

# Heritability estimates for pre-weaning growth traits in the Adelaide Boer goat flock

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Data consisting of records from 3 040 animals, born of 59 sires and 597 dams, were collected from 1978 to 1991 and analysed to estimate variance components for birth weight, weaning weight, average daily gain (ADG) and Kleiber ratio. Birth year, age of dam, sex and rearing status (a combination of birth and weaning status) were included in the analysis as fixed effects. Methods employed were Henderson's Method 3, fitting a sire model, and Restricted Maximum Likelihood, using a derivative-free algorithm and fitting four different animal models. The following ranges of heritabilities were obtained from the different models: 0.162–0.327 for birth weight; 0.162–0.350 for weaning weight; 0.176–0.257 for ADG; and 0.130–0.231 for Kleiber ratio. Estimates from animal models which excluded maternal genetic effects were biased upwards, while the inclusion of maternal genetic effects resulted in lower and presumably more realistic variance components. Maternal effects were large for birth weight and small for the other three traits. Selection for weaning weight or average daily gain is suggested.

Produksiedata wat bestaan uit rekords van 3 040 diere, die nageslag van 59 vaars en 597 moeders, is van 1978 tot 1991 van die Boerbokkudde op Adelaide Proefstasie versamel en gebruik om variansiekomponente vir geboortemassa, speenmassa, gemiddelde daaglikse toename (GDT) en die Kleiberverhouding te beraam. Vier vaste effekte, naamlik geboortjaar, ooi-ouderdom, geslag en meerlingstatus ('n kombinasie van geboorte- en speenstatus), is in die ontleding ingesluit. Verskillende metodes is toegepas, naamlik Henderson se Metode 3, vir die passing van 'n vadermodel, asook Beperkte Maksimum Waarskynlikheid (REML), vir die gebruik van 'n afgeleide vrye algoritme en die passing van vier verskillende dieremodelle. Die volgende reeks erfbaarhede is met die verskillende modelle verkry: 0.162–0.327 vir geboortemassa; 0.162–0.350 vir speenmassa; 0.176–0.257 vir GDT; en 0.130–0.231 vir die Kleiberverhouding. Beramings met dieremodelle wat nie materne effekte in ag neem nie, het opwaartse sydigheid getoon, terwyl die insluiting van materne effekte laer en waarskynlik meer realistiese beramings tot gevolg gehad het. Die invloed van materne komponente was groot op geboortemassa en klein op die ander drie eienskappe. Seleksie vir speenmassa of GDT word voorgestel.

**Keywords:** Boer goats, heritabilities, variance components.

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## Introduction

The Improved Boer goat has been developed over the last 60 years, mainly to fulfil the need for browsing animals that utilize shrubs and control bush encroachment. Although there is an increasing national and international interest in Boer goats for stud as well as commercial farming, relatively little attention in the field of quantitative genetics has been paid to this breed.

Improving growth performance is an important way of increasing meat output in a lamb production system. To date, no genetic parameters for growth traits have been estimated. To allow the development of a sensible breeding programme for Boer goats, knowledge of parameters for important traits are vital. The database of records of the Adelaide Boer goat flock provided an opportunity to estimate variance components for growth traits.

## Materials and methods

### Animals, environment and management

The Adelaide Improved Boer goat flock of approximately 90 breeding does is kept at the Adelaide Experimental Farm (32°40'S, 26°17'E) in the Eastern Cape Province of South Africa. It covers an area of 475 ha in the false thornveld region of the Eastern Cape. This veld type (Acocks type 21)

forms part of the dry bush community (Acocks, 1988). The region receives an average annual rainfall of approximately 448 mm, mainly during the summer months from October to February, resulting in a dry winter. Average maximum (minimum) temperatures during the period of study were 29°C (14°C) for January and 18°C (6°C) for July.

The farm was divided into 24 fields and nine lambing paddocks. An open rotation grazing system was followed, with cattle and goats utilizing the fields simultaneously. Diets of does were supplemented with chocolate maize (ureum and molasses coated grain) during the last two months of pregnancy. During dry periods, lucerne hay or pellets were supplemented *ad libitum* to all animals.

Four to six bucks were selected and made available annually by the Boergoat Breeders' Association. An individual mating system was followed, with 20 to 30 does allocated to each buck. In most cases, bucks were used for one breeding season only. The autumn mating season of 42 days starts in the last week of March.

At weaning age (five months), kids were selected for growth according to an index system which corrects for birth status and age of dam. Buck kids were marketed shortly after weaning. Doe kids from multiple births were preferred as replacements to improve fecundity (kids born/doe kidded). At

18 months of age, does were finally selected on the basis of growth and breed standards.

### Recording and processing of data

Data collected from 1978 to 1991 (14 years) were used for this study. After incomplete records were removed, performance data of 3 040 individuals, the progeny of 59 sires and 597 dams, remained. Sires had an average number of 52 offspring each.

Variance components were estimated for the pre-weaning traits of birth weight (BW), weaning weight (WW), average daily gain (ADG) and the Kleiber ratio (KR). Weaning weight was corrected beforehand to 150 days of age by using the formula:

$$\text{Corrected weight} = [(\text{true weight} - \text{BW}) \times 150 / \text{true age}] + \text{BW}$$

The Kleiber ratio was calculated as  $\text{ADG}/\text{WW}^{0.75}$ , using the age corrected weaning weight.

### Statistical analysis

A multivariate analysis of variance was performed to determine the influence of birth year, age of dam, sex and rearing status (a combination of birth and weaning status) on the production traits. All fixed effects proved to be significant ( $P < 0.01$ ). These five fixed effects were included accordingly in the models used during the analysis.

Different methods were used to estimate variance components. Firstly, the LSMLMW-PC1 computer program of Harvey (1988) was used to employ Henderson's Method 3 (Henderson, 1953), fitting the following sire model:

$$Y_{ijklmn} = \mu + A_i + s_{ij} + d_k + r_l + g_m + e_{ijklmn}$$

where

- $Y_{ijklmn}$  = progeny records for the production traits
- $\mu$  = population average
- $A_i$  = fixed effect of the  $i^{\text{th}}$  year of birth ( $i = 1, \dots, 14$ )
- $s_{ij}$  = random sire effect nested in  $A_i$
- $d_k$  = fixed effect of  $k^{\text{th}}$  age of dam ( $k = 2, \dots, 9$ )
- $r_l$  = fixed effect of  $l^{\text{th}}$  rearing status ( $l = 11, 21, 22, 31, 32, \dots, 44$ )
- $g_m$  = fixed effect of  $l^{\text{th}}$  sex ( $m = 1, 2$ )
- $e_{ijklmn}$  = random residual error

Interactions between the random effects and fixed effects are assumed to be negligible.

The DFREML program of Meyer (1988) was used to analyse the data by Restricted Maximum Likelihood, using a derivative-free algorithm and the univariate option. Four different animal models, denoted Models 1 to 4, were fitted. Statistically, the models can be explained as follows:

$$\text{Model 1: } Y_{ijk} = \mu + F_i + a_j + e_{ijk}$$

$$\text{Model 2: } Y_{ijkl} = \mu + F_i + a_j + c_k + e_{ijkl}$$

$$\text{Model 3: } Y_{ijkl} = \mu + F_i + a_j + m_k + e_{ijkl}$$

$$\text{Model 4: } Y_{ijkl} = \mu + F_i + a_j + m_k + c_k + e_{ijkl}$$

with

- $Y_{ijkl}$  = progeny record of production traits,
- $\mu$  = population average,
- $F_i$  = fixed effects,
- $a_j$  = direct additive genetic effect of the  $j^{\text{th}}$  animal,
- $m_k$  = maternal additive genetic effect of the  $k^{\text{th}}$  dam,
- $c_k$  = permanent environmental effect due to the  $k^{\text{th}}$  dam and

$e_{ijkl}$  = random residual error.

Meyer (1992) describes Model 1 as a simple animal model, because no additional random effects are included. With Model 2, the common environmental dam effect ( $c$ ) was fitted as a second random effect. An additional random effect, the maternal genetic effect ( $m$ ), was included in Model 3. While solving these three models, it was assumed that  $\text{Cov}(a, m') = \text{Cov}(a, c') = \text{Cov}(m, c') = 0$  and that  $e$  is uncorrelated with all other effects.

Because the co-variance between the direct and maternal genetic effects have an effect on heritability, it is important to have an estimation of this covariance. Model 4 was then solved, which includes direct, maternal and permanent environmental effects simultaneously, taking into account the covariances between these parameters.

### Heritabilities

Using the variance components from the sire model, heritabilities were estimated as follows:

$$h^2 = 4\sigma_s^2 / (\sigma_s^2 + \sigma_e^2) \quad (\text{Falconer, 1985}).$$

From the variance components obtained from Animal Models 1 and 2, only the direct additive heritability was estimated, but the maternal environmental effect was included in the heritability estimates from Model 2.

When both direct additive and maternal additive variance components are available, as estimated with Models 3 and 4, different types of heritabilities could be estimated, namely, direct heritability, maternal heritability and heritability for the total genetic effect, according to the methods described by Willham (1972).

The genetic correlation between the direct and maternal variances (Table 5) was estimated to be:

$$r_{\text{Gam}} = \sigma_{am} / (\sigma_a^2 \sigma_m^2)^{0.5}$$

### Results and discussion

Heritabilities and genetic correlations for birth weight (BW), weaning weight (WW), average daily gain (ADG) and the Kleiber ratio (KR) obtained with the sire model are shown in Table 1. The results coincide with heritability estimates available for small stock, which ranged from 0.10 to 0.21 (Yalcin, 1982; Nicoll *et al.*, 1989; Burfening & Carpio, 1993; Van Wyk *et al.*, 1993a), also using a sire model analysis.

All genetic correlations were positive, except between birth weight and the Kleiber ratio, where a low negative correlation was found. The large standard error (SE) of this value, however, places its reliability in question. The high correlations between weaning weight, average daily gain, and Kleiber

**Table 1** Heritabilities\* and genetic correlations ( $\pm$ SE) (LSMLMW sire model)

	Birth weight	Weaning weight	Average daily gain	Kleiber ratio
BW	0.178(0.044)	0.356(0.183)	0.251(0.197)	-0.016(0.223)
WW	-	0.191(0.046)	0.995(0.003)	0.929(0.038)
ADG	-	-	0.189(0.045)	0.970(0.023)
KR	-	-	-	0.130(0.037)

\* Heritabilities on the diagonal

ratio exist because weaning weight are included in the formulas of average daily gain and the Kleiber ratio.

Estimated genetic correlations between BW and WW, and between BW and ADG were higher than the values of 0.12 to 0.16 and -0.01 to 0.01 obtained by Maria *et al.* (1993) in Romanov sheep and Van Wyk *et al.* (1993b) in Dorner sheep for the two correlations respectively. The genetic correlation between WW and ADG was similar to the correlation of 0.988 reported by Van Wyk *et al.* (1993b), but higher than the value of 0.59 reported by Maria *et al.* (1993). Van Wyk *et al.* (1993b) reported genetic correlations between WW, ADG and KR of 0.888 and 0.942 respectively, which are similar to the results of this study.

Analysis with an animal model (DFREML-Model 1) yielded higher estimates than the sire model. These results appear in Table 2.

Heritabilities computed from this analysis were all lower than figures obtained by van Wyk *et al.* (1993a), who estimated heritabilities of 0.422, 0.341, 0.312 and 0.261 for BW, WW, ADG and KR respectively.

Because this model takes into account all relationships between animals, maternal effects are also included in the heritabilities, but are possibly confounded with the direct variance. According to Van Wyk *et al.* (1993a), this could cause heritabilities to be upwardly biased. Waldron *et al.* (1993) reported that animal models which ignore maternal effects tend to overestimate direct heritability. Potential response to selection based on these values would therefore also be overestimated.

Since maternal effects could play a significant role in the expression of pre-weaning traits, it is important to know the extent of both maternal genetic and environmental effects in

**Table 2** Variance components estimated with DFREML Model 1

Component	Birth weight	Weaning weight	Average daily gain	Kleiber ratio
LS-means ±SE	3.5±0.05	26.8±0.33	0.16±0.002	1.31±0.070
CV (%)	13.6	13.9	15.9	6.3
$\sigma^2_a$	0.1007	4.7705	0.1918	0.1563
$\sigma^2_e$	0.2070	12.7258	0.5543	0.5785
$\sigma^2_p$	0.3078	17.4962	0.7461	0.7348
$h^2$	0.3273	0.2727	0.2570	0.2127

**Table 3** Variance components estimated with DFREML Model 2

Component	Birth weight	Weaning weight	Average daily gain	Kleiber ratio
$\sigma^2_a$	0.0515	3.9868	0.1710	0.1711
$\sigma^2_c$	0.2555E-05	0.2142E-04	0.9187E-06	0.2002E-05
$\sigma^2_e$	0.2403	13.2371	0.5679	0.5688
$\sigma^2_p$	0.2919	17.2239	0.7389	0.7399
$h^2$	0.1765	0.2315	0.2315	0.2313

addition to the direct additive component.

Robison (1981) mentioned that an understanding of the genetic variation in maternal effects and the relationship between direct genetic effects and maternal effects are essential for formulating optimum breeding programmes, and that selection efficiency may be reduced if maternal effects are not measured or considered in a breeding programme. The data were therefore analysed by fitting DFREML Model 2, which separates the permanent maternal environmental effect from the additive effect. Estimates are presented in Table 3.

The permanent environmental variance ( $\sigma^2_c$ ) proved to be very small in all four traits, with resulting zero  $c^2$  values. The  $\sigma^2_c$  component obviously did influence heritability, as lower values were obtained than with DFREML Model 1.

By fitting DFREML Model 3, direct additive variances and maternal additive variances could be estimated separately, thereby removing the confounding effect mentioned earlier. Interestingly, the direct additive heritabilities ( $h^2_a$ ) estimated with Model 3 (Table 4) did not differ much from those estimated with the sire model.

Direct heritability was the highest for weaning weight, but the larger maternal component of birth weight gave it the higher total heritability. Values for maternal heritability ( $h^2_m$ ) for WW, ADG, and KR were similar in size and about 50% less than  $h^2_m$  for BW.

The results of the DFREML Model 4 analysis appears in Table 5. Heritability values for sheep fall within the range of estimates by other researchers. Burfening & Kress (1993), Van Wyk *et al.* (1993a) and Tosh & Kemp (1994) estimated  $h^2_T$  values of 0.11 to 0.33, 0.018 to 0.22, 0.18 and 0.15 for BW, WW, ADG and KR, respectively.

Different results for both cattle and sheep are found in the literature as far as the co-variance between direct genetic effects and maternal genetic effects ( $\sigma_{am}$ ) are concerned. Negative co-variances are reported by Bertrand & Benyshek (1987), Cantet *et al.* (1988), Trus & Wilton (1988), Burfening & Kress (1993), Maria *et al.* (1993) and Van Wyk *et al.* (1993a). Meyer (1992) and Waldron *et al.* (1993) obtained both positive and negative values.

The estimation of  $\sigma_{am}$  for this data set yielded negative co-variances for BW and WW, but positive values for ADG and KR (Table 5).

WW had the largest negative  $\sigma_{am}$ . The importance of this co-variance can be noticed in the difference between  $h^2_T$  val-

**Table 4** Variance components estimated with DFREML Model 3

Component	Birth weight	Weaning weight	Average daily gain	Kleiber ratio
$\sigma^2_a$	0.0348	2.5466	0.1050	0.0841
$\sigma^2_m$	0.0486	1.2250	0.0487	0.0485
$\sigma^2_e$	0.2197	13.4266	0.5810	0.5954
$\sigma^2_p$	0.3030	17.1983	0.7347	0.7280
$h^2_a$	0.1148	0.1481	0.1429	0.1155
$h^2_m$	0.1602	0.0712	0.0663	0.0666
$h^2_T$	0.1949	0.1837	0.1760	0.1488

**Table 5** Variance components estimated with DFREML Model 4

Component	Birth weight	Weaning weight	Average daily gain	Kleiber ratio
$\sigma^2_a$	0.0449	2.7941	0.1146	0.0804
$\sigma^2_m$	0.0402	0.7030	0.0350	0.0143
$\sigma_{am}$	-0.0126	-0.2065	0.0072	0.0168
$\sigma^2_c$	0.0165	0.9490	0.0386	0.0375
$\sigma^2_e$	0.1965	11.2872	0.4829	0.5604
$\sigma^2_p$	0.2856	15.5270	0.6784	0.7095
$r_{Gam}$	-0.2958	-0.1473	0.1137	0.4955
$h^2_a$	0.1572	0.1800	0.1690	0.1134
$h^2_m$	0.1406	0.0453	0.0516	0.0202
$c^2$	0.0579	0.0661	0.0570	0.0528
$h^2_T$	0.1616	0.1623	0.2107	0.1590

ues estimated by Model 3, where  $\sigma_{am}$  was assumed to be zero, and the  $h^2_T$  values from Model 4, where  $\sigma_{am}$  was included.

Contrary to what Bertrand & Benyshek (1987) and Cantet *et al.* (1988) found for beef cattle, BW had a higher maternal heritability than WW. For BW, the maternal heritability was even higher than direct heritability in the Model 3 analysis. The estimates for  $h^2_m$  of 0.13 to 0.31 for BW and 0.02 to 0.25 for WW in sheep by Burfening & Kress (1993), Maria *et al.* (1993), and Tosh & Kemp (1994) also illustrate the higher values for birth weight.

Values for  $h^2_a$  and  $h^2_m$  were similar in the Model 4 analysis. Burfening & Kress (1993) maintain that the portion of the selection differential realized is expected to be low when selecting for a maternally influenced trait. Selection for birth weight is therefore expected to have a low response.

Model 2 and Model 4 differed substantially in  $c^2$  estimates, with Model 4 yielding the higher values. However, these  $c^2$  values were still much lower than those cited by Tosh & Kemp (1994) for three different sheep breeds, namely, 0.27 to 0.37 for BW and 0.12 to 0.20 for WW in three sheep breeds. The  $c^2$  values of 0.10 for BW, 0.0 for WW and 0.02 for ADG reported by Maria *et al.* (1993) are more in line with the results of this study.

Values for  $c^2$  did not differ much between traits, indicating a constant maternal environmental effect for Boer goats from birth to weaning age.

The difference between maternal values in cattle and goats could probably also be explained by the high occurrence of multiple births (92.4% in this data set) in the Boer goat, compared to cattle, which limits direct genetic expression of birth weight. For the accurate and unbiased analyses of maternal and permanent environmental variance components, very large data sets are required. With a data set of the size ( $N = 3\ 040$ ) used in this study, such deviations can be expected.

## Conclusions

Heritability estimates varied between 0.15 and 0.35 for the traits examined, and selection for any of these traits should be successful. Animal models which excluded maternal effects overestimated heritabilities. Maternal heritability was similar in size to direct heritability for birth weight, but less than half that of  $h^2_a$  for weaning weight, average daily gain, and the Kleiber ratio. The genetic correlation between direct and maternal genetic effects was small and should have little effect on selection response.

Although selection for any of the traits studied should be successful, selection on weaning weight or average daily gain is recommended, because these two traits had the highest direct and total heritabilities and they are easy to measure. The positive correlations of weaning weight and average daily gain with birth weight should not be a problem, as the high occurrence of multiple births will limit birth weight.

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