoek Experimental Farm. The general management of the flock and description of the study area are as described by Duguma (2001). A total of 8310 lambs born from 2538 ewes and sired by 681 rams, raised over the period from 1970 to 1998 were used in this study. Liveweight at birth (BW), weaning (WW) and preweaning average daily gain (ADG) were the growth traits investigated. To identify the effects to be included in the fixed part of the

model, an analysis of variance was performed on birth year (1970 to 1998), sex (male, female), birth type (single, multiple), age of dam (2- to 6-yr old) and group (group of animals selected for increased clean fleece weight and the unselected control). The effects tested were significant ($p < 0.001$) for all traits and hence included in the operational model.

Variance components were estimated by Restricted Maximum Likelihood procedures (REML) applying the VCE 4.2.5 package of Groeneveld (1998). An animal model including maternal additive genetic and maternal permanent environmental effects as additional random effects was fitted for all three traits. By using estimated (co)variance components, direct heritabilities (h^2), maternal heritabilities (m^2), maternal permanent environmental variances (c^2) and the correlations between the direct and

maternal additive genetic effects (r_{am}) were obtained. Total heritabilities (h^2_t) were calculated as defined by Willham (1972). All models involved the same fixed effects.

The following model was fitted for all traits:

$$y = X\mathbf{b} + Z\mathbf{a} + M\mathbf{m} + P\mathbf{c} + e \qquad\qquad Cov(a, m) = A\sigma_{am}$$

where:

y = the vector of records

$\mathbf{b}$ = the vector of fixed effects

X = the matrix that associates $\mathbf{b}$ with Y

$\mathbf{a}$ = the vector of breeding values for direct additive genetic effects Z = the

matrix that associates $\mathbf{a}$ with Y

$\mathbf{m}$ = the vector of breeding values for maternal genetic effects M = the

matrix that associates $\mathbf{m}$ with Y

$\mathbf{c}$ = the vector of permanent environmental effects due to dam P = the

matrix that associates $\mathbf{c}$ with Y

$\mathbf{e}$ = the vector of residual effects.

Further, with $\mathbf{A}$ the numerator relationship matrix between animals, $\mathbf{I}_n$ an identity matrix with order the number of animals and $\mathbf{I}$ an identity matrix with order the number of records, the (co)variance structure of the random effects in the analysis can then be described as:

$V(a) = \sigma^2_a \mathbf{A}$, $V(m) = \sigma^2_m \mathbf{A}$, $V(c) = \sigma^2_c \mathbf{I}_n$, $V(e) = \sigma^2_e \mathbf{I}$ and $Cov(a, m) = \mathbf{A}\sigma_{am}$, where σ^2_a is the additive genetic variance, σ^2_m, the maternal additive

genetic variance, $\sigma^2{}_c$, the maternal permanent environmental variance, $\sigma^2{}_e$, the residual variance and σ_{am}, the direct and maternal genetic covariance. It was assumed that all effects in the models are independent with the exception of the direct and maternal additive genetic effects.

Results

Estimates of (co)variance components, direct (h^2) and maternal (m^2) heritabilities, values for the maternal permanent environmental effects (c^2) and the correlations between the direct and maternal additive genetic effects (r_{am}) for each trait are shown in Table 1. Standard errors of heritability estimates were unavailable. Estimates of the various correlations between traits are presented in Table 2.

Table 1. Variance components and genetic parameters for BW, WW and ADG estimated in multitrait analysis

Item	BW	WW	ADG
Variance components			
$\sigma^2{}_a$	0.11	8.71	850.67
$\sigma^2{}_m$	0.15	0.33	6.13
σ_{am}	-0.01	-0.17	-11.71
$\sigma^2{}_c$	0.02	0.38	23.06
$\sigma^2{}_e$	0.26	12.98	1264.21
$\sigma^2{}_p$	0.54	22.22	2132.35
Genetic parameters			
h^2	0.21	0.40	0.40
m^2	0.27	0.02	0.01
R_{am}	-0.02	-0.10	-0.16
$h^2{}_t$	0.34	0.39	0.39
c^2	0.05	0.02	0.01
e^2	0.48	0.59	0.60

$\sigma^2{}_a$, direct additive genetic variance; $\sigma^2{}_m$, maternal additive genetic variance; σ_{am}, direct-maternal genetic covariance; $\sigma^2{}_c$, maternal permanent environmental variance; $\sigma^2{}_e$, residual variance; $\sigma^2{}_p$, phenotypic variance; h^2, direct heritability; m^2, maternal heritability; r_{am}, direct-maternal genetic correlation; $h^2{}_t$, total heritability; c^2, ratio of maternal permanent environmental effect; e^2, ratio of residual effect.

The h^2 estimates for body weight varied from 0.21 to 0.40 between BW, WW and ADG with a tendency of an increasing age trend. For BW, maternal additive genetic variance components and heritabilities (m^2) were larger than both the direct additive genetic and maternal permanent environmental effects. However, for WW and ADG, both maternal additive genetic and maternal permanent environmental effects were smaller than

the direct additive genetic effects. In all cases, the correlations between direct and maternal additive genetic effects (r_{am}) were nearly zero and negative in sign.

Table 2. Estimated direct genetic, maternal genetic, maternal permanent environmental and residual correlations (above diagonal) and the corresponding diagonal) covariances (below between BW, WW and ADG from multitrait analyses.

Trait	BW	WW	ADG
Direct additive genetic effects			
BW	-	0.16	0.04
WW	0.16	-	0.99
ADG	0.42	85.49	-
Maternal additive genetic effects			
BW	-	0.93	0.60
WW	0.20	-	0.85
ADG	0.57	1.21	-
Maternal permanent environmental effects			
BW	-	0.89	0.82
WW	0.08	-	0.99
ADG	0.60	2.92	-
Residual effects			
BW	-	0.16	0.02
WW	0.30	-	0.99
ADG	0.41	126.83	-

Direct genetic correlations between BW and WW and between BW and ADG were small positive, while that between WW and ADG was almost unity. The maternal genetic correlations between BW and WW, BW and ADG and WW and ADG were all high positive. The maternal permanent environmental correlation estimates between the different weight traits were positive and high.

Discussion

Estimates of h² for BW obtained in the present study are within the range of the animal model estimates, which varied from 0.04 (Cloete *et al.*, 1998) to
0.42 (Van Wyk *et al.*, 1993). Estimates of h² for WW obtained were also within the literature ranges which varied from 0.09 (Burfening & Kress, 1993) to 0.50 (Fadili *et al.*, 2000). The estimates for ADG ranged from 0.19 (Yazdi *et al.*, 1997) to 0.42 (Fadili *et al.*, 2000). The estimates for all three traits also well

correspond to those reported by Heydenrych (1975), which was based on part of the same data set as was used in the present study but using sib analysis. The estimates were also within the range of unitrait estimates reported by Duguma (2001), which was used the same data set.

In the present study, the magnitude of m^2 estimates obtained for BW were substantial, being greater than both the h^2 and c^2 estimates (Table 1). The m^2 estimates, however, were lower than h^2 estimates for WW and ADG. Yazdi *et al*. (1997) found comparable results and indicated that this was presumably due to poor quality of pasture that prevented the genetic ability of ewes to provide sufficient milk for their lambs to be expressed. Thus, inadequate milk yield could mask the expression of the maternal ability of ewes. The value for m^2 obtained in BW was lower than those reported by Burfening & Kress (1993) and Van Wyk *et al*. (1993). These authors reported m^2 estimates ranging from 0.30 to 0.65 depending on the model applied for BW, but without considering the effect of maternal permanent environmental effects. These high m^2 values might have been including effects due to the permanent environmental effects of the dam. It has been indicated by Snyman *et al*. (1995) that the exclusion of the maternal permanent environmental effect, when it has a significant influence, could cause estimates of m^2 to be biased upwards.

The c^2 estimate computed for BW was in general agreement with those reported by Cloete *et al*. (2001). These authors found an estimate of 0.07 for the permanent environmental effect of the dam in BW. It was, however, larger than a zero c^2 estimate reported by Maria *et al*. (1993), but lower than those reported by Snyman *et al*. (1995) and Neser *et al*. (2001). Both Snyman *et al*. (1995) and Neser *et al*. (2001) reported an estimate of 0.12 for the permanent environmental effect of the dam in BW. They ascribed this value to uterine environment provided by the dam and the effect of multiple births. Likewise, Maria *et al*. (1993) indicated that the permanent environmental effect is due to uterine capacity, feeding level during late gestation and the maternal behaviour of the ewe. Maternal behaviour is likely to be associated with the rearing ability of a dam. In the present study, relatively lower c^2 estimates were obtained for WW and ADG. Literature results indicated that early growth of a ewe has an effect on the amount of milk she gives to her lambs during her early life (Gould & Whiteman, 1975).

Generally, results showed a trend of an increasing direct additive but decreasing maternal variance ratios from birth to weaning at 100 days of age. Other studies reported a similar pattern (Maria *et al.*, 1993; Burfening & Kress, 1993; Tosh & Kemp, 1994; Fadili *et al.,* 2000). The increasing h² of lamb weight at weaning is most likely caused by an increased expression of genes with direct additive effects on body development (Yazdi *et al.*, 1997). This also confirms the idea of Robison (1981) and Snyman *et al.* (1995), who concluded that maternal effects in mammals diminish with age. In general, results of this study showed that maternal effects, genetic and environmental, are important for BW and need to be considered in any selection programme.

The estimates of correlations obtained between direct and maternal additive genetic effects (r_{am}) for BW are lower than in most of the estimates reported in the literature (Maria *et al.*, 1993; Abegaz & Duguma, 2000; Neser *et al.*,
2001). The estimate of 0.35 reported by Neser *et al.* (2001) for BW opposed the negative estimates found in this study. This same study reported a high negative correlation estimate in WW. In the present study, the signs of these estimates for WW was opposed to those reported by Näsholm & Danell (1996), Snyman *et al.* (1996) and Yazdi *et al.* (1997). They reported positive genetic correlations ranging from 0.18 to 0.57. The very low negative genetic correlations obtained in the present study suggested that selection for increased liveweight of the lamb would not negatively affect the maternal ability of the ewe. Cloete *et al.* (2001) also found no significant correlation between the direct additive and maternal additive effects in Merino flock. According to Meyer (1997) a negative estimate of the direct and maternal additive genetic covariance has mostly been observed in field data while it has by and large been absent in experimental data sets. She has indicated that this could have been attributed to factors like more uniform management and lack of preferential treatment. Alternatively, it may also reflect better identification of contemporary or management groups.

Early growth traits in sheep are mostly characterised by negative r_{am}
estimates (Maria *et al.*, 1993; Fadili *et al.*, 2000; Al-Shorepy, 2001; Neser *et al.*, 2000; 2001). These estimates may be considerable and could be affected by small data sets (Maria *et al.*, 1993; Fadili *et al.*, 2000; Al-Shorepy, 2001), the models fitted or poor pedigree structure that is inadequate for obtaining estimates of both direct and maternal heritabilities and the genetic correlations between animal effects (Kominakis *et al.*, 1998; Lee *et al.*, 2000).

The effects of management practices on the direct and maternal genetic correlations have also been indicated. Both Meyer (1992) and Swalve (1993) suggested that environmental covariances between dam and offspring that is not accounted for may bias the direct and maternal genetic correlation downwards. The difficulty of statistically separating the direct and maternal component (Meyer, 1992), and the design of fixed effects were also suggested as a factor that could have a strong influence on the reliability of the estimation of the direct and maternal additive genetic correlation (Gerstmayr, 1992). In beef cattle, Robinson (1996) indicated that the negative correlation between direct and maternal genetic variances could result from other effects in the data rather than a true negative genetic relationship.

Genetic correlations between growth traits of the Tygerhoek Merino lambs were positive and varied from low to high. In his extensive review, Fogarty (1995) reported a weighted average genetic correlation estimate between BW and WW of 0.39. The low direct genetic correlations between BW and WW might be beneficial for avoiding lambing difficulties, which could result in loss of lambs and dams. A significant reduction in survival rate of lambs was observed in this flock as lambs became heavier at birth (Duguma, 2001).

Conclusions

Heritability estimates of early growth traits ranged from moderate to moderately high and showed a trend for increasing direct additive and decreasing maternal variance ratios from birth to weaning at 100 days of age. Estimates of direct genetic correlatons between WW and BW were low, indicating that selecting for WW may not result in lambing difficulties. The genetic antagonisms between direct and maternal additive genetic effects obtained were also not large enough to prevent genetic improvement if selection is based on individual weight performance.

Acknowledgements

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