Estimates of variances due to parent of origin for weights of Australian beef cattle

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Abstract

Estimates of variances due to differential expression of paternally and maternally derived genes can be obtained from animal model type analyses by fitting appropriate gametic effects. This is feasible for large scale analyses, as the inverse of the gametic relationship matrix can be set up directly from a list of pedigrees.

We present a series of analyses applying such model for large sets of records for birth, weaning, yearling and final weights of Australian Angus and Hereford cattle. Results show that maternal genetic effects on these traits are largely confounded with maternal parent of origin effects, so that it is difficult to reliably separate the respective variance components. On the other hand, paternal parent of origin effects tend to act similarly to sire × herd effects so that estimates of their variance are inflated by any effects not modelled and contributing to such apparent interaction.

Fitting an animal model with both parent of offspring effects, maternal genetic and permanent environmental effects as well as sire × herd and maternal grand-sire × herd of origin of dam interactions as additional random effects yielded estimates of the variance due to paternal parent of origin effects of 5 to 7% of the phenotypic variation for birth and weaning weights and of 0 to 1% for yearling and final weights. Corresponding estimates for maternal parent of origin effects were 0 to 11% for birth and weaning weights and 7 to 8% for yearling and final weights, while sire and maternal grand-sire interaction effects explained from 0 to 4% of the phenotypic variance.

1 Introduction

So-called 'parent of origin' effects refer to the phenomenon that the expression of genes may depend on the sex of the parent from which they were inherited. Paternal imprinting

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describes the scenario where alleles from the father are not or only partially expressed in his progeny, and, conversely, maternally imprinted genes are those inherited from the mother which are silenced in her offspring. This is predominantly attributed to differential DNA methylation during transcription (Ferguson-Smith, 2001); see Reik and Walter (2001) for a more detailed review. There are many reports for such mode of gene action in various species (e.g. Morison et al., 2005). Prominent examples for imprinted genes in livestock are the Callipyge gene in sheep (e.g. Georges et al., 2003) and DGAT-1 in dairy cows (Kuehn et al., 2007).

As illustrated by Hill and Keightley (1988), imprinting changes the expectation of covariances among relatives. In a mixed model setting, this can be accommodated by fitting a model with animals' gametic effects. This is feasible for large scale problems as the inverse of the gametic relationship matrix can be set up analogously to the inverse of the numerator relationship matrix from a list of pedigree information (Schaeffer et al., 1989). Alternatively, as proposed by Tier and Sölkner (1993), imprinting effects can be estimated by augmenting the standard animal model by gametic effects due to one parent, treating gametes as homozygous diploid individuals. Estimates of variances due to imprinting obtained fitting such model have been reported for growth of pigs (Vries et al., 1994), carcass characteristics of beef cattle (Engellandt and Tier, 2002) and dairy- and fitness-related traits recorded on dairy cows (Kaiser et al., 1998; Essl and Voith, 2002b). However, these analyses were limited to considering imprinting from one parent only. Essl and Voith (2002a) suggested to employ separate sire and dam model analyses to assess the difference between paternal and maternal imprinting. More recently Neugebauer et al. (2010a,b) fitted a model with correlated sire and dam gametes to estimate imprinting variances for both sexes simultaneously, considering growth and carcass traits in pigs and beef cattle. However these analyses lacked constraints appropriate to the parameterisation chosen, resulting in negative estimates of variances in several instances.

As discussed by Tier and Meyer (2011), in principle there are seven parameters to fully describe gene action with imprinting under the infinitessimal model: The additive genetic variance due to non-imprinted genes, the variances due genes fully imprinted maternally or paternally, and the corresponding variances due to partially imprinted alleles together with the respective degrees of imprinting. However, in practice, effects to the different groups of genes can not be separated – we can only distinguish between variances due animals' maternal and paternal gametes and the covariance between them, i.e. estimate three parameters. Thus, a common assumption is that there is no partial imprinting.

Conceptually, modelling in the presence of imprinting is most transparent by considering variances due to gametes originating from different parents. We can then fit a gametic model with random effects due to animals' maternal and paternal gametes, and interpret the covariance between them as representing half of the additive genetic variance due to non-imprinted genes, whilst the differences in estimates of the gametic variances and the covariances yield estimates of the corresponding variances due to the parents of origin. For such model to yield estimates of the causal components within the parameter space, estimation needs to constrain estimates of the covariance to be no greater than either variance and be non-negative. Alternatively, an equivalent model is given by an animal model fitting both maternal and paternal gametic effects as additional, uncorrelated random effects. Tier and Meyer (2011) recently applied such models to carcass characteristics of beef cattle measured by live ultrasound scanning, and reported estimates of variances due to the parent of origin (POO) effects of up to 25% of the total genetic variance.

So far, estimates of variances due to POO effects have only been reported for traits not subject to maternal effects. For several types of the most common covariances between relatives occurring in the analysis of data routinely collected in livestock improvement programmes, maternal additive genetic effects are confounded with maternal POO effects. Thus maternal effects may produce the same pattern of variation as the latter, and data spanning several generation or genomic information may be required to successfully differentiate between them (Hager et al., 2008). This paper investigates the scope for estimation of variances due to POO effects for early weights of Australian beef cattle, traits which are subject to both additive genetic and permanent environmental maternal effects.

2 Material and Methods

Records for birth (BW), weaning (WW), yearling (YW) and final (FW) weights of Australian Angus and Hereford cattle were extracted from the National Beef Recording Scheme (NBRS) data base, selecting the largest herds. Ages at recording considered were 80 to 300 days, 301 to 500 days and 501 to 700 days for WW, YW and FW, respectively. For animals with more than one measurement in a given age range, only the first record was selected. Any weights recorded prior to 1985 and records for twins were disregarded. Additional edits eliminated records more than 2.5 standard deviations from the mean, records for animals with unknown sex, and any offspring of dams less than 19 months or more than 184 months old. Further,

any records in small contemporary group subclasses (defined below) comprising less than 5 measurements were discarded. All pedigree information available for animals in the data and their parents was extracted recursively. Characteristics of the data structure are summarized in Table 1.

Univariate analyses for all traits were carried out by restricted maximum likelihood fitting a series of models with increasing number of variance components. Model A was an animal model, fitting animals' additive genetic as well as maternal genetic and permanent environmental effects as random effects. Models P and M fitted the same effects as model A and a single parental POO effect in addition, paternal and maternal respectively. Model F was model A augmented by both parental POO effects, treated as uncorrelated. Finally, model E extended model F by fitting the two corresponding POO effects for maternal genetic effects. These models were further expanded by fitting sire × herd (S×H) effects, denoted as models *X*S (for *X*=A, P, M, F, E), or S×H as well as maternal grand-sire × herd of origin of dam (Z×H) effects in addition (denoted as models *X*Z). Furthermore, models were fitted either assuming direct-maternal genetic correlations were zero or allowing for such covariance, denoted by subscript 0 and *r*, respectively, in the following. POO effects on direct and maternal genetic effects fitted in model E, however, were assumed to be uncorrelated. This yielded up to 30 different analyses per trait and breed.

For all models, contemporary groups were fitted as fixed effects. These were defined as subclasses given by herd, date of weighing, sex of calf and management groups. Date used was the calendar date, except for BW where date was defined as year-month. If the range of ages at weighing represented in a subclass exceeded 45 days for WW or 60 days for YW and FW, classes were subdivided further, a practice refereed to as 'age slicing'. In addition, age at weighing was fitted as a linear covariable, nested within sex of calf (except for BW). Systematic differences due to age at dam where taken into account by fitting it as a linear and quadratic covariable as well as fitting a so-called heifer factor, i.e. a cross-classified fixed effect distinguishing between heifers (calving at less than 29 months old) and cows.

Analyses were carried out using our software package Wombat (Meyer, 2007). For models other than model A, this required the inverse of the gametic relationship matrix to be set up and its determinant to be calculated externally, and to be supplied as a 'user-defined' covariance matrix. This task was performed using the procedure described by Tier and Meyer (2011) (Fortran code given in the appendix of their paper). To reduce computational requirements, models F and E were fitted as the equivalent gametic models (*c.f.* Tier and

Meyer (2011)), unless constraints to ensure non-negative estimates of variances due to POO effects were required. Significance of random effects was assessed by comparing nested models with a likelihood ratio test, and standard errors of estimates were obtained from the inverse of the average information matrix.

To investigate the effect of data and pedigree structure on estimates under the different models, additional analyses were carried out for simulated data. This was done replacing the data for the largest subset (WW for Angus) by records obtained sampling random effects in the full model (F_0) from Normal distributions with population variances for direct, additive genetic effects, maternal additive genetic and permanent environmental effects, paternal and maternal POO effects, and residuals of 50, 20, 30, 10, 10 and 80, respectively, and a direct-maternal genetic correlation of zero. While no fixed effects were simulated, these were fitted in the analyses. A total of 10 replicates were sampled and analysed.

3 Results

3.1 Variances from different models

Estimates of variance components the 30 different analyses for weaning weights of Angus cattle are summarized in Table 2. Corresponding values for selected analyses for the other traits are shown in Table 3 for Angus and Table 4 for Herefords.

3.1.1 Modelling weights of beef cattle

Results for the 'standard' models ignoring POO effects were, by and large, comparable to those reported previously for these traits and breeds (e.g. Meyer, 1992b; Meyer et al., 2004). As observed in various other studies, allowing for a non-zero direct-maternal genetic covariance (σ_{am}) yielded a substantial, negative estimate (model A_r), accompanied by higher estimates for both the direct (σ^2_A) and maternal (σ^2_M) genetic variance, compared to results obtained assuming σ_{am} was zero (model A_0), and dramatically increased value of the log likelihood ($\log \mathcal{L}$).

While a weak, antagonistic genetic relationship between direct and maternal genetic effects for WW in the range of -0.1 to -0.2 is generally accepted as plausible, larger estimates (absolute value) are usually treated with justified scepticism. There has thus been much

debate of whether a non-zero σ_{am} should be fitted or not. For field data on beef cattle, it is not uncommon that cows remain in their mating groups until their calves are weaned. If such management groups are not judiciously recorded, this can lead to classification of contemporary groups which does not fully account for systematic environmental effects. In turn, this may result in records for progeny of a sire being more similar than due to their degree of relationship alone, causing the estimate of σ_{am} to be biased downwards and those of σ^2_A and σ^2_M to be inflated. Other factors which can contribute to implausible estimates of σ_{am} are negative, direct-maternal environmental covariances which are not taken into account or inappropriate definition of genetic groups (Meyer, 1992a, 1997; Robinson, 1996).

Fitting a sire × herd interaction has been shown to alleviate these symptoms and has thus been adopted as a pragmatic solution to counteract potential deficiencies in modelling in genetic evaluation schemes for beef cattle such as BreedPlan (Graser et al., 2005). However, in estimating genetic parameters it is not unproblematic as analyses fitting such models often yield estimates where a substantial proportion of the direct additive genetic variance is partitioned into the sire × herd component. As expected, fitting S×H effects did reduce (absolute value) the estimate of σ_{am} substantially, with the magnitude of the direct-genetic correlation estimate for WW reduced from −0.57 (A_r) to −0.38 (AS_r) in Angus and −0.53 to −0.37 in Herefords. This was accompanied by a reduction in the estimate of σ^2_A by more than 40% compared to analyses not fitting S×H effects and a dramatic increase in log likelihood ($\log \mathcal{L}$). With about 90% of S×H effects pertaining to sires used in a single herd only (*c.f.* Table 1) this was not surprising, as there were less contrasts between sire and S×H effects than might be desirable. S×H effects were most influential for WW – any unidentified groups are generally broken up at weaning, so that an influence on later weights is expected to reflect a carry-over effect only.

Meyer (2003) demonstrated that repartitioning of genetic variance into the variance due to S×H effects (σ^2_S) is reduced with increasing proportion of records on progeny of sires used in multiple herds. Data extraction in this study, however, aimed at obtaining records on several generations of animals in large herds and herds with a substantial number of calves resulting from embryo transfer, so as to maximize the types of covariances between relatives available and thus the scope for disentangling variances due to different types of genetic effects. Selecting records to allow S×H effects to be better estimated would have counteracted this aim and was thus disregarded. Moreover, our interest in S×H effects *per se* was limited – the main reason for considering these was the potential for paternal POO

effects to act in a similar fashion and thus to be inflated by the variation otherwise accounted for by σ^2_S.

Similarly, maternal grand-sire × herd of origin of dam effects were considered here primarily for their potential to interact with estimates of paternal imprinting on maternal genetic effects in model E – with Z×H effects expected to be analogous to S×H effects for paternal imprinting of direct genetic effects. Maternal grand-sire effects in animal model analyses are rarely considered in the literature, though Dodenhoff et al. (1999) reported genetic effects for maternal grand-dams to account for 2 – 7% of σ^2_P for WW of Angus cattle and to reduce (absolute value) negative estimates of σ_{am}. Fitting Z×H effects again increased $\log \mathcal{L}$ dramatically over the models fitting S×H only, with the corresponding variance (σ^2_Z) explaining almost 3% of the phenotypic (σ^2_P) variance, and reduced the magnitude of estimates of σ^2_M, σ_{am} and σ^2_S. As for S×H effects, most Z×H effects represented sires occurring in one herd only. In addition, a large proportion (83% for WW in Angus; see Table 1) was represented by only record, i.e. the scope for successfully disentangling Z×H and genetic effects was limited.

3.1.2 Fitting a single parent of offspring effect

Fitting paternal POO effects only (models P) increased $\log \mathcal{L}$ substantially over the models (A) ignoring such effects. Somewhat disconcertingly, the estimate of σ_{am} for model P_r was positive, corresponding to a direct-maternal genetic correlation of unity in 7 of the 8 trait × breed combinations, whilst not or only just significantly (at an error probability of 95%) increasing $\log \mathcal{L}$, compared to model P_0. Occurrence of such estimates usually represents a stern warning that the data and pedigree structure does not allow all parameters fitted to be estimated, or that the model of analysis comprises other random effects which have not been modelled adequately. At the same time estimates of σ^2_A were reduced drastically, while estimates of the variance due to paternal POO effects (σ^2_{IP}) for models P_0 and P_r ranged from 5% to 19% of σ^2_P. This emphasized serious problems in the partitioning of variation. Fitting S×H effects then reduced estimates of σ^2_{IP} dramatically, suggesting that, when S×H effects were not fitted paternal POO effects acted in a similar fashion to sire × herd effects. Conversely, this implied that estimates of σ^2_{IP} from models P_0 and P_r were substantially biased upwards. Fitting Z×H effects in addition (models PZ) yielded some further reduction in estimates of σ^2_{IP}. In addition, fitting S×H effects restored estimates of σ_{am} to negative values similar to those obtained from models AS and AZ.

In constrast, fitting maternal POO effects improved $\log \mathcal{L}$ much less. For σ_{am} equal to zero (model M_0), analyses for WW for both breeds yielded estimates of the variance due to maternal POO effects (σ^2_{IM}) close to zero, whilst estimates of σ^2_M and $\log \mathcal{L}$ remained virtually unchanged compared to model A_0. In an opposing pattern, estimates of σ^2_M for YW and FW were essentially zero and estimates of σ^2_{IM} amounted from 5% to 10% of σ^2_P. This was accompanied by a substantial increase in $\log \mathcal{L}$ and some decrease in estimates of σ^2_A while the sum of estimates, σ^2_P, remained more or less constant. Similarly, estimates of the maternal, permanent environmental variance (σ^2_C) were virtually unaffected by POO effects fitted. This suggested that all maternal genetic variation for YW and FW was interpreted as variance due to maternal POO effects, while the opposite held for WW (both breeds) and BW in Angus.

Allowing of a non-zero σ_{am} yielded by and large the same pattern in estimates for YW and FW than models assuming σ_{am}=0. For BW and WW, estimates of σ_{am} from model M_r were similar to those obtained fitting A_r, but some estimates of σ^2_M were markedly lower with the difference again being partitioned into σ^2_{IM}. As for models A, fitting S×H and Z×H effects reduced estimates of σ^2_M. Similarly, fitting Z×H effects tended to decrease non-zero estimates of σ^2_{IM}.

3.1.3 Fitting both paternal effects

Accounting for both POO effects (models F), estimates of σ^2_{IP} were generally of similar magnitude or slightly lower than for model P. This indicates that ignoring maternal POO effects had little effect on estimates of σ^2_{IP}, i.e. that variation due to maternal POO effects was not 'picked up' as $\hat{\sigma}^2_{IP}$, and was consistent with the pattern observed by Tier and Meyer (2011) in corresponding analyses of carcass traits recorded by ultra-sound scanning for the same breeds. When fitting S×H effects though, the reduction in estimates of σ^2_{IP} tended to be somewhat less than encountered under models P.

For σ^2_{IM}, however, values were in several instances higher than obtained for model M. In particular, estimates which were previously zero increased to 7% (WW in Angus) and 12% (BW in Hereford) of σ^2_P, along with a significant increase in $\log \mathcal{L}$ for model F over that for model M. This was accompanied by some reduction in estimates of the residual variance (σ^2_E) or of σ^2_A and σ^2_M. When determining random effects to be included in the model of analysis in a 'step-up' fashion, it is common practice to omit sources of variation which have been found insignificant from further steps. Results suggest that for models comprising

effects that are at least partially confounded and thus subject to substantial repartitioning of variation when the model is altered, this might be premature and lead to elimination of important effects. When fitting both POO effects, allowing for a non-zero direct-maternal genetic covariance (model F_r) yielded little changes in estimates and log $\mathcal{L}$ compared to model F_0, and as observed earlier, estimates of σ_{am} were limited by a corresponding correlation of unity (absolute value).

Fitting S×H and Z×H effects again resulted in marked reductions in estimates of variances due to POO effects, following similar patterns as described above for the models fitting a single parental effect. Shown in Table 3 and Table 4 are estimates for models A, AZ, F and FZ omitting any results for analyses allowing for a non-zero σ_{am} if this did not increase log $\mathcal{L}$ significantly. For all 8 trait × breed combinations, fitting POO effects (models F) raised log $\mathcal{L}$ substantially and significantly compared to the corresponding base model (Models A), with increases being lowest when Z×H effects were included in the model of analysis.

3.1.4 Parent of offspring effects on maternal genetic effect

Extending the model to allow for imprinting of maternal genetic effects (model E) yielded analyses with up to 11 covariance components to be estimated. On the whole, a similar repartitioning of variation to that observed for direct genetic effects was observed. Estimates of variances due to maternal imprinting on maternal genetic effects (σ^2_{MM}), however, were close to zero throughout. The corresponding paternal component (σ^2_{MP}) appeared important only for WW. Whilst estimates of σ^2_{MP} were significant for BW in both breeds and YW in Herefords when no interaction effects were fitted (models E), this eroded when maternal grand-sire × herd effects were included in the model (models EZ). As shown in Table 2 for WW of Angus, estimates of σ^2_{MP} from models E were less than half of those obtained from models E. Corresponding values for WW in Herefords were 30.1 and 13.5, i.e. fitting Z×H effects reduced $\hat{\sigma}^2_{MP}$ by almost 60%.

3.2 Simulation results

To gain further insight into the partitioning of variation when both maternal effects and POO effects are fitted, data for WW in Angus was replaced by simulated records. Population values for variance components and mean estimates across replicates are given in Table 5. For all models, the estimate of σ^2_P agreed with the population values which emphasizes

that drastically different estimates were indeed a 'partitioning of variation' problem. As observed for the real data, estimates of σ^2_C were virtually unaffected by the model of analysis. When ignoring POO effects (models A), estimates of σ^2_A were inflated most, but some of the imprinting variances appeared to be picked up in estimates of σ^2_M and σ^2_E as well. Interestingly, allowing for a non-zero σ_{am} (model A_r) resulted in negative estimate of this component. This suggests that differential expression of maternal and paternal gametes should be added to our list of potential causes resulting in implausible, negative estimates of the direct-maternal genetic covariance.

Fitting paternal POO effects only, the estimate of the corresponding variance component, σ^2_{IP}, recovered most of the variation simulated. Mean estimates of σ^2_E and σ^2_M for models P_0 and A_0 were very similar, indicating that maternal imprinting effects not modelled predominantly inflated these components. However, allowing for maternal and ignoring paternal POO effects (model M_0) resulted in estimates for σ^2_{IM} of zero – as observed for the real data – for 9 of the 10 replicates. This suggests that paternal POO effects not modelled may suppress the expression of their maternal counterparts. Allowing for a direct-maternal genetic covariance (M_r) removed this restriction, but resulted in an even larger (absolute value) estimate of σ_{am} and an underestimate of σ^2_E.

Finally, analyses fitting the model under which the data were simulated (F_0) resulted in mean estimates close to the population values, demonstrating that the data and pedigree structure were suitable to disentangle all seven sources of variation. Conversely, this implies that some of the more puzzling differences in estimates form different models in the real data have to be attributed to other reasons.

Corresponding analyses fitting S×H and Z×H effects in addition yielded mean estimates of σ^2_Z of less than 0.1 and of σ^2_S between 0.1 and 0.4 while estimates of the other variances were essentially the same as those from the corresponding models omitting these effects. This indicates that such interaction effects were not prone to 'automatically' remove genetic variation in our data, i.e. that the data structure could support estimation of all the genetic components fitted. Conversely, it implies that the substantial reductions in estimates of variances due to POO effects observed when fitting S×H and Z×H effects largely reflected overestimation in their absence.

3.3 Estimates of genetic parameters

Estimates of variance ratios for genetic effects and of the direct-maternal genetic correlation (r_{AM}) together with their approximate, lower bound sampling errors (s.e.) for analyses fitting models A and F are summarized in Table 6 for Angus and Table 7 for Herefords, omitting results for model F_r and for FZ_r for those cases where allowing for σ_{am} did not increase $\log \mathcal{L}$ significantly.

With estimates based on large data sets, s.e. were small throughout, with values of 0 denoting s.e. of less than 0.005. Fitting POO effects increased s.e.for estimates of direct (h^2) and maternal (m^2) heritabilities substantially, to approximately double those observed for model A_0. In contrast, estimates of the proportion of variance due maternal, permanent environmental effects (c^2) and their standard errors (not shown) differed little between the two models of analyses, indicating that this component was virtually unaffected by repartitioning of variation when POO effects were fitted.

Estimates of h^2, m^2 and c^2 from analyses not fitting POO effects were again well in the range of corresponding values reported in the literature. Allowing for POO effects reduced estimates of both direct and maternal heritabilities substantially compared to values obtained from the base mode, A_0. While we would expect estimates of h^2 to be somewhat inflated if POO existed and were ignored and, conversely, anticipate some decrease in estimates from models F compared to models A, a number of these reductions appeared implausibly large. This held especially for WW where virtually all direct genetic variance was 'picked up' as variance due to imprinting. For the other traits, the reduction in h^2 was less but estimates of m^2 from models F were essentially zero. This suggested that estimates of the proportion of variance due to paternal (i_P^2) and maternal (i_M^2) imprinting were inflated by maternal genetic variation.

Estimates of variances due to POO effects from model F_0 ranged from $5-17\%$ of σ_P^2 for paternal and $0-12\%$ of σ_P^2 for maternal effects, with respective means of 10.4% and 8.4% and substantially higher than corresponding estimates for other traits available in the literature. Fitting S×H and Z×H effects (model F_r, not shown) reduced estimates, especially for paternal effects, with means (ranges) of 3.0% $(0-7)$ of σ_P^2 and 6.8% $(0-11)$ of σ_P^2 for estimates of i_P^2 and i_M^2, respectively. For most analyses under models F_r and FZ_r estimates of r_{AM} were close to unity (absolute value), accompanied by failure to approximate the corresponding s.e.. This was due to estimates of σ_M^2 or σ_A^2 close to zero. These estimates of r_{AM} were thus regarded as

spurious.

4 Discussion

There has been much research effort concerned with modelling of traits subject to maternal effects, especially weaning weight. Reliable estimation of maternal effects and their variances has always been problematic as direct and maternal effects are inherently confounded (Willham, 1980). For beef cattle, models explicitly accounting for direct-maternal environmental covariances have been proposed (Meyer, 1997; Quintanilla et al., 1999), but have found little uptake. Instead, sire × herd effects are commonly fitted, as this tends to counteract implausible estimates of the direct-maternal genetic correlation. Results from this study suggest that fitting maternal grand-sire × herd (of origin of dam) effects in addition may be beneficial.

Results emphasize the difficulties in partitioning variance components due different modes of gene action even for large and relatively well structured data sets. Table 8 summarizes the expectation of selected types of covariances between relatives when maternal and POO effects are present. As shown, for several of the covariances most common in our type of data, coefficients for σ^2_M and σ^2_{IM} are the same, i.e. estimates of these components are likely to be hard to separate. To estimate the 6 components in model F_r (omitting σ^2_E), at least 6 types of covariances between relatives are required. However, considering the first 6, 7 or 8 covariances in Table 8 only would not allow for a unique solution for all causal components. Using all 12 covariances listed would yield sufficient contrasts, but result in strong sampling correlations between estimates, especially between σ^2_A and σ^2_{IP} and between σ^2_M and σ^2_{IM}.

Recently, Imumorin et al. (2011) reported maternal and paternal POO effects for 18 quantitative trait loci affecting growth of beef cattle, explaining between 1 and 4% of σ^2_P each. While our results present evidence for differential expression of genes for weights of beef cattle depending on the parent they came from, estimates of the corresponding variances are likely to be, to some extent at least, inflated by other sources of variation. When fitted, paternal POO effects tended to act similarly to sire × herd effects and thus to 'pick up' some the variation accounted for by these effects. As shown, there was considerable repartitioning between estimates of σ^2_M and σ^2_{IM}. For model FZ_r, estimated sampling correlations between these components (obtained from the inverse of the average information matrix) for the 8 cases (trait × breed) ranged from −0.82 to −0.92.

5 Conclusions

Genetic imprinting is known to affect a wide range traits, including growth. While estimation of variances due to parent of offspring effects is feasible utilizing the gametic relationship matrix, it is hampered by inherent confounding with maternal genetic effects. Results indicate that a small proportion of the phenotypic variance in weights of beef cattle may be attributed to differential expression of genes from the two parents.

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Table 1: Characteristics of the data (BW: birth, WW: weaning, YW: yearling and FW: final weight).

		Angus				Hereford			
		BW	WW	YW	FW	BW	WW	YW	FW
No. records		246419	258843	195975	171896	137392	199616	153497	148840
No. animals		278760	289836	230473	221531	180096	240613	208820	218142
No. sires	A[a]	5661	6435	5881	7221	4129	5739	6153	7434
	B[b]	70.8	69.2	64.3	42.8	47.0	52.1	41.2	25.6
No. genetic dams	T[c]	100210	105390	91197	98139	76765	92510	94995	105870
	A[a]	81874	89066	73692	74543	48872	66044	61497	68604
	B[b]	72.5	68.8	63.8	52.2	62.1	70.3	56.3	45.5
	1[d]	35.1	37.9	40.3	47.3	35.9	32.4	40.0	46.4
	2[e]	21.3	20.2	22.3	21.6	21.5	20.5	22.9	23.8
No. raising dams		88786	94887	79447	79477	52837	70049	64507	71002
No. contemp. groups		7455	6816	6335	7201	6205	6894	6454	6995
No. herds		30	30	30	52	36	39	52	88
No. S×H[f]		9715	10758	9273	10244	6369	11665	10434	10674
	C[g]	27.3	27.1	23.4	16.5	31.1	47.5	37.4	25.1
	D[h]	90.5	90.8	90.2	90.4	89.7	89.0	88.2	86.5
No. Z×H[i]		25825	41259	28020	24942	11255	18199	15809	18351
	C[g]	73.5	82.9	76.8	67.6	54.1	63.1	55.0	53.2
	D[h]	86.7	87.2	86.9	87.4	87.9	87.8	87.3	85.2
Weight (kg)	$\bar{x}$[j]	35.88	226.0	342.8	491.7	38.24	220.4	342.4	479.9
	sd[k]	5.52	49.5	75.5	99.3	5.65	51.6	79.5	110.5
Age (days)	$\bar{x}$	–	197.4	393.1	567.5	–	201.4	399.2	570.2
	sd	–	41.2	40.8	41.9	–	42.9	41.6	42.4
Dam age (yrs)	$\bar{x}$	4.40	4.46	4.47	4.95	4.83	4.96	4.91	5.07
	sd	2.29	2.25	2.26	2.49	2.34	2.37	2.35	2.36

[a] With progeny in the data
[b] Proportion (in %) with records themselves
[c] Total, after pruning
[d] Proportion (in %) with only 1 calf
[e] Proportion (in %) with 2 calves
[f] Sire × herd effects
[g] Proportion (in %) of effects with only one record
[h] Proportion of sires (in %) represented in only one herd
[i] Maternal grand-sire × herd of origin effects
[j] Mean
[k] Standard deviation

Table 2: Estimates of variance components[a] (in kg^2) for weaning weights of **Angus** cattle from different models (see text)

Model	σ^2_P	σ^2_E	σ^2_A	σ^2_M	σ_{am}	σ^2_C	σ^2_S	σ^2_Z	σ^2_{IP}	σ^2_{IM}	σ^2_{MP}	σ^2_{MM}	$\log \mathcal{L}^b$	$\Delta\mathcal{L}^c$
A_0	536.9	291.7	104.6	39.6	–	101.0	–	–	–	–	–	–	0	
A_r	538.7	262.1	161.8	76.3	-63.6	102.1	–	–	–	–	–	–	358.9	358.9
AS_0	532.8	309.6	56.2	39.4	–	103.2	24.3	–	–	–	–	–	706.9	
AS_r	535.1	291.9	92.2	56.3	-27.3	103.0	19.1	–	–	–	–	–	749.1	42.2
AZ_0	534.5	305.5	61.2	26.0	–	103.1	23.2	15.5	–	–	–	–	951.5	
AZ_r	536.3	290.9	91.0	40.0	-22.7	103.1	19.0	15.0	–	–	–	–	981.3	29.8
P_0	546.2	284.2	29.1	46.2	–	102.5	–	–	84.3	–	–	–	474.8	
P_r	546.6	289.9	4.7	38.9	13.5	102.8	–	–	96.9	–	–	–	477.6	2.8
PS_0	536.5	302.4	39.7	42.4	–	103.2	17.5	–	31.3	–	–	–	743.7	
PS_r	535.6	293.5	81.9	53.9	-22.3	103.0	18.5	–	7.1	–	–	–	749.4	5.7
PZ_0	537.4	299.4	47.8	28.4	–	103.3	17.6	15.2	25.8	–	–	–	978.0	
PZ_r	536.7	292.4	81.3	37.7	-17.9	103.1	18.5	15.0	6.7	–	–	–	981.7	3.7
M_0	536.9	291.7	104.6	39.6	–	101.0	–	–	–	0.0	–	–	0.0	
M_r	538.6	247.3	161.1	66.7	-70.0	102.7	–	–	–	30.8	–	–	368.3	368.3
MS_0	532.8	309.6	56.2	39.4	–	103.2	24.3	–	–	0.0	–	–	706.9	
MS_r	534.9	280.8	91.7	49.2	-32.4	103.4	19.0	–	–	23.3	–	–	754.0	47.1
MZ_0	534.5	305.5	61.2	26.0	–	103.1	23.2	15.5	–	0.0	–	–	951.5	
MZ_r	535.9	278.3	90.0	32.0	-28.5	103.6	18.9	15.0	–	26.6	–	–	987.5	36.0
F_0	546.6	269.3	9.2	30.8	–	103.0	–	–	94.6	39.8	–	–	487.9	
F_r	546.8	272.4	1.0	28.7	5.3	103.1	–	–	98.8	37.4	–	–	488.6	1.7
FS_0	536.5	295.0	30.9	34.7	–	103.6	17.1	–	36.3	18.9	–	–	746.8	
FS_r	535.0	282.4	78.4	45.1	-25.8	103.4	18.1	–	8.9	24.6	–	–	776.6	29.8
FZ_0	537.3	291.1	37.3	19.3	–	103.8	17.3	15.2	31.4	21.9	–	–	982.1	
FZ_r	536.4	279.8	78.7	29.3	-23.2	103.6	18.3	15.0	7.8	27.1	–	–	987.9	5.8
E_0	548.7	264.7	11.6	4.2	–	96.9	–	–	92.4	48.7	30.1	0.0	651.8	
E_r	548.7	266.9	8.0	2.1	4.0	97.2	–	–	94.2	45.9	30.4	0.0	652.4	0.6
ES_0	538.5	291.3	36.6	8.9	–	97.6	17.3	–	32.1	24.7	30.0	0.0	911.9	
ES_r	537.6	280.0	77.7	19.0	-23.1	97.5	18.3	–	8.7	30.0	29.6	0.0	917.7	5.8
EZ_0	537.9	289.8	38.1	10.8	–	101.1	17.3	11.5	31.0	24.8	13.5	0.0	1015.3	
EZ_r	536.9	278.9	77.9	20.5	-22.5	100.9	18.2	11.4	8.3	30.0	13.3	0.0	1020.8	5.5

[a] σ^2_P: phenotypic, σ^2_E: residual, σ^2_A: direct, additive genetic, σ^2_M: maternal additive genetic, σ^2_C: maternal, permanent environmental, σ^2_S: sire × herd, σ^2_Z: maternal grand-sire × herd of origin of dam, σ^2_{IP}: direct genetic paternal imprinting and σ^2_{IM}: direct genetic maternal imprinting variance; σ_{am}: direct-maternal genetic covariance

[b] log likelihood, as deviation from value for model A

[c] Difference in log $\mathcal{L}$ between corresponding models allowing for and not fitting σ_{am}

Table 3: Estimates of variance components (in kg^2; see Table 2 for acronyms) for birth, yearling and final weights of **Angus** cattle from different models

Model	σ^2_P	σ^2_E	σ^2_A	σ^2_M	σ_{am}	σ^2_C	σ^2_S	σ^2_Z	σ^2_{IP}	σ^2_{IM}	$\log \mathcal{L}$
					Birth weight						
A_0	17.75	8.83	6.92	0.98	–	1.02	–	–	–	–	0
A_r	17.99	7.84	8.92	1.49	-1.35	1.09	–	–	–	–	116.5
AZ_0	17.76	8.93	6.48	0.74	–	1.06	0.44	0.12	–	–	339.6
AZ_r	17.89	8.43	7.50	0.97	-0.58	1.08	0.36	0.12	–	–	353.8
F_0	17.95	7.75	4.82	0.00	–	1.14	–	–	2.04	2.20	212.8
F_r	17.91	7.36	5.56	0.05	-0.55	1.16	–	–	1.60	2.71	216.6
FZ_0	17.71	8.24	5.09	0.00	–	1.12	0.32	0.11	0.90	1.93	400.3
FZ_r	17.63	7.56	6.58	0.17	-1.05	1.16	0.35	0.11	0.00	2.75	414.7
					Yearling weight						
A_0	818.3	517.3	220.4	27.5	–	53.1	–	–	–	–	0
A_r	820.9	495.6	263.1	41.4	-35.7	56.4	–	–	–	–	49.3
AZ_0	820.2	523.3	186.1	15.7	–	55.9	31.9	7.4	–	–	564.3
AZ_r	818.7	532.0	168.0	12.2	10.7	54.7	33.7	7.4	–	–	568.7
F_0	825.6	480.1	137.2	0.0	–	55.6	–	–	76.6	76.1	170.3
FZ_0	815.5	511.2	155.2	0.0	–	54.3	32.7	6.7	0.0	55.4	605.2
					Final weight						
A_0	1290.4	811.7	427.2	35.5	–	16.1	–	–	–	–	0
A_r	1291.7	792.6	465.5	43.6	-30.9	20.9	–	–	–	–	15.6
AZ_0	1292.3	816.8	392.2	20.5	–	21.3	35.7	5.8	–	–	264.2
AZ_r	1290.7	829.4	365.9	17.2	16.0	18.6	37.9	5.7	–	–	268.2
F_0	1294.6	768.8	329.5	0.0	–	17.8	–	–	78.4	100.0	111.5
FZ_0	1285.3	797.5	343.3	0.0	–	16.8	35.4	4.7	1.6	85.9	304.9

Table 4: Estimates of variance components (in kg^2; see Table 2 for acronyms) for weights of **Hereford** cattle from selected models (see text)

Model	σ^2_P	σ^2_E	σ^2_A	σ^2_M	σ_{am}	σ^2_C	σ^2_S	σ^2_Z	σ^2_{IP}	σ^2_{IM}	$\log \mathcal{L}$
					Birth weight						
A_0	17.82	8.70	7.04	1.37	–	0.70	–	–	–	–	0
A_r	18.02	7.50	9.40	2.09	-1.80	0.82	–	–	–	–	118.4
AZ_0	17.97	8.92	6.29	1.02	–	0.79	0.78	0.17	–	–	268.1
AZ_r	18.08	8.28	7.58	1.35	-0.77	0.83	0.64	0.17	–	–	282.1
F_0	18.09	7.45	4.60	0.27	–	0.92	–	–	2.70	2.15	174.1
FZ_0	17.94	8.09	4.97	0.18	–	0.91	0.57	0.17	1.19	1.86	294.3
FZ_r	17.89	7.54	6.91	0.62	-1.12	0.92	0.62	0.17	0.04	2.19	297.4
					Weaning weight						
A_0	655.0	338.0	96.2	64.8	–	156.0	–	–	–	–	0
A_r	653.9	312.8	144.0	105.1	-65.7	157.6	–	–	–	–	226.4
AZ_0	652.4	354.9	51.3	37.3	–	160.6	20.5	27.7	–	–	637.9
AZ_r	653.1	341.5	78.3	55.7	-26.6	160.6	16.3	27.3	–	–	667.3
F_0	657.1	340.5	6.6	73.8	–	157.3	–	–	78.9	0.0	289.6
FZ_0	653.9	352.0	23.8	42.7	–	160.6	14.4	27.3	33.0	0.0	674.5
					Yearling weight						
A_0	926.7	578.5	213.2	46.3	–	88.7	–	–	–	–	0
A_r	926.6	556.4	256.1	62.4	-42.8	94.5	–	–	–	–	48.9
AZ_0	925.8	592.9	168.3	29.2	–	94.0	30.3	11.1	–	–	281.1
F_0	928.6	533.6	122.3	0.0	–	96.2	–	–	75.7	100.8	132.2
F_r	929.3	546.3	101.8	1.9	13.8	94.8	–	–	86.8	83.9	134.3
FZ_0	923.6	565.7	136.9	0.0	–	93.7	30.0	10.4	8.4	78.5	315.4
					Final weight						
A_0	1296.0	816.5	386.0	43.1	–	50.4	–	–	–	–	0
A_r	1297.2	793.3	431.7	54.9	-40.3	57.6	–	–	–	–	21.6
AZ_0	1297.8	827.8	344.7	26.9	–	55.9	33.1	9.4	–	–	155.3
F_0	1296.3	774.4	295.6	0.0	–	54.8	–	–	65.9	105.5	79.8
FZ_0	1293.0	801.2	299.5	0.0	–	52.0	33.3	7.8	5.6	93.6	190.3

Table 5: Mean estimates of variance components (see Table 2 for acronyms) for simulated data

	σ^2_P	σ^2_E	σ^2_A	σ^2_M	σ_{am}	σ^2_C	σ^2_{IP}	σ^2_{IM}	$\log \mathcal{L}$
Pop.[a]	200.0	80.0	50.0	20.0	0.0	30.0	10.0	10.0	
A_0	199.9	84.5	61.8	24.5	–	29.0	–	–	0
A_r	200.3	80.8	68.9	27.8	-6.5	29.2	–	–	28.22
P_0	200.9	83.2	56.0	24.5	–	29.3	7.9	–	38.60
P_r	201.0	84.4	50.8	23.0	2.9	29.3	10.6	–	39.46
M_0	199.8	84.4	61.7	24.4	–	29.1	–	0.3	0.06
M_r	199.5	75.9	66.6	23.9	-9.2	29.8	–	12.4	38.19
F_0	200.2	80.2	49.8	20.1	–	29.8	9.9	10.4	46.25
F_r	200.2	79.8	50.9	20.3	-0.7	29.8	9.3	10.8	46.45

[a] Population values

Table 6: Estimates of genetic parameters[a] (×100) for **Angus** cattle together with their approximate standard errors, for estimates ignoring (models A) and fitting both paternal and maternal parent of origin effects (models F).

Trait[b]		A_0	A_r	AZ_0	AZ_r	F_0	FZ_0	FZ_r
BW	h^2	39±1	50±1	36±1	42±1	27±1	29±1	37±3
	m^2	6±0	8±0	4±0	5±0	0±1	0±1	1±1
	i_P^2	–	–	–	–	11±1	5±1	0±2
	i_M^2	–	–	–	–	12±2	11±2	16±2
	r_{AM}	–	-37±2	–	-21±3	–	–	-100±37
WW	h^2	19±1	30±1	11±1	17±1	2±1	7±1	15±3
	m^2	7±0	14±1	5±0	7±1	6±1	4±1	5±1
	i_P^2	–	–	–	–	17±1	6±1	1±2
	i_M^2	–	–	–	–	7±1	4±1	5±1
	r_{AM}	–	-57±1	–	-38±3	–	–	-48±9
YW	h^2	27±1	32±1	23±1	21±1	17±1	19±1	
	m^2	3±0	5±0	2±0	1±0	0±1	0±1	
	i_P^2	–	–	–	–	9±1	0±1	
	i_M^2	–	–	–	–	9±2	7±2	
	r_{AM}	–	-34±3	–	24±10	–	–	
FW	h^2	33±1	36±1	30±1	28±1	25±1	27±1	
	m^2	3±0	3±0	2±0	1±0	0±1	0±1	
	i_P^2	–	–	–	–	6±1	0±1	
	i_M^2	–	–	–	–	8±2	7±2	
	r_{AM}	–	-22±4	–	20±8	–	–	

[a] h^2: direct heritability, m^2: maternal heritability, c^2: proportion of variance due to permanent environmental effects, i_P^2: proportion of variance due to paternal parent of origin effects, and i_M^2: proportion of variance due to maternal parent of origin effects, r_{AM}: direct-maternal genetic correlation

[b] BW: birth, WW: weaning, YW: yearling and FW: final weight

Table 7: Estimates of genetic parameters (×100; see Table 6 for acronyms) for **Hereford** cattle together with their approximate standard errors, for estimates ignoring (models A) and fitting both paternal and maternal parent of origin effects (models F).

Trait[a]		A_0	A_r	AZ_0	AZ_r	F_0	FZ_0	FZ_r
BW	h^2	40±1	52±1	35±1	42±2	25±2	28±2	39±5
	m^2	8±0	12±1	6±1	7±1	1±1	1±1	3±1
	i_P^2	–	–	–	–	15±1	7±1	0±3
	i_M^2	–	–	–	–	12±2	10±2	12±2
	r_{AM}	–	-40±2	–	-24±4	–	–	-54±14
WW	h^2	15±1	22±1	8±1	12±1	1±1	4±1	
	m^2	10±0	16±1	6±0	9±1	11±1	7±1	
	i_P^2	–	–	–	–	12±1	5±1	
	i_M^2	–	–	–	–	0±2	0±2	
	r_{AM}	–	-53±2	–	-40±4	–	–	
YW	h^2	23±1	28±1	18±1	17±1	13±1	15±1	
	m^2	5±0	7±1	3±0	3±0	0±1	0±1	
	i_P^2	–	–	–	–	8±1	1±1	
	i_M^2	–	–	–	–	11±2	8±2	
	r_{AM}	–	-34±3	–	10±8	–	–	
FW	h^2	30±1	33±1	27±1	26±1	23±1	23±1	
	m^2	3±0	4±0	2±0	2±0	0±1	0±1	
	i_P^2	–	–	–	–	5±1	0±1	
	i_M^2	–	–	–	–	8±2	7±2	
	r_{AM}	–	-26±4	–	4±7	–	–	

[a]BW: birth, WW: weaning, YW: yearling and FW: final weight

Table 8: Expectation of covariances between relatives in terms of causal variances (see Table 2 for acronyms)

Covariance between relatives	σ_A^2	σ_M^2	σ_{AM}	σ_C^2	σ_{IP}^2	σ_{IM}^2
Sire-offspring	½	0	¼	0	½	0
Dam-offspring	½	½	¼	0	0	½
Paternal half sibs	¼	0	0	0	½	0
Maternal half sibs	¼	1	1	1	0	½
Full sibs	½	1	1	1	½	½
Paternal grand parent-offspring	¼	0	⅛	0	¼	0
Maternal grand parent-offspring	¼	¼	⅝	0	0	¼
First cousins: sires full-sibs	⅛	0	0	0	¼	0
First cousins: dams full-sibs	⅛	½	½	0	0	¼
First cousins: opposite sexes full sibs	⅛	0	¼	0	0	0
Paternal uncle -nephew/niece	¼	0	¼	0	¼	0
Maternal aunt-nephew/niece	¼	½	¾	0	0	¼