

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

Karin Meyer and Bruce Tier

Animal Genetics and Breeding Unit¹, University of New England, Armidale NSW 2351,
Australia

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 \times 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 \times herd and maternal grand-sire \times 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 infinitesimal 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.

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

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

79 **2 Material and Methods**

80 Records for birth (BW), weaning (WW), yearling (YW) and final (FW) weights of Australian
81 Angus and Hereford cattle were extracted from the National Beef Recording Scheme (NBRS)
82 data base, selecting the largest herds. Ages at recording considered were 80 to 300 days, 301
83 to 500 days and 501 to 700 days for WW, YW and FW, respectively. For animals with more
84 than one measurement in a given age range, only the first record was selected. Any weights
85 recorded prior to 1985 and records for twins were disregarded. Additional edits eliminated
86 records more than 2.5 standard deviations from the mean, records for animals with unknown
87 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 \times herd (S \times H) effects, denoted as models XS (for X=A, P, M, F, E), or S \times H as well as maternal grand-sire \times herd of origin of dam (Z \times H) effects in addition (denoted as models XZ). 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 referred 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 were 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

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

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

133 3 Results

134 3.1 Variances from different models

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

138 3.1.1 Modelling weights of beef cattle

139 Results for the 'standard' models ignoring POO effects were, by and large, comparable
140 to those reported previously for these traits and breeds (e.g. Meyer, 1992b; Meyer et al.,
141 2004). As observed in various other studies, allowing for a non-zero direct-maternal genetic
142 covariance (σ_{am}) yielded a substantial, negative estimate (model A_r), accompanied by higher
143 estimates for both the direct (σ_A^2) and maternal (σ_M^2) genetic variance, compared to results
144 obtained assuming σ_{am} was zero (model A_0), and dramatically increased value of the log
145 likelihood ($\log \mathcal{L}$).

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

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

158 Fitting a sire \times herd interaction has been shown to alleviate these symptoms and has thus
159 been adopted as a pragmatic solution to counteract potential deficiencies in modelling in
160 genetic evaluation schemes for beef cattle such as BREEDPLAN (Graser et al., 2005). However,
161 in estimating genetic parameters it is not unproblematic as analyses fitting such models
162 often yield estimates where a substantial proportion of the direct additive genetic variance
163 is partitioned into the sire \times herd component. As expected, fitting S \times H effects did reduce
164 (absolute value) the estimate of σ_{am} substantially, with the magnitude of the direct-genetic
165 correlation estimate for WW reduced from -0.57 (A_r) to -0.38 (AS_r) in Angus and -0.53 to
166 -0.37 in Herefords. This was accompanied by a reduction in the estimate of σ_A^2 by more than
167 40% compared to analyses not fitting S \times H effects and a dramatic increase in log likelihood
168 ($\log \mathcal{L}$). With about 90% of S \times H effects pertaining to sires used in a single herd only (*c.f.*
169 Table 1) this was not surprising, as there were less contrasts between sire and S \times H effects than
170 might be desirable. S \times H effects were most influential for WW – any unidentified groups are
171 generally broken up at weaning, so that an influence on later weights is expected to reflect a
172 carry-over effect only.

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

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

184 Similarly, maternal grand-sire \times herd of origin of dam effects were considered here primar-
 185 ily for their potential to interact with estimates of paternal imprinting on maternal genetic
 186 effects in model E – with Z \times H effects expected to be analogous to S \times H effects for paternal
 187 imprinting of direct genetic effects. Maternal grand-sire effects in animal model analyses are
 188 rarely considered in the literature, though Dodenhoff et al. (1999) reported genetic effects for
 189 maternal grand-dams to account for 2–7% of σ_p^2 for WW of Angus cattle and to reduce (abso-
 190 lute value) negative estimates of σ_{am} . Fitting Z \times H effects again increased $\log \mathcal{L}$ dramatically
 191 over the models fitting S \times H only, with the corresponding variance (σ_Z^2) explaining almost
 192 3% of the phenotypic (σ_p^2) variance, and reduced the magnitude of estimates of σ_M^2 , σ_{am} and
 193 σ_S^2 . As for S \times H effects, most Z \times H effects represented sires occurring in one herd only. In
 194 addition, a large proportion (83% for WW in Angus; see Table 1) was represented by only
 195 record, i.e. the scope for successfully disentangling Z \times H and genetic effects was limited.

196 3.1.2 Fitting a single parent of offspring effect

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

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

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

229 3.1.3 Fitting both paternal effects

230 Accounting for both POO effects (models F), estimates of σ_{IP}^2 were generally of similar
 231 magnitude or slightly lower than for model P. This indicates that ignoring maternal POO
 232 effects had little effect on estimates of σ_{IP}^2 , i.e. that variation due to maternal POO effects
 233 was not ‘picked up’ as $\hat{\sigma}_{IP}^2$, and was consistent with the pattern observed by Tier and Meyer
 234 (2011) in corresponding analyses of carcass traits recorded by ultra-sound scanning for the
 235 same breeds. When fitting S×H effects though, the reduction in estimates of σ_{IP}^2 tended to be
 236 somewhat less than encountered under models P.

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

244 effects that are at least partially confounded and thus subject to substantial repartitioning
 245 of variation when the model is altered, this might be premature and lead to elimination of
 246 important effects. When fitting both POO effects, allowing for a non-zero direct-maternal
 247 genetic covariance (model F_7) yielded little changes in estimates and $\log \mathcal{L}$ compared to model
 248 F_0 , and as observed earlier, estimates of σ_{am} were limited by a corresponding correlation of
 249 unity (absolute value).

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

257 3.1.4 Parent of offspring effects on maternal genetic effect

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

269 3.2 Simulation results

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

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

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

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

296 Corresponding analyses fitting $S \times H$ and $Z \times H$ effects in addition yielded mean estimates
297 of σ_Z^2 of less than 0.1 and of σ_S^2 between 0.1 and 0.4 while estimates of the other variances
298 were essentially the same as those from the corresponding models omitting these effects.
299 This indicates that such interaction effects were not prone to ‘automatically’ remove genetic
300 variation in our data, i.e. that the data structure could support estimation of all the genetic
301 components fitted. Conversely, it implies that the substantial reductions in estimates of
302 variances due to POO effects observed when fitting $S \times H$ and $Z \times H$ effects largely reflected
303 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

336 spurious.

337 4 Discussion

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

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

356 Recently, Imumorin et al. (2011) reported maternal and paternal POO effects for 18 quan-
357 titative trait loci affecting growth of beef cattle, explaining between 1 and 4% of σ_p^2 each.
358 While our results present evidence for differential expression of genes for weights of beef
359 cattle depending on the parent they came from, estimates of the corresponding variances
360 are likely to be, to some extent at least, inflated by other sources of variation. When fitted,
361 paternal POO effects tended to act similarly to sire \times herd effects and thus to 'pick up' some
362 the variation accounted for by these effects. As shown, there was considerable repartitioning
363 between estimates of σ_M^2 and σ_{IM}^2 . For model FZ_r , estimated sampling correlations between
364 these components (obtained from the inverse of the average information matrix) for the 8
365 cases (trait \times 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

^aWith progeny in the data

^bProportion (in %) with records themselves

^cTotal, after pruning

^dProportion (in %) with only 1 calf

^eProportion (in %) with 2 calves

^fSire × herd effects

^gProportion (in %) of effects with only one record

^hProportion of sires (in %) represented in only one herd

ⁱMaternal grand-sire × herd of origin effects

^jMean

^kStandard deviation

Table 2: Estimates of variance components^a (in kg²) for weaning weights of **Angus** cattle from different models (see text)

Model	σ_P^2	σ_E^2	σ_A^2	σ_M^2	σ_{am}	σ_C^2	σ_S^2	σ_Z^2	σ_{IP}^2	σ_{IM}^2	σ_{MP}^2	σ_{MM}^2	$\log \mathcal{L}^b$	$\Delta \mathcal{L}^c$
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_P^2 : phenotypic, σ_E^2 : residual, σ_A^2 : direct, additive genetic, σ_M^2 : maternal additive genetic, σ_C^2 : maternal, permanent environmental, σ_S^2 : sire \times herd, σ_Z^2 : maternal grand-sire \times herd of origin of dam, σ_{IP}^2 : direct genetic paternal imprinting and σ_{IM}^2 : direct genetic maternal imprinting variance; σ_{am} : direct-maternal genetic covariance

^blog likelihood, as deviation from value for model A

^cDifference 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_P^2	σ_E^2	σ_A^2	σ_M^2	σ_{am}	σ_C^2	σ_S^2	σ_Z^2	σ_{IP}^2	σ_{IM}^2	$\log \mathcal{L}$
<i>Birth weight</i>											
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
<i>Yearling weight</i>											
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
<i>Final weight</i>											
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 kg²; see Table 2 for acronyms) for weights of **Hereford** cattle from selected models (see text)

Model	σ_P^2	σ_E^2	σ_A^2	σ_M^2	σ_{am}	σ_C^2	σ_S^2	σ_Z^2	σ_{IP}^2	σ_{IM}^2	$\log \mathcal{L}$
<i>Birth weight</i>											
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
<i>Weaning weight</i>											
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
<i>Yearling weight</i>											
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
<i>Final weight</i>											
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_P^2	σ_E^2	σ_A^2	σ_M^2	σ_{am}	σ_C^2	σ_{IP}^2	σ_{IM}^2	$\log \mathcal{L}$
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

^aPopulation values

Table 6: Estimates of genetic parameters^a ($\times 100$) 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

^bBW: birth, WW: weaning, YW: yearling and FW: final weight

Table 7: Estimates of genetic parameters ($\times 100$; 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	–	–	

^aBW: 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	1/2	0	1/4	0	1/2	0
Dam-offspring	1/2	1/2	5/4	0	0	1/2
Paternal half sibs	1/4	0	0	0	1/2	0
Maternal half sibs	1/4	1	1	1	0	1/2
Full sibs	1/2	1	1	1	1/2	1/2
Paternal grand parent-offspring	1/4	0	1/8	0	1/4	0
Maternal grand parent-offspring	1/4	1/4	5/8	0	0	1/4
First cousins: sires full-sibs	1/8	0	0	0	1/4	0
First cousins: dams full-sibs	1/8	1/2	1/2	0	0	1/4
First cousins: opposite sexes full sibs	1/8	0	1/4	0	0	0
Paternal uncle -nephew/niece	1/4	0	1/4	0	1/4	0
Maternal aunt-nephew/niece	1/4	1/2	3/4	0	0	1/4