

Multitrait estimation of direct and maternal (co)variances for growth and efficiency traits in a multibreed beef cattle herd

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Estimates of (co)variance components were obtained for growth and efficiency traits in a multibreed synthetic beef cattle herd. Components were estimated simultaneously by fitting four alternative seven-trait models. Direct heritabilities varied according to the model fitted but were higher for preweaning than for postweaning traits. Applying a model which also included maternal heritabilities, the direct-maternal covariance and the permanent environmental effect, direct heritabilities of weaning weight, weaning index, preweaning Kleiber ratio, preweaning relative growth rate, cow efficiency, postweaning Kleiber ratio and postweaning relative growth rate were 0.57, 0.40, 0.35, 0.71, 0.54, 0.16 and 0.13, respectively. In general, maternal heritabilities varied from 0.03 for postweaning Kleiber ratio to 0.45 for cow efficiency. Direct-maternal correlations were negative and varied from -0.31 to -0.58 for weaning weight related traits, but was -0.77 for cow efficiency.

Beramings van kovariansiekomponente is vir groei- en doeltreffendheidseienskappe in 'n multiras sintetiese vleisbeeskudde verkry. Komponente is tegelykertyd met die passing van vier alternatiewe sewe-eienskapmodelle beraam. Direkte oorerflikhede het gevarieer volgens die model wat gebruik is, maar was hoër vir voorspeeneienskappe en laer vir naspeeneienskappe. Met die passing van 'n model wat ook materne oorerflikhede, direk-materne kovariansies en die permanente omgewingseffek ingesluit het, was die direkte oorerflikhede vir speengewig, speenindeks, voorspeense Kleiberverhouding, voorspeense relatiewe groeitempo, koeidoeltreffendheid, naspeense Kleiberverhouding en naspeense relatiewe groeidoeltreffendheid onderskeidelik 0.57, 0.40, 0.35, 0.71, 0.54, 0.16 en 0.13. Oor die algemeen het die materne oorerflikhede vanaf 0.03 vir naspeense Kleiberverhouding tot 0.45 vir koeidoeltreffendheid gevarieer. Direk-materne korrelasies was negatief en het vir speengewigverwante eienskappe van -0.31 tot -0.58 gevarieer, maar was -0.77 vir koeidoeltreffendheid.

Keywords: Beef cattle, (co)variance components, efficiency, growth, multitrait

Introduction

The importance of a fast growth rate and high weaning weights in beef cattle is clearly not debatable. Unfortunately, high weaning weights are being associated with increased birth weights and thus with an increase in calving difficulties. Similarly, high weaning weights are being associated with high mature weights and corresponding increases in maintenance requirements of the breeding female (Burrow *et al.*, 1991). Consequently, researchers have considered some alternative criteria to overcome these undesirable correlated responses. Fitzhugh & Taylor (1971) suggested proportional or relative growth rate as a strategy to alter the shape of the growth curve, while Scholtz &

Roux (1988) proposed the use of the Kleiber ratio (growth rate/metabolic size) as another alternative to improve growth efficiency. A restricted selection index, which allows for selection for weaning weight while restricting change in birth weight is another way of altering the shape of the growth curve (Dickerson *et al.*, 1974; Bourdon & Brinks, 1982; Mendoza & Slinger, 1985; Winder *et al.*, 1990). All these criteria have either been evaluated using limited data or without taking the maternal components thereof into consideration.

Restricted Maximum Likelihood (REML) under an animal model has become popular in the estimation of variance components. Such analyses allow the separation of animal's direct, maternal direct, maternal permanent environmental and (co)variance components. Mostly, to date, only uni-trait or pairwise two-trait analyses have been carried out. The VCE 4 REML package of Groeneveld (1994; 1997) enables the simultaneous estimation of all (co)variance components of a number of traits on the basis of exact first derivatives. It has been demonstrated that by the inclusion of additional information from correlated traits in multitrait analyses, more accurate estimates of (co)variance components would be obtained. This package was applied by Groeneveld *et al.* (1998), Mostert *et al.* (1998) and Rust *et al.* (1998) on four traits of South African beef cattle breeds.

The objective of this analysis was to separate direct additive, direct maternal, permanent environmental of the dam and (co)variance components in a multibreed synthetic beef cattle population using multitrait analysis. Besides the ordinary weight traits, relative growth or efficiency traits were additionally included in the analysis.

Material and methods

Data

Data were obtained from a multibreed synthetic beef cattle herd (Bovelder) of the Johannesburg Metropolitan Council and consisted of 13122 birth and weaning weight records collected from 1988 to 1993. The herd is kept on two different farms on an intensive management system (Patterson *et al.*, 1980). Breed development started in 1962 with the first initial crosses. Ten foundation sire breeds were included in the crossbreeding programme (namely Holstein, Hereford, Simmentaler, Charolais, Afrikaner, Aberdeen Angus, South Devon, Brahman, Bonsmara and Brown Swiss) and were mated to crossbred cows of varying types, a large percentage of which were purchased from commercial herds. Numerous crossbred cow types were in the herd in the early stages. However, at the later stages of the project they became more uniform.

Females were artificially inseminated using the same sires across the two farms. Heifer calves were first inseminated so as to calve for the first time at approximately two years of age. The average age of dams at calving was 4.9 years (Table 1) and ranged between 2 and 14 years.

The number of sires used was 149, with an average of 88 calves per sire which varied between 18 and 357 calves per sire. Between 20 and 32 sires were used annually, with 102 sires used for one year only. The rest (namely 47) were used for more than one year with only three used for four and more years. On average, sires were used for 1.46 years only. In order to increase the number of genetic ties and to gain in precision of estimation, the pedigree file was extended by additionally including back-pedigree information of identified sires and paternal and maternal grandsires since 1985. The number of animals in the pedigree file was 22472. The number of dams was 4686 with an average of 2.8 calves per dam.

Although cows calved almost throughout the year, the majority of calves (92 %) were born in winter (June to September), while the rest were born during December through March. Season of birth was therefore recorded as either 'summer born' or 'winter born'. Season of birth was not confounded with age of dam. Dam weights (DW) were recorded after parturition.

Postweaning growth records in feedlot of 2703 heifer and bull calves were also obtained. Average daily gain from weaning to an average age of 17.4 months was 0.88 kg/day with an average final weight (FW) of 490 kg (Table 1).

Table 1 Data information

Traits and covariables	Number of records	Mean	CV (%)
Birth weight (BW) (kg)	13122	36.0	17.6
Weaning weight (WW) (kg)	13122	220.8	13.3
Preweaning gain (kg/day)	13122	0.86	17.1
Weaning age (days)	13122	214.5	4.7
Weaning index (Index)	13122	159.2	18.7
Preweaning Kleiber ratio (Pre-K) $\times 10^4$	13122	150.1	8.7
Preweaning Relative growth rate (Pre-RGR) $\times 10^4$	13122	84.7	10.6
Dam weight (DW) (kg)	13122	508.9	12.1
Dam age (years)	13122	4.9	55.9
Cow efficiency ratio (WW/DW ^{0.75}) $\times 100$	13122	210.0	16.6
Final weight (FW) (kg)	2703	489.6	9.3
Final age (days)	2703	522.7	5.1
Postweaning gain (kg/day)	2703	0.88	19.1
Postweaning Kleiber ratio (Post-K) $\times 10^4$	2703	85.0	19.4
Postweaning Relative growth rate (Post-RGR) $\times 10^4$	2703	26.0	21.3

Trait description

In addition to birth weight (BW), weaning weight (WW) and dam weight (DW) recorded, the following derived traits, giving expression to efficiency, were also calculated:

- Preweaning Kleiber ratio (Pre-K) = Preweaning average daily gain/WW^{0.75}.
- Preweaning relative growth rate (Pre-RGR) = (in WW – in BW)/Weaning age (Fitzhugh & Taylor, 1971).
- Cow efficiency = WW/DW^{0.75}
- Owing to the positive genetic correlation between WW and BW ($r_g = 0.51$) (Table 2), a restricted selection index was calculated to facilitate selection for WW without a correlated increase in BW. Variances and covariances were obtained by applying a seven-trait model as is described in the following section. The index was subsequently calculated by applying the following simple procedure described by Cunningham *et al.* (1970):

$$\text{Cov (BW, Index)} = a[\text{Cov (BW, WW)}] - b[\text{VarBW}]$$

where:

$$\text{Cov (BW, Index)} = \text{Additive genetic covariance between the Index and BW}$$

- Cov (BW, WW) = Additive genetic covariance between BW and WW
 Var (BW) = Additive genetic variance of BW
 a = a weighing factor for WW
 b = a weighing factor for BW.

The Cov (BW, Index) was assumed to be 0 and (a) assumed to be 1. Solving for (b), resulted in the following Index:

$$\text{Index (weaning)} = \text{WW} - 1.71 \text{ BW}$$

Individual index values were subsequently calculated for each calf.

- Postweaning Kleiber ratio (Post-K) = Postweaning average daily gain/FW^{0.75}
- Postweaning relative growth rate (Post-RGR) = (in FW - in WW)/Final age - Weaning age

The ratio's were then multiplied by 10⁴ to avoid scaling problems, except the cow efficiency ratio which was multiplied by 100. All ratios were measured as traits of the calf. Data information is presented in Table 1.

Statistical analysis

The data were analysed using the REML VCE 4.2.5 package of Groeneveld (1994; 1997) and Groeneveld & Gracia-Cortés (1998) which optimises the log likelihood by analytical gradients and converges when the gradients approach zero.

In an initial seven-trait analysis only the direct genetic effect was included in the model. This was done to obtain Var (BW) and Cov (BW, WW) in order to calculate the restricted weaning index (Index). Fixed effects included were the HYS (herd-year-season) concatenation with 21 levels and sex with two levels. Age of dam (fitted as a linear and quadratic covariable) and age at weaning (fitted as a linear or quadratic covariable for the weaning traits) were also included.

Subsequently, four multitrait genetic models were fitted alternatively to the seven traits to estimate heritabilities and genetic correlations. These models allow for the simultaneous estimation of seven heritabilities and all (21) genetic correlations between the traits and included the weaning index, while BW was omitted. These models accounted for:

- Model 1: h_a^2
- Model 2: h_a^2 and h_m^2
- Model 3: h_a^2 , h_m^2 and r_{am}
- Model 4: h_a^2 , h_m^2 , r_{am} and c^2

It was assumed that the means for the direct effect, maternal effect, permanent environmental effect of the dam and the residual effect were zero, and furthermore that:

$$\begin{aligned} \text{Var (a)} &= A\sigma_a^2, \\ \text{Var (m)} &= A\sigma_m^2, \\ \text{Var (c)} &= I\sigma_c^2, \\ \text{Var (e)} &= I\sigma_e^2, \text{ and} \\ \text{Cov (a, m)} &= A\sigma_{am} \end{aligned}$$

$$\text{and Var (y)} = \sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_{am} + \sigma_e^2,$$

where: A = the numerator relationship matrix,

I = the identity matrix,

σ_a^2 = additive genetic variance,

σ_m^2 = maternal genetic variance,

σ_c^2 = variance due to the permanent environmental effects of the dam,

σ_{am} = genetic covariance between direct and maternal effects, and
 σ_e^2 = residual variance.

All other covariances were assumed to be zero.

Applying the likelihood ratio test (Swalve, 1993), Model 4 was found to be most reliable for the estimation of (co)variance components. However, estimates obtained from this model will be compared to those obtained from the other models as well.

Total heritabilities (h^2_T), which give expression of the regression of total genotypic variance on total phenotypic variance, were calculated using the following equation of Willham (1972):

$$h^2_T = (\sigma_a^2 + 0.5 \sigma_m^2 + 1.5 \sigma_{am}) / \sigma_p^2$$

Total maternal effects were also calculated, using the following equation (Notter, 1998):

$$t_m = h_m^2 + c^2 + \frac{1}{4}h_a^2 + h_m h_a r_{am}$$

Results and discussion

Heritability estimates and genetic correlations for the seven traits from the initial analysis (with BW) applying an animal model accounting for direct effects only, are presented in Table 2.

Table 2 Heritabilities (on diagonal) and genetic correlations between seven growth and efficiency traits (Model 1)

	BW	WW	Pre-K	Pre-RGR	WW/DW ^{0.75}	Post-K	Post-RGR
Birth weight (BW)	0.62	0.51	0.00	-0.61	0.19	0.46	0.17
Weaning weight (WW)		0.52	0.85	0.36	0.72	0.39	-0.28
Pre-K			0.43	0.79	0.74	0.19	-0.43
Pre-RGR				0.46	0.47	-0.13	-0.44
WW/DW ^{0.75}					0.45	0.13	-0.39
Post-K						0.10	0.76
Post-RGR							0.07

Birth weight

Heritability for birth weight (BW) was 0.62 (Table 2), which tends to be much higher than those reported elsewhere (Winder *et al.*, 1990; Meyer, 1992a; Bullock *et al.*, 1993; Mohiuddin, 1993; Koots *et al.*, 1994a). An almost identical direct heritability of 0.65 was reported by Tawah *et al.* (1993) in a synthetic herd in Cameroon. BW was positively correlated with WW ($r_g = 0.51$), which closely corresponds to the unweighted estimates reviewed by Woldehawariat *et al.* (1977) ($r_g = 0.55$; $n = 26$), Mohiuddin (1993) ($r_g = 0.50$; $n = 31$) and Koots *et al.* (1994b) ($r_g = 0.47$; $n = 77$). An almost identical correlation ($r_g = 0.52$) was also reported by Prinsloo (1997). The fact that BW was negatively correlated ($r_g = -0.61$) with Pre-RGR, suggests that selection for Pre-RGR would decrease BW, which may be undesirable. Almost identical correlations between BW and Pre-RGR

Direct components

In general, direct heritabilities tend to be higher than those reported in most other studies except for the postweaning relative growth traits. Direct heritabilities for WW varied from 0.38 (Model 2) to 0.57 (Model 4) (Table 3), which are considerably higher than corresponding estimates reported elsewhere (Woldehawariat *et al.*, 1977; Meyer, 1992a; Mohiuddin, 1993; Koots *et al.*, 1994a). Average heritabilities reported in those reviews were 0.22 ($n = 53$), 0.25 ($n = 21$), 0.24 ($n = 83$) and 0.27 ($n = 239$), respectively. Most of these estimates were, however, obtained from either single trait or two-trait analyses. Mostert *et al.* (1998) and Rust *et al.* (1998) obtained direct heritabilities for WW in six South African beef cattle breeds which varied from 0.21 to 0.33 where a four-trait analysis was carried out applying a model accounting for both direct and maternal effects. Their values were, however, probably under-estimated, since the negative direct-maternal covariances were omitted in the calculation of the total phenotypic variance (Groeneveld, pers. comm.). Meyer (1992a) obtained average heritabilities of 0.26 when the maternal effects were excluded and estimates ranging from 0.085 to 0.241 where maternal effects were included in the models and concluded that the exclusion of maternal effects tends to inflate heritability estimates. In this study, h^2_a 's for WW were higher where the direct-maternal covariances were accounted for, compared to where they were ignored. A similar effect was indicated by Robinson (1996). The higher than expected direct heritabilities for WW, but also for BW, in this study may be related to the possible inclusion of a 'breed effect', since the population consists of several breeds, which was not accounted for. Quite variable estimates for different herd-line (body size) combinations were also reported by Rodriguez-Almeida *et al.* (1995) and they suggested that most of the non-additive genetic variance (28% for WW) was accounted for by dominance effects. The dominance effect was not included in our models and being a crossbred population, it could be a reason for the variable and sometimes high estimates and a potential source of biased estimates.

Direct heritabilities for the preweaning relative growth traits applying the four models varied from 0.34 to 0.43 for Pre-K and from 0.36 to 0.71 for Pre-RGR. They were generally higher than corresponding estimates reported elsewhere. Bergh (1990), Köster *et al.* (1994) and Prinsloo (1997) reported heritabilities for Pre-K of between 0.21 and 0.31. These parameters were, however, obtained from unitraait analyses with smaller datasets and could in the strict sense not be compared. Heritabilities for Pre-RGR reported in the literature varied from 0.05 (Smith & Cundiff, 1976) to 0.67 (Smith *et al.*, 1976) but ranged from 0.20 to 0.30 in other studies (Fitzhugh & Taylor, 1971; Winder *et al.*, 1990; Bullock *et al.*, 1993; Prinsloo, 1997). Heritabilities for cow efficiency were high (0.32 to 0.54), while those for the postweaning relative growth traits were variable, and low, except for Model 2. It seems as though the exclusion of the direct-maternal covariance inflates the direct component for the postweaning relative growth traits. This difference is not obvious but it may be related to the sometimes unpredictable behaviour of ratios as was pointed out by Gunsett (1984), Essl (1989) and Rowe (1995).

Total heritabilities (h^2_r) were moderate to high (0.22 to 0.57) for the weaning traits but varied for cow efficiency (0.41 in Model 3 and 0.15 in Model 4) and moderate (Model 3) to low (Model 4) for the postweaning relative growth parameters. They, therefore, differed substantially between the two models for the same trait.

Direct genetic correlations between the various traits were mostly positive and mostly moderate to high (Table 4) where preweaning part-whole relationships exist. Correlations between preweaning traits and postweaning traits were negative and mostly low. The direct correlation, applying Model 2, were considerably higher than those obtained from Models 3 and 4. These correlations may also be overestimated owing to the exclusion of negative direct-maternal covariances between those traits. Additionally, some of the preweaning traits were positively correlated with Post-K but

negatively correlated with Post-RGR. Differences in estimates between the different models are difficult to explain, but it may be related to the inclusion of environmental covariances or possible negative sampling correlations and large sampling errors as was pointed out by Meyer (1992b). Meyer (1993a) indicated that there is a tendency for estimates of r_A to be reduced when allowing for σ_{am} and noted that fitting models allowing for non-zero direct-maternal genetic covariances occasionally produces somewhat erratic partitioning of phenotypic variances. It was not obvious in this study. Including the covariance between direct and maternal effects raised h^2_a for WW from 0.38 (Model 2) to 0.55 (Model 3) and to 0.57 (Model 4), but lowered h^2_a for Post-K from 0.48 (Model 2) to 0.29 (Model 3) and to 0.16 (Model 4). These erratic changes seem to occur mostly in traits with small genetic contributions relative to the total variance. The small number of observations may also have an influence on the erratic behaviour of the postweaning relative growth traits. In Meyer's (1994) study only pairwise two-trait analyses were carried out. With more traits in multitrait analyses this could be aggravated. No comparable results for these traits where multitrait models were fitted, were found in the literature.

Predicted direct and correlated responses to single-trait selection, based on the parameter estimates in Table 4, are presented in Table 5. Direct responses per generation (at $i = 1.0$) would vary from 3.12% for Post RGR to 9.76% for WW. Selection for any preweaning trait would cause positive correlated responses in any other preweaning trait, though they were small in some cases. Selection for Pre-K would cause a small correlated increase (5.13%) in WW compared to a direct response of 9.76%, while selection for WW would cause a positive correlated response of 2.60% in Pre-K and a negative response of 0.74% in Pre-RGR. The 2.60% response in Pre-K is not much less than the respective direct response of 3.05%. Postweaning relative growth traits may be adversely affected, although the responses would be relatively small. Selection for the Index would cause a 7.20% correlated response in WW (compared to a 9.76% direct response in WW) and a 3.07% in Pre-K. If the objective is an increase in WW, the Index is preferred to Pre-K. Similarly, selection for cow efficiency ($WW/DW^{0.75}$) would cause an 8.36% correlated response in WW, while it is lowly correlated with BW (Table 2). Both the Index and cow efficiency therefore seem to be obvious selection criteria which would increase WW without a possible detrimental effect on BW.

Table 5 Predicted direct (bold) and correlated responses to unit selection intensity expressed as a percentage of the mean*

(%) Selected trait	Responses in direct and correlated traits						
	WW	Index	Pre-K	Pre-RGR	WW/DW ^{0.75}	Post-K	Post-RGR
WW	9.76	8.97	2.60	-0.74	8.04	0.01	-1.70
Index	7.20	8.53	3.07	2.15	5.55	0.56	-1.63
Pre-K	5.13	7.51	3.05	3.45	3.75	0.26	-1.48
Pre-RGR	1.20	4.32	2.83	6.80	2.05	-1.11	-0.88
WW/DW ^{0.75}	8.36	7.14	1.97	1.32	8.59	-1.03	-1.60
Post-K	1.03	0.54	0.10	-0.54	-0.78	3.08	2.77
Post-RGR	-1.31	-1.56	-0.58	-0.42	-1.19	2.73	3.12

* Derived from data in Table 1 and 4

Maternal components

Maternal heritabilities were lower than the direct heritabilities for all traits and varied from 0.03 to 0.45 (Table 3). Maternal heritabilities for WW varied from 0.12 (Model 3) to 0.24 (Model 2) (Table 3) and agree well with those reported in some other studies (Meyer, 1992a; 1993a; Koots *et al.*, 1994a). Maternal heritabilities tended to be higher when the direct-maternal covariances were not accounted for in the weaning weight related traits, but lower for the postweaning relative growth traits (Model 1). The inclusion of c^2 (Model 4) decreased h^2_m estimates of the postweaning relative growth traits, while it had almost no effect on the estimates of the preweaning related traits except for Pre-RGR and cow efficiency. In Meyer *et al.* (1993), h^2_m were in some analyses in Hereford cattle larger than h^2_a . In their review, Koots *et al.* (1994a) reported an unweighted mean h^2_m of 0.20 ($n = 38$) for WW, while values obtained by Groeneveld *et al.* (1998), Mostert *et al.* (1998) and Rust *et al.* (1998) varied from 0.08 to 0.19. These values which varied from 0.08 to 0.19 were probably also biased owing to the exclusion of the direct-maternal covariance. For WW related traits (Index, Pre-K, Pre-RGR and WW/DW^{0.75}), h^2_m estimates were similar in magnitude to that of WW, except for Pre-RGR and WW/DW^{0.75} where estimates were substantially higher. Cow efficiency could, therefore, be improved by selecting on both direct and maternal breeding values.

Maternal correlations between the various traits (Table 4) were mostly positive but lower than the corresponding direct correlations. Preweaning relative growth traits were, however, negatively correlated with some of the postweaning relative growth traits (Post-K and Post-RGR), although these correlations were mostly small.

Maternal environmental effects (c^2) explained only a small portion of the total variance, ranging from 0.02 for Post-K to 0.20 for cow efficiency (Table 3). The high c^2 estimate for cow efficiency is apparently related to a high repeatability of dam weight. In general, c^2 estimates were smaller than h^2_m estimates which are in agreement with several other comparable investigations (Bertrand & Benyshek, 1987; Hetzel *et al.*, 1990; Meyer, 1992a; Swalve, 1993). Estimates of c^2 were larger than h^2_m in studies using field data (Meyer, 1993a, b; Van Vleck *et al.*, 1996). In both Meyer (1994) and Robinson (1996), c^2 only became smaller than h^2_m when r_{am} was included in their models. The permanent environmental effect of the dam is therefore relatively small in this study for all traits, except for cow efficiency where it plays an important role. Total maternal effects (t_m) were fairly consistent but low for preweaning traits (0.22 to 0.26) and almost zero for the two postweaning traits. In contrast, the maternal effect was fairly large for cow efficiency (0.41) indicating a moderate repeatability thereof.

Direct-maternal components

Correlations between direct and maternal values (r_{am}) were negative for all traits (Table 4), varying from -0.31 for Index to -0.77 for cow efficiency (WW/DW^{0.75}). Fitting Model 3, larger corresponding correlations which varied from -0.01 for Post-K to -0.21 for cow efficiency, were obtained indicating a possible bias in the estimation of these parameters. The direct-maternal correlation for WW (Model 4) was -0.37, which agreed with most estimates reported in the literature (Meyer, 1992a; 1994; Meyer *et al.*, 1993; Swalve, 1993; Waldron *et al.*, 1993; Robinson, 1996). Meyer (1994) obtained positive r_{am} estimates of approximately 0.20 for Angus cattle, while those for Zebu crosses were approximately -0.70, demonstrating that breed differences exist for these parameters. Similarly, Núñez-Domínguez *et al.* (1993) obtained r_{am} estimates of 0.38 and 0.03 for weaning weight in purebred and crossbred populations, respectively. Direct-maternal correlations for WW related traits were almost identical to that of WW (approximately -0.35). One exception is the -0.77 for cow efficiency. No comparable estimates were found in the literature for those traits. Large nega-

tive estimates, as were reported in numerous studies (Baker, 1980; Cantet *et al.*, 1988; Meyer, 1992a), were according to Meyer (1992b), due to management practices or environmentally induced negative dam-offspring covariances and do not always reflect true adverse genetic relationships between growth and maternal performance. The latter may probably be a reason for the high correlation for cow efficiency related to the early calving of heifers. According to Robinson (1996), negative estimates are more likely the consequence of additional variation between sires or sire \times year variation than a true negative genetic relationship.

The cross-correlations (i.e. off-diagonal components of the direct \times maternal correlation matrix) are presented in Table 6 for WW, Index, Pre-K and cow efficiency. These estimates varied considerably, but were in all cases also negative. The direct effect of cow efficiency was lower correlated with the maternal effects of WW, Index and Pre-K (-0.16, -0.04 and -0.01, respectively) than the correlations between maternal effects of cow efficiency with the direct effects of WW, Index and Pre-K (-0.72, -0.58 and -0.39, respectively). The cause of these differences is not clear at all. However, despite these differences, strong evidence exists for a negative relationship between direct and maternal effects, both within and between traits.

Table 6 Cross-correlations between direct and maternal effects for WW, Index Pre-K and cow efficiency (Model 4)

		Direct effect			
		WW	Index	Pre-K	WW/DW ^{0.75}
Maternal effect	WW	-0.37^a	-0.34	-0.30	-0.16
	Index	-0.26	-0.31	-0.39	-0.04
	Pre-K	-0.18	-0.32	-0.38	-0.01
	WW/DW ^{0.75}	-0.72	-0.58	-0.39	-0.77

^a Maternal heritabilities on diagonal

Conclusions

Estimates of direct and maternal heritabilities in this study tended to be larger than in most comparable investigations. The large variation in breed types in this multibreed herd may be the reason for this. Estimates for weaning related traits increased with the inclusion of more components (i.e. permanent environmental and direct-maternal covariances). With estimates of this size, prospects for improvement in preweaning traits seem to be more than reasonable. It applies to both weaning weight and the preweaning efficiency traits. Selection for weaning weight caused reasonable correlated responses in preweaning relative growth traits, the selection index and dam efficiency without any adverse influence on postweaning efficiency traits. With the simple model, when maternal effects (both direct and permanent environmental) were excluded, negative correlations were obtained between preweaning and postweaning traits. Several reasons might have contributed to this and it should be further investigated.

Estimates of the correlations between direct genetic and maternal genetic effects were negative for all traits, which is a common feature, but were smaller than in many other reports. Since the data of

this study originated from one genetic herd but maintained on two different farms, the negative r_{am} estimates could be effected by unidentified differences in management procedures not taken into consideration in this analysis, as is indicated by the differences in r_{am} between Models 3 and 4. The index or cow efficiency is recommended as the most appropriate selection criterion when the objective is to increase weaning weight without a corresponding increase in birth weight.

Total heritability (h^2_T) estimates, were higher for weaning weight than for the index and preweaning traits, but variable for cow efficiency (0.41 in Model 3 and 0.15 in Model 4). This is caused by the high negative direct-maternal covariance for cow efficiency despite a high maternal heritability (h^2_m).

Multitrait animal model analyses, fitting both genetic and environmental effects seem to be feasible as a routine procedure for the simultaneous estimation of variances and covariances for several traits. Computationally it is, however, very demanding with an increase in the number of traits and components to be estimated.

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