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Maternal body composition in seedstock herds. 3. Multivariate analysis using factor analytic models and cluster analysis

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Abstract. Considerable information exists on genetic relationships of body composition and carcass quality of young and finished beef cattle. However, there is a dearth of information on genetic relationships of cow body composition over time and, also, relationships with young-animal body-composition measures. The aim of the present study is to understand genetic relationships among various cow body-composition traits of Angus cows over time, from yearling to weaning of a second calf at ~3.5 years. To determine genetic correlations among various composition traits over time, a multi-trait–multi-time analysis is required. For the Maternal Productivity Project, this necessitates modelling of five traits (namely weight and ultrasound measure for loin eye muscle area (EMA), rib fat, P8 rump fat and intramuscular fat) by five time combinations (recordings at yearling then pre-calving and weaning in first and second parity). The approach was based on including all 25 trait-by-time combinations in an analysis using factor analytic models to approximate the genetic covariance matrix. Various models for the residual covariance structure were investigated. The analyses yielded correlations that could be compared with those of past studies reported in the literature and, also, to a set of bivariate analyses. Clustering of the genetic multi-trait–multi-time correlation structure resulted in a separation of traits (weight and EMA, and the fat traits) and also of time effects into early (heifer = before first lactation) and late (cow = post-first lactation) measurements.

Additional keywords: genetic correlations, mixed models, multi-trait–multi-time.

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Introduction

The Beef CRC Maternal Productivity Project (Pitchford *et al*. 2017) sought to understand how cow body composition was associated with various measures of maternal productivity. An important part of this is developing a detailed understanding of the underlying genetic relationships between cow body composition traits including weight (WT, kg) and ultrasound measures of rib fat depth (RIB, mm), P8 rump fat depth (P8, mm), intramuscular fat percent (IMF, %) and loin eye muscle area (EMA, cm^2). In addition, understanding how various trait and genetic relationships may change during development, from the yearling ultrasound scan to weaning of the second calf, provides an insight as to how such traits could be handled for genetic evaluation.

Many studies have reported genetic-parameter estimates (genetic variances and correlations) for WT and body composition measured on young animals and some have included multiple measurement time points. These studies have typically demonstrated moderate to strong correlations of the same trait among times, e.g. start and end of finishing phase in steers (Johnston *et al*. 2003). While several studies have reported strong genetic relationships between cow height and weight (Northcutt *et al.* 1992; Gregory *et al*. 1995), and strong correlations for cow weight (Koots *et al*. 1994; Arango *et al*. 2002; Williams *et al*. 2009) over time, few studies have reported genetic-parameter estimates for body-composition traits for cows and relationships with cow WT.

As part of the Beef CRC Maternal Productivity Project, Donoghue *et al*. (2017) reported variance and genetic correlation estimates between body-composition traits from a set of bivariate analyses for Angus and Hereford cows at pre-calving and weaning in first and second parity; the analyses conducted provide a subset of the full set of possible bivariate analyses. The analyses provided an insight into the underlying genetic basis for cow body-composition traits, with heritability estimates for ultrasound-scan traits for Angus ranging from 0.22 (EMA, pre-calving second parity) to 0.59 (rib fat depth, weaning first parity). Donoghue *et al*. (2017) reported moderate to high genetic correlations between measurements of the same trait at pre-calving and weaning within parity. In addition,

Donoghue *et al*. (2017) reported that genetic correlations with corresponding yearling measures of body composition were consistently positive and high for the first parity, but lower for the second parity.

The present study seeks to build on the work of Donoghue *et al*. (2017) by determining genetic-variance estimates and correlations for Angus heifers and cows using multivariate (multi-trait–multi-time) analyses, with the aim of producing estimates that are suitable for use in genetic evaluation. One approach to investigating the full set of correlations between multi-trait–multi-time data is to construct the full covariance matrix via bivariate analyses between all pairs of trait-by-time combinations. This is the approach considered by Stewart *et al*. (2012; among others) to estimate genetic parameters for horses in a large multi-trait dataset. An issue with this approach is that because the correlations are estimated from many separate analyses, the resulting covariance matrix may not be positive definite and adjustments (Higham 2002; Jorjani *et al.* 2003) may be required to make the matrix positive definite. The individual analyses also do not make best use of all the information available. An alternative approach is to fit a single full multi-trait–multi-time covariance model using factor analytic models (Smith *et al.* 2001). In a series of papers, Meyer (2007, 2009*a*, 2009*b*) investigated the use of reduced rank and factor analytic models and applied these models in multivariate analyses of carcass traits for Angus cattle. Tyrisevä *et al*. (2011) used factor analytic models in the estimation of genetic correlations among countries for dairy bulls. An issue with this approach is the large computational burden these analyses impose when the number of trait-by-time combinations is large. A further issue is the choice of residual model and the impact that this may have. The present study investigates the use of factor analytic models with several residual models to estimate the genetic correlations among multi-trait–multi-time Angus body-composition traits from the Beef CRC Maternal Productivity Project.

Materials and methods

Animals and measurements

The Angus cows used for the present study were a subset of the Cooperative Research Centre for Beef Genetic Technologies' (Beef CRC) Maternal Productivity Project. Details regarding selection of herds that participated in the Industry subproject, along with types and timing of records collected, were described by Pitchford *et al*. (2017). Briefly, body-composition measurements of 5901 Angus heifers were undertaken at the following four times: pre-calving first parity (PC1), weaning of first calf (W1), pre-calving second parity (PC2) and weaning of second calf (W2; Table 1). The body-composition measurements at the four time points included WT (kg), as well as ultrasound measures of P8 (mm), 12 and 13th RIB (mm), EMA (cm^2) and intramuscular fat percentage (IMF, %). Yearling records (500 day) collected for use in BREEDPLAN genetic evaluation (Graser *et al*. 2005) for WT, RIB, P8, EMA, IMF were also included as a fifth time point in the analysis. The average age of the animals for the yearling records was 461 days. The yearling BREEDPLAN records were pre-adjusted for age of calf and age of dam before analysis (Graser *et al*. 2005). All ultrasound measurements were made by accredited scanners with a B-mode Aquila Vet ultrasound (Esaote, Genova, Italy), equipped with 18-cm linear-array probe (3.5 MHz). All data reported in the present study for P8, RIB, EMA and IMF are based on ultrasound measurements.

Table 1. Number of observations (*n*), the mean value ($\bar{x}$) and the standard deviation (s.d.) for each trait-by-time combination for Angus cows

Both P8 rump fat depth (P8) and rib fat depth (RIB) are on the log scale. EMA, eye muscle area; IMF, intra-muscular fat; WT, weight; 500, yearling record at 500 days; PC1, pre-calving first parity; PC2, pre-calving second parity; W1, weaning of first calf; W2, weaning of second calf

Trait	Measurement	500	PC1	W1	PC2	W2
EMA	*n*	4704	4821	3679	3550	2543
	$\bar{x}$	58.4	56.7	59.4	60.7	63.1
	s.d.	9.2	10.3	9.1	9.5	9.5
IMF	*n*	4707	4694	3677	3552	2538
	$\bar{x}$	4.76	5.18	5.53	5.52	6.05
	s.d.	2.04	2.05	1.91	2.14	1.90
P8	*n*	4707	4821	3679	3551	2543
	$\bar{x}$	1.88	1.83	1.84	1.88	2.08
	s.d.	0.42	0.42	0.42	0.45	0.48
RIB	*n*	4706	4821	3679	3551	2543
	$\bar{x}$	1.68	1.66	1.72	1.71	1.94
	s.d.	0.36	0.37	0.38	0.40	0.43
WT	*n*	4695	4820	3678	3551	2542
	$\bar{x}$	392.6	487.7	516.0	554.1	582.9
	s.d.	63.2	70.7	65.7	68.8	73.2

The dataset was extremely unbalanced, as not all animals had measurements at all times. For all analyses, the variables RIB and P8 were transformed using a natural log-transformation ($\log(x+1)$) to better approximate the assumed normal distribution for the residual errors. The number of observations, and the mean and standard deviation for each trait-by-time combination are given in Table 1.

Formation of contemporary groups and data editing

Contemporary groups (CGs) were formed so as to group animals that had been treated alike until the measurement date. Yearling CG definition included yearling group (Graser *et al*. 2005), herd of origin, birth year and calving season (spring or autumn). Similarly, CG definition at pre-calving in parity one included herd of origin, birth year, calving season (spring or autumn) and cattle owner-defined management group. Subsequent CG definition was sequential, with the CG at weaning in parity one including the previous pre-calving CG subdivided for weaning management group. The same process was followed for pre-calving and weaning in parity two. Initial data editing identified outliers, defined as records that were more than four standard deviations from the CG mean, for each trait. For most traits, the numbers of outliers were low (generally $\leq$5 records). The outliers were removed before the analyses. CGs with fewer than five animals were excluded from the analysis. There were 448 contemporary groups, with sizes ranging from 5 to 421.

Statistical analyses

To estimate the covariance structure between the 25 trait-by-time combinations, a single complete analysis was undertaken using factor analytic models (Smith *et al.* 2001; Meyer 2007). Cluster-

analysis methods (Cullis *et al.* 2010) were applied to the resulting genetic correlation matrix, with the aim of grouping traits and times according to their similarity, to aid in interpretation.

The linear mixed model was the basis of all models fitted and was of the form

$$y = X\tau + Z_g u_g + e,$$

where y is the vector of observations (25 trait-by-time combinations by the number of animals, n), fixed effects are given by $X\tau$, the random genetic effects by $Z_g u_g$ and the residual effects by e. It is assumed that e is normally distributed, with a zero mean and covariance matrix R.

For the Maternal Productivity data, the fixed effects consist of a mean for each trait-by-time combination, CG for each trait, and, for cows, a regression on the age of the animal for each trait-by-time combination, a regression on days elapsed from PC measurement until calving (for pre-calving traits) for animals that calved (for each trait) and a regression on days elapsed from calving until weaning (for weaning traits), again for each trait. Visscher and Goddard (1993) discussed the issue of fitting CG as fixed or random and pointed out that while information may be lost by fitting the CG as fixed effects when there are many small sized CGs, fitting them as random effects may cause bias if there is association between sires (or animals in our case) and CGs. Therefore, the CGs were fitted as fixed effects.

Maternal genetic and permanent environmental effects were investigated separately for each trait for the 500-day measurements and were taken as random effects. In each case, these effects were non-significant and so were not included in the analyses of all trait-by-time combinations.

The genetic effects u_g are combinations of trait, time and genotype; these effects are assumed independent of the other random effects, are normally distributed and have a mean of zero. The multi-trait–multi-time model used in the present paper treats the trait-by-time combinations as a single component. It is assumed that the variance matrix of u_g is given by

$$var(u_g) = G_s \otimes A, \quad (1)$$

where G_s is the genetic covariance matrix for the trait-by-time combinations, $\otimes$ is the Kronecker product, and A is the additive relationship matrix as determined by the pedigree. Eqn 1 is an example of a separable variance matrix of two components, with one component being for the trait-by-time combinations (G_s) and one for the animals (given by the relationship matrix A). For the Maternal Productivity data, pedigree information was available on 11 627 animals (n = 5901 with records) and spanned about seven generations.

Various forms for G_s could be used in the analysis. If there are s trait-by-time combinations, and a fully parameterised or unstructured (US) covariance matrix is used, G_s has $s(s+1)/2$ parameters to be estimated. For the Maternal Productivity data, s = 25 and there are 325 parameters to be estimated.

A reduced form for G_s, which is a parsimonious alternative to the US form, is the factor analytic (FA) covariance matrix (Smith *et al.* 2001). In this case,

$$G_s = \Lambda\Lambda^T + \Psi, \quad (2)$$

where Λ is a $s \times k$ matrix of loadings (k is the number of factors) and Ψ is a diagonal matrix of the so-called specific variances. As the number of factors, k, increases, the approximation to a fully US form generally improves. This is the model used in the majority of analyses. Note that the maximal FA model has 18 factors with 322 parameters. From a practical point of view, a model with a small or modest number of factors is desirable.

The residual effects have a covariance matrix R that can be modelled in various ways. If R_s is the $s \times s$ covariance matrix for the s trait-by-time combinations, it follows that for trait-by-animal effects,

$$R = R_s \otimes I_n.$$

The US covariance matrix could be used for R_s and 325 parameters would need to be estimated. FA models (suitably parameterised to ensure a positive definite matrix) could be used to reduce the number of parameters.

Another possible model that is often used in plant-based analyses is a separable structure for R_s, namely

$$R_s = R_T \otimes R_t,$$

where for T traits and t times, the matrices in this separable form represent covariance matrices for traits (R_T) and times (R_t) separately.

The matrices R_T and R_t can themselves be modelled using various structures. For example, US or FA models could be used for the trait or time components. Alternatively, autoregressive models or ante-dependence of order one (Kenward 1987) could be used for the time component. The first-order heterogeneous autoregressive (ar1h) covariance structure has variances σ_t^2 for the tth time, and covariance between the tth time and the sth time is given by $\rho^{|t-s|}\sigma_t\sigma_s$, where ρ is the correlation between consecutive time points. For the autoregressive process, the time spacing should, therefore, be uniform. An ante-dependence model of order r assumes that the jth observation ($j > r$) given the preceding r observations is independent of all other preceding observations (Gabriel 1962). The model is more flexible than is the autoregressive model because it allows both different variances and so-called ante-dependence parameters. The ante-dependence structure is best specified by the inverse covariance matrix. For an order-one process (ante1), the inverse covariance matrix is tri-diagonal with zeros elsewhere; however, note that the covariance matrix can have non-zero values for all entries. For five times, there are five distinct diagonal elements and four distinct off-diagonal elements on the leading off-diagonal in the inverse covariance matrix. Thus, there are nine parameters, whereas the heterogeneous autoregressive process will have six parameters.

The analysis requires appropriate variance models for the genetic (G_s) and residual effects (R_s). Four different residual models were fitted. The first three were separable structures for which the trait covariance matrix was always unstructured, and the time covariance matrices were ar1h, ante1 and US respectively. In these models, the first variance in the trait covariance matrix was fixed at 1, so as to ensure identifiability of parameters in the model. This is a consequence of fitting a separable covariance model with heterogeneous variances in the

components of the separable structure, as multiplying one structure by a constant and dividing the other structure by the same constant results in the same overall structure, demonstrating the lack of identifiability. The fourth residual model was the US covariance matrix for the full trait-by-time combinations. For each of these residual models, FA models were fitted for the genetic effects. A series of FA models (2) were fitted. A residual likelihood-ratio test was used to decide on the final order of the FA model.

Smith *et al*. (2015) discussed the problem of selecting a factor model when it is difficult to fit such models. They proposed the use of what they termed the percentage of variance explained by the factors (%VAF), to determine whether a model can be used for prediction of genetic effects and estimation of covariance components. If λ_{ij} is the factor loading for the ith trait-by-time combination and the jth factor (the (i, j) element of Λ), and ψ_i is the ith specific variance, the percentage variance explained by the factors (k in number) for the ith trait-by-time combination is given by

$$\frac{\sum_{j=1}^{k}\lambda_{ij}^2}{\sum_{j=1}^{k}\lambda_{ij}^2+\psi_i}\times 100. \qquad (3)$$

The overall percentage variance explained across all trait-by-time combinations is

$$\frac{\sum_{i=1}^{25}\sum_{j=1}^{k}\lambda_{ij}^2}{\sum_{i=1}^{25}(\sum_{j=1}^{k}\lambda_{ij}^2+\psi_i)}\times 100. \qquad (4)$$

Smith *et al*. (2015) chose a value for Eqn 4 of at least 80%, with all individual values of Eqn 3 of at least 60% for the model to be acceptable (in their analysis), but these values are arbitrary.

The stability of estimated correlations and variances for successive factor models is also indicative of an acceptable order for the factor model. Thus, if we form a vector of the estimated pairwise correlations, ρ_r and $\rho_{r\text{-}1}$ for models with r and $r-1$ factors respectively, a measure of the change between the two models is the relative L_2 norm as a percentage, namely

$$\frac{\sqrt{(\rho_r-\rho_{r-1})^T(\rho_r-\rho_{r-1})}}{\sqrt{\rho_{r-1}^T\rho_{r-1}}}\times 100, \qquad (5)$$

with a similar definition for the estimated variances. These measures can also be used for the estimated residual correlations and variances.

The FA model gives an estimate of the trait-by-time genetic covariance matrix G_s, which can be converted to a correlation matrix C_s. To investigate the genetic correlations between traits and times, a cluster analysis using the agnes package in R was performed, using I - C_s as the dissimilarity matrix. (Cullis *et al.* 2010; De Faveri *et al.* 2015; Smith *et al.* 2015). A heatmap was used to represent the genetic correlations with the ordering of the trait-by-time combinations on the basis of the order obtained from the cluster analysis. This aids in the interpretation of the correlation structure as the trait-by-time combinations that are highly correlated are located close together on the heatmap.

Results

Multi-trait–multi-time analysis using FA models

Several models were fitted using ASReml (Butler *et al.* 2009; Gilmour *et al.* 2009) and a subset of these are listed in Table 2. This table also includes a residual likelihood-ratio statistic for successive models presented in the table, the degrees of freedom and the P-value for the test that an additional factor is required, the Akaike information criterion (AIC) for each model, the overall percentage of variance accounted for by the factors for each model using Eqn 4 and measures of stability for the estimated genetic and residual correlations and variances using relative norms of the form given by Eqn 5.

Table 2. Summary of models fitted

The genetic model G_s is denoted by a factor analytic model with k factors (FAk). The residual model is R_s. US, ar1h and ante1 denote unstructured, first-order heterogeneous autoregressive and first-order ante-dependence covariance matrices respectively. Residual log-likelihoods (first model set to 0), residual likelihood-ratio statistics (RLRS) for the test of successive models, degrees of freedom (d.f.), P-values, Akaike information criterion (AIC), %variance accounted for (%VAF), and relative norms for the estimated correlations and variances of successive models are presented

		Residual						Norm of genetic		Norm of residual	
G_s	R_s	log-likelihood	RLRS	d.f.	P-value	AIC	%VAF	Correlations	Variances	Correlations	Variances
FA1	US × ar1h	0.0				5414.2	27.6				
FA1	US × ante1	193.2	386.4	3	0	5033.8	26.6				
FA1	US × US	1010.5	1634.6	6	0	3411.2	33.7				
FA1	US	2469.9	2918.8	296	0	1084.4	59.6				
FA2	US	2594.3	248.8	24	0	883.6	64.0	10.18	7.45	2.95	0.87
FA3	US	2781.4	374.2	23	0	555.4	79.6	41.23	14.76	8.68	1.93
FA4	US	2924.1	285.4	22	0	314.0	92.1	38.70	27.56	6.85	3.83
FA5	US	3039.9	231.5	21	0	124.5	95.4	73.71	44.63	22.23	8.48
FA6	US	3117.3	154.9	20	0	9.6	96.4	29.82	40.47	15.61	11.43
FA7	US	3139.6	44.5	19	0.001	3.1	97.1	2.95	1.21	2.51	0.44
FA8	US	3159.1	39.1	18	0.003	0.0	97.8	3.89	1.24	2.77	0.44
FA9	US	3175.0	31.8	17	0.016	2.2	98.1	2.93	2.63	1.96	1.03
FA10	US	3183.0	15.8	16	0.466	18.3	98.5	3.17	2.69	2.10	1.13
FA11	US × US	2781.4				259.4	96.5	26.79	90.48	62.81	30.58

The models presented in Table 2 represent a subset of the full set of models fitted. The four residual models considered are all presented for a genetic model with a single factor. The residual likelihood-ratio statistics indicated the improvement of fit as the model complexity increases, and the fully US covariance matrix was clearly the best fit. Subsequent models (apart from the last) are for genetic models of increasing numbers of factors with the fully US residual covariance matrix.

The residual likelihood-ratio test for each additional factor is presented in Table 2 as the statistic, its degrees of freedom and a *P*-value. The additional factors are significant until the 10th factor, so that the model chosen is the FA9. The AIC suggested that the FA8 could be used. Note that the best model for the separable US trait by US time residual model was the FA11 (presented in Table 2). The AIC was clearly larger for the separable model (the likelihood-ratio test could not be performed as the models were not nested).

The percentage variance accounted for by the factors, using Eqn 4, for the FA9 model was 98% and all the individual values using Eqn 3 were above 80%. The stability measures for the genetic and residual correlations and variances are presented in Table 2. These measures showed large relative changes in the estimated genetic and residual correlations and variances up to the FA6 model. Thereafter, the change was between 1% and 3%, suggesting that the estimates had settled down. Note that the last model in the table was compared with the FA9 model to illustrate that the unstructured residual model does indeed make a big difference compared with the separable US model.

The estimated genetic variances (diagonal of the matrix), correlations (upper triangle of the matrix) and their standard errors (lower triangle) for the 25 trait-by-time combinations are given in Table 3. The strongest correlations were for the same trait measured at different times. RIB and P8 fat depth were highly correlated, which was expected, as they are both measures of subcutaneous fat. IMF was less highly correlated with subcutaneous (RIB and P8) fat, but more highly than with WT and muscle (EMA). EMA was more highly correlated with WT than with fat traits.

The estimated (co)variance parameters of the residual effects for the model with a genetic FA structure with nine factors are presented in Table 4. The residual variances are on the diagonal, the correlations (multiplied by 100) are given in the upper triangular part of the matrix and the standard errors of the residual correlations are presented in the lower triangular part.

To aid in understanding the structure in what is a large number of genetic correlations, a clustering algorithm was used as in Cullis *et al*. (2010). A heat map of the estimated correlations is given in Fig. 1. The trait-by-time combinations are ordered as in the clustering, to highlight groupings. The heat map confirmed the two broad groupings of EMA and weight, and the fat traits, with further refinement within these two groups into early (yearling and PC1) and late (W1, PC2, W2) measurements.

Discussion

Grouping of trait-by-time combinations

The analyses showed that the traits could be grouped together into two main groups, namely WT and muscle (EMA), and the fat traits (P8, RIB, IMF). In addition, grouping of times generally separated out into heifer (yearling and PC1) and cow (W1, PC2, W2). Genetic correlations were high (~0.9 for all traits except IMF, where the correlation was 0.7) between the two early measurements of yearling and PC1, and similar high correlations (~0.9) were found among the later measurements (PC1, W1, PC2) for the same trait (Table 3, Fig. 1). Correlations between the early measures and later measures averaged ~0.7.

On the basis of literature estimates of genetic correlations for developing animals, the grouping of RIB, P8 and IMF in heifer and first- and second-parity cows was expected. For Angus heifers, Reverter *et al*. (2000) and Meyer (2005) estimated genetic correlations of 0.96 and 0.85 respectively, between RIB and P8 fat depth. IMF has been reported to be moderately correlated with P8 and RIB in heifers (Reverter *et al*. 2000; Meyer *et al*. 2004; Meyer 2005). In these studies, the correlations between IMF and P8 ranged from 0.47 to 0.57 and, for IMF and RIB, they ranged from 0.49 to 0.65. The correlations in the present paper between IMF and P8 and IMF and RIB for heifers ranged from 0.49 to 0.63 and from 0.50 to 0.67 respectively, which are similar to those found in the previous studies.

Several studies have reported low to moderate genetic correlations between WT and subcutaneous fat for animals at various stages of maturity, thus providing supporting evidence for fat traits to be clustered separately from WT (Fig. 1); see, for example, Johnston *et al*. (2003) and Barwick *et al*. (2009). Barwick *et al*. (2009) and Wolcott *et al*. (2014) also found correlations between WT and EMA in heifers ranging from 0.54 to 0.61, which are similar to those found in the present paper (0.39–0.55).

For growing animals, genetic correlations between EMA and subcutaneous fat are low (Moser *et al*. 1998; Reverter *et al*. 2000; Yokoo *et al*. 2008), providing support for the separate grouping of EMA from fat traits observed in the present study. Similar to subcutaneous fat, estimates of genetic correlations between IMF and EMA are low. Reverter *et al*. (2000) estimated genetic correlations between scan IMF and EMA of 0.19 for Angus heifers, while Meyer (2005) reported genetic correlations of 0.18 for Angus heifers. The estimates reported indicate that genetic separation of EMA and IMF appears consistent with that found in other studies.

It is apparent that there is a decline in strength of genetic correlation for the same trait measured across time as animals mature. Moreover, the genetics of body composition of heifers and cows indicated that moderate but important changes in genetic relationships take place during first gestation, parturition and lactation. However, despite a reduction in the strength of correlations of the same measurement between time points, the correlations remained strong such that selection on young-animal body composition is likely to confer change in the same direction for cow body composition. The results in the present paper were similar to those found in previous studies (Koots *et al*. 1994; Arango *et al*. 2004; Barwick *et al*. 2009; Wolcott *et al*. 2014) and matched the relationships reported by Lee *et al*. (2017) and Donoghue *et al*. (2017).

Estimating correlation structure for cow body composition

Modelling many trait-by-time combinations in a single analysis can be difficult. A common approach is to conduct bivariate

Table 3. A matrix with estimated genetic variances down the diagonal, estimated genetic correlations multiplied by 100 in the upper triangle, and standard errors of the estimated genetic correlations (also multiplied by 100) in the lower triangular portion

The estimates are from the model with an FA9 structure for the genetic model and an unstructured residual model. 500, 500 days; PC1, pre-calving first parity; PC2, pre-calving second parity; W1, weaning of first calf; W2, weaning of second calf

Trait				EMA					IMF					P8					RIB					WT		
	Time	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2
	500	10.3	86	69	78	59	17	14	11	0	-2	13	12	14	6	8	21	11	12	11	11	39	39	30	36	32
	PC1	2.8	11	69	85	61	30	33	20	12	6	35	35	17	21	18	38	31	15	23	19	50	55	38	47	39
EMA	W1	3.9	3.2	13.8	90	93	14	15	45	34	36	21	26	55	46	52	22	21	53	49	55	19	29	49	49	52
	PC2	3.7	2.8	2.6	13.2	87	17	21	36	27	26	21	28	39	38	40	19	23	37	39	40	27	41	48	54	53
	W2	5.0	5.4	2.4	3.6	13.1	5	9	46	31	46	14	16	50	42	54	13	10	47	41	53	17	34	59	57	67
	500	6.1	7.3	8.1	8.1	9.1	0.57	90	72	73	62	49	55	42	41	33	53	66	48	54	40	14	17	0	2	-8
	PC1	5.4	6.3	7.1	7.2	8.5	3.2	0.79	81	82	72	54	63	43	48	39	50	67	45	55	40	13	22	5	7	-2
IMF	W1	4.8	6.0	6.0	6.5	6.9	5.3	3.5	1.23	93	94	44	54	73	67	69	40	57	76	74	71	2	16	28	23	24
	PC2	5.5	6.8	7.1	7.4	8.3	5.6	4.0	2.6	0.9	85	44	58	66	67	58	41	64	72	78	68	-6	7	17	13	7
	W2	6.4	7.6	7.6	8.2	7.8	6.7	5.4	2.6	4.4	0.89	32	38	61	56	62	29	42	63	60	62	-8	11	26	20	29
	500	4.8	5.3	6.1	6.4	7.4	5.3	5.2	5.7	6.3	7.3	0.02	92	63	76	68	86	83	58	66	63	20	16	6	5	-3
	PC1	4.3	4.6	5.5	5.8	7.0	5.2	4.1	4.9	5.3	6.9	2.0	0.03	74	88	76	77	90	68	78	70	11	12	5	8	-4
P8	W1	3.8	4.4	4.4	5.2	5.4	6.3	5.4	3.2	4.6	5.4	4.7	3.6	0.05	93	94	54	68	96	89	92	-3	1	23	18	17
	PC2	4.2	4.7	5.1	5.3	6.0	6.4	5.3	3.9	4.2	5.9	3.9	2.4	1.7	0.04	94	58	77	87	89	88	-5	4	19	19	14
	W2	4.8	5.4	5.4	5.9	5.5	7.0	6.3	4.4	5.7	5.1	4.9	4.0	1.8	1.8	0.05	51	63	87	83	91	6	15	36	33	35
	500	4.6	5.3	6.1	6.4	7.4	5.0	5.3	5.8	6.4	7.3	2.1	3.3	5.0	4.9	5.7	0.02	87	60	68	64	28	18	5	3	-8
	PC1	4.1	4.9	5.7	6.0	7.1	4.2	3.7	4.6	5.0	6.7	2.9	1.5	4.0	3.4	4.9	2.6	0.02	74	87	74	13	14	3	7	-8
RIB	W1	3.5	4.3	4.5	5.3	5.6	5.9	5.1	2.9	4.0	5.2	4.8	3.9	0.7	2.2	2.6	4.6	3.4	0.04	96	97	0	5	26	22	17
	PC2	3.7	4.6	5.1	5.5	6.3	5.8	4.9	3.3	3.3	5.6	4.5	3.2	2.2	1.5	3.1	4.4	2.6	1.3	0.04	95	3	11	25	24	15
	W2	4.4	5.2	5.2	5.9	5.7	6.7	6.1	3.9	4.8	5.0	5.1	4.3	2.0	2.5	1.6	5.0	4.1	1.3	1.6	0.04	13	20	41	36	33
	500	4.2	4.4	5.5	5.1	7.4	7.0	6.3	6.4	7.1	7.7	5.7	5.7	5.7	5.9	6.5	5.4	5.6	5.6	5.9	6.3	432	91	76	74	63
	PC1	3.8	3.7	4.8	4.5	7.1	6.9	5.9	5.9	6.7	7.4	5.7	5.4	5.4	5.6	6.1	5.5	5.3	5.2	5.5	5.9	1.6	649	87	90	82
WT	W1	4.6	4.8	4.7	5.2	5.9	7.8	6.9	6.2	7.1	7.5	6.5	6.2	5.7	6.0	6.0	6.5	6.2	5.5	5.8	5.8	3.6	2.5	767	96	95
	PC2	4.2	4.2	4.3	4.5	5.9	7.4	6.5	6.0	6.9	7.4	6.2	5.8	5.5	5.6	5.8	6.1	5.8	5.3	5.5	5.7	3.5	2.0	1.4	882	95
	W2	4.5	4.8	4.6	5.4	5.2	7.7	6.8	6.3	7.3	7.2	6.5	6.2	5.8	6.0	5.8	6.4	6.1	5.7	6.0	5.8	4.5	3.0	1.8	1.6	1410

Table 4. A matrix with estimated residual variances down the diagonal, estimated residual correlations multiplied by 100 in the upper triangle, and standard errors of the estimated residual correlations (also multiplied by 100) in the lower triangular portion

The estimates are from the model with an FA9 structure for the genetic model and an unstructured residual model. 500, 500 days; PC1, pre-calving first parity; PC2, pre-calving second parity; W1, weaning of first calf; W2, weaning of second calf

Trait				EMA					IMF					P8					RIB					WT		
	Time	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2	500	PC1	W1	PC2	W2
	500	25.7	35	29	29	26	25	15	14	12	7	36	22	17	15	14	29	20	16	11	11	51	36	25	23	20
	PC1	2.2	26.9	33	34	26	13	33	24	22	12	16	39	22	20	13	10	36	23	17	10	26	29	21	22	13
EMA	W1	2.3	2.2	31.4	49	42	13	20	47	31	27	15	18	54	40	30	14	17	53	36	27	36	31	58	45	39
	PC2	2.4	2.4	2.2	32.4	40	12	17	30	42	24	10	17	38	45	27	11	16	38	44	24	26	27	39	41	28
	W2	2.7	3.0	2.7	2.6	35.7	12	16	27	28	42	15	20	36	32	54	12	16	33	28	52	29	22	36	29	47
	500	2.3	2.6	2.9	2.9	3.2	1.7	28	24	24	20	46	21	13	14	15	42	22	15	14	16	25	15	10	10	14
	PC1	2.5	2.5	3.0	3.1	3.6	2.5	1.56	33	32	22	26	51	22	24	17	29	47	25	24	19	14	19	13	11	13
IMF	W1	2.8	3.0	2.8	3.3	3.7	3.0	2.9	1.75	51	43	24	29	62	42	28	25	27	63	40	32	18	15	42	31	25
	PC2	2.7	3.0	3.0	2.7	3.2	2.8	2.9	2.5	1.96	44	22	26	47	62	34	22	25	48	56	35	13	14	31	36	26
	W2	3.1	3.5	3.4	3.3	3.0	3.2	3.5	3.1	2.8	1.92	20	21	40	40	62	21	20	40	38	67	14	15	27	25	37
	500	2.6	2.9	3.3	3.4	3.8	2.4	3.1	3.7	3.5	4.0	0.03	37	24	23	22	61	29	22	20	19	35	19	12	12	15
	PC1	2.5	2.4	3.0	3.2	3.7	2.8	2.3	3.3	3.3	3.9	3.1	0.04	26	28	21	33	70	26	26	19	19	28	13	13	15
P8	W1	2.8	2.9	2.6	3.2	3.5	3.4	3.5	2.5	3.1	3.7	4.0	3.6	0.05	58	38	20	20	83	54	35	26	24	60	48	41
	PC2	2.7	2.8	2.8	2.6	3.1	3.1	3.2	3.0	2.2	3.2	3.6	3.3	2.5	0.06	38	19	26	54	81	36	19	14	37	43	30
	W2	3.2	3.4	3.4	3.2	2.7	3.5	3.8	3.8	3.3	2.6	4.1	4.0	3.6	3.1	0.06	21	17	35	38	85	17	13	29	23	49
	500	2.7	3.2	3.5	3.6	4.0	2.6	3.3	4.0	3.7	4.2	2.3	3.4	4.3	3.9	4.4	0.02	36	25	25	23	28	19	14	11	15
	PC1	2.5	2.5	3.1	3.3	3.8	2.8	2.4	3.3	3.3	3.9	3.3	1.6	3.8	3.4	4.1	3.3	0.03	26	27	19	17	24	14	11	13
RIB	W1	2.7	2.9	2.6	3.2	3.6	3.4	3.4	2.4	3.0	3.7	4.0	3.6	1.2	2.6	3.7	4.1	3.60	0.04	55	36	24	21	59	45	38
	PC2	2.7	2.9	3.0	2.7	3.3	3.2	3.2	3.0	2.3	3.3	3.7	3.4	2.7	1.2	3.3	3.9	3.40	2.5	0.05	38	15	11	36	38	29
	W2	3.1	3.3	3.4	3.3	2.8	3.4	3.7	3.6	3.1	2.4	4.1	4.0	3.6	3.1	1.2	4.3	4.00	3.5	3.1	0.06	14	11	27	21	49
	500	2.3	2.7	3.2	3.1	3.9	3.2	3.6	4.2	4.0	4.5	3.8	3.9	4.5	4.1	4.6	4.0	3.90	4.5	4.2	4.5	419	60	50	50	49
	PC1	2.5	2.5	3.0	3.1	4.1	3.4	3.5	4.1	4.0	4.5	4.1	3.7	4.4	4.1	4.7	4.3	3.80	4.3	4.1	4.6	2.4	593	45	48	43
WT	W1	2.4	2.5	2.0	2.6	3.0	3.0	3.1	3.0	3.1	3.5	3.6	3.4	3.1	3.2	3.6	3.8	3.40	3.0	3.2	3.5	2.8	2.7	1412	68	57
	PC2	2.6	2.7	2.6	2.6	3.3	3.3	3.5	3.6	3.3	3.8	4.0	3.8	3.8	3.2	3.9	4.2	3.80	3.7	3.3	3.8	3.0	2.9	1.8	1137	52
	W2	3.0	3.3	3.1	3.3	3.1	3.7	4.0	4.2	3.9	3.8	4.5	4.4	4.4	3.9	3.6	4.8	4.40	4.4	4.0	3.6	3.7	3.7	2.5	2.7	1601

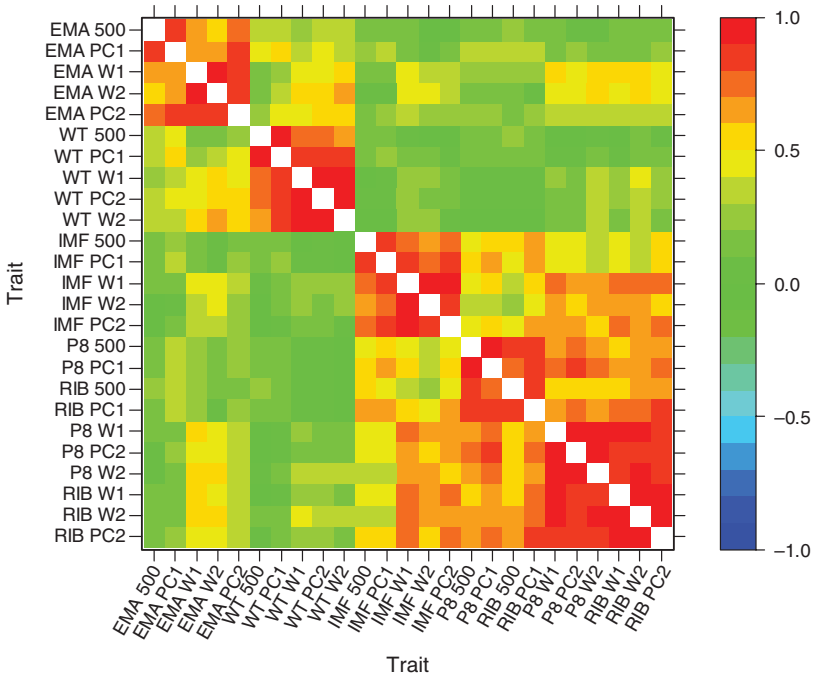

Fig. 1. Heat-map representation of correlations among traits at different times, based on the genetic correlation matrix estimated from FA9 model for genetic effects and an unstructured residual covariance model in the multi-trait–multi-time analysis. Traits are ordered on the basis of a cluster analysis.

analyses for all combinations, to assemble the full correlation matrix and then adjust it to make it positive definite. A more comprehensive approach examined in the present paper was to perform a full multi-trait–multi-time analysis using FA models for the genetic covariance structure. The correlations estimated from a complete single multi-trait–multi-time analysis make best use of as much available information among the multiple traits as possible. For this reason, it would be expected that these analyses would yield more accurate correlations than a piecemeal approach of performing 300 bivariate analyses.

The estimated genetic (and residual) correlations found using bivariate analyses are presented in Table S1 (available as Supplementary material for this paper). In many cases, the correlations are similar; however, there are clear and substantial differences with the results in Table 3. The L_2 norm of the bivariate estimates relative to those from the multi-trait–multi-time analysis using Eqn 5 was 13%, indicating a substantial overall difference.

The choice of residual model used in single stage multi-trait–multi-time genetic analyses is an important consideration. Fitting a restrictive residual model can cause problems of partitioning of the overall covariance matrix into genetic and residual components. This occurred for the separable residual models and the problem persisted even when higher-order FA models were fitted. The separable model assumes that the correlation between each pair of times is the same for each trait and the correlation between each pair of traits is the same for each time. In the present paper, the estimated residual correlations for WT across times were much higher than those for other traits and estimated correlations among traits were not consistent. Therefore, the separable residual models considered were not adequate when compared with a fully US model.

The FA analyses were computationally demanding and were performed using high-performance computing resources. It took weeks to run the full set of FA models required to adequately estimate the covariance structure for the full multi-trait–multi-time model. Meyer (2005) reported on both an analysis of multi-trait data on Angus cattle and on a simulation study for reduced-rank methods of analysis. The computational burden in achieving such analyses is discussed in that paper and mirrors those found in the current study. Despite the computational issues, the time and resources used for analysis were a small component when compared with the design and data acquisition of the Maternal Productivity Project.

The practical approach to fit the multi-trait–multi-time models is important. For FA models, there may be a need for good starting values to achieve convergence of the fitting process. For the analyses reported in the present paper, the approach was to fit an initial model omitting the genetic model (that is the FA model) and purely estimating the residual covariance matrix. The estimated parameters from this initial analysis were then used in the analysis for each FA model. This approach proved very successful, and although many iterations were required for convergence, it is our recommended method of analysis.

Model selection, or how many factors to include in the model, is another important consideration. Smith *et al*. (2015) suggested the %VAF could be used to decide on the appropriate FA order and suggested that the residual likelihood-ratio test may imply the need for fitting too many factors. Given that the aim of our

analysis was estimating genetic correlations, we recommend examining the stability of estimates of correlations and variances as the number of factors in the model increases, in conjunction with residual likelihood-ratio tests and the AIC. In our analyses, the %VAF was high for low numbers of factors but the corresponding stability measures were large. The final model selected by the residual likelihood-ratio test (and the AIC) displayed low stability measures as is desirable.

While the FA models are one approach that may be suitable for modelling the genetic covariance structure in multi-trait–multi-time genetic datasets, there are other approaches that may make use of the time covariance structure of the traits and, specifically, the fact that correlations usually decrease as the time between measurements decreases. Separable models for the genetic effects using ante-dependence or autoregressive ar1 models for the time component are one option, but these models are restrictive. They were attempted for this dataset (results not presented here) but did not fit as well as the FA models. An alternative approach may be a multi-trait random coefficients model, multivariate autoregressive models (De Faveri 2013) or structured ante-dependence models (Jaffrézic *et al*. 2003), which may be used to model multivariate data over time.

Conclusions

In conclusion, the FA genetic models were a suitable approach for a single multi-trait–multi-time analysis but required significant computing resources and time. In addition, the cluster analyses implemented in the present paper were helpful in aiding biological understanding of genetic relationships among traits over time. The results presented aid the understanding of genetic relationships of WT and RIB, P8, IMF and EMA for Angus cattle from yearling to weaning of second calf. Importantly, it is apparent that the strength of genetic correlation for the same trait declines over time. However, traits clearly cluster in before first lactation and after first lactation. The strength of correlation across the time points indicated that the selection on young animal traits would confer change in the same direction for cows after first lactation. If highly accurate breeding values are required to describe cow body composition, then measurement of traits post first lactation would be required as genetic correlations between composition at yearling and W2 ranged from 0.59 to 0.68.

Conflicts of interest

The authors declare no conflicts of interest.

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