THE EFFECT OF IMPRINTED GENES ON CARCASS TRAITS IN AUSTRALIAN ANGUS AND HEREFORD CATTLE

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SUMMARY

Imprinted loci are those where the level of expression of an allele depends upon the allele's parent of origin. Imprinting is a widespread phenomenon and parent-of-origin effects have been reported for many qualitative and quantitative traits, in particular carcass traits. The effect of parent-of-origin effects on three quantitative traits – eye muscle area and fat depth at the P8 and $12/13^{th}$ rib sites – measured on Angus and Hereford heifers and bull calves was examined. Parent-of-origin effects accounted for 12-45% of the total genetic variation for these traits.

INTRODUCTION

What is imprinting? An imprinted locus is a locus where, during gametogenesis, alleles are temporarily modified by a parent, so that their expression is either completely, or partially, suppressed in its progeny. Suppression lasts for one generation: alleles imprinted in one generation can be expressed in the subsequent generation if the parent is of the right gender. Thus an imprinted allele from a dam(sire) will not be expressed by an individual, but will be by its progeny if the individual is a bull(cow) but not if it is a cow(bull). Imprinting is also known as 'parent-of-origin' effects. Imprinting of genes is a common phenomenon – in mice more than 120 imprinted loci have been found (Morison *et al.* 2005). Imprinting can also affect quantitative traits with important implications for breeding programs, as it limits inheritance of some desirable alleles to one parent. Thus selection within one generation has different effects on the following and subsequent generations. Parent-of-origin effects also have consequences for QTL detection methods and genome wide association studies. An important example of imprinting in cattle is DGAT1, where the two types of heterozygotes have different effects (Kuehn *et al.* 2007).

Modeling imprinting. Imprinting in quantitative characters is modeled at the gametic level. Each individual has two gametes, one inherited from each parent and observations are assigned directly to either or both gametes. Covariances amongst gametes inherited from each parent are functions of separate gametic relationship matrices. When modeling imprinting, it is important to consider other types of effects that may be partially confounded with imprinting effects. These include any effects that relate to sires and dams such as maternal, Y-chromosomal and mitochondrial effects. Effects of imprinting have been found for carcass traits in both pigs (de Vries *et al.* 1994) and beef cattle (Engellandt and Tier 2002). In these analyses imprinting models were limited to the analysis of an additive genetic effect and the effect of either the paternal or maternal gamete. However, as quantitative traits are the function of many loci, it is possible that alleles at some loci are imprinted by the sire and at other loci by the dam. Thus it is possible that the effect of both paternally and maternally imprinted genes could affect quantitative traits. By modeling both maternal and paternal gametic effects simultaneously, Neugebauer *et al.* (2010a, 2010b) estimated variances for the additive and both imprinted gametic effects for carcass traits in both beef cattle and swine.

This paper presents estimates for the effects of imprinting in ultrasonic measures of carcass traits in Australian Angus and Hereford cattle.

MATERIALS AND METHODS

Traits. Three carcass traits measured by live ultrasonic scanning were analysed as separate traits for heifer and bull calves. These were fat depth measured between the 12-13th rib (RIB) and on the rump at the P8 site and eye muscle area (EMA), when calves were between 300 and 700 days old.

Data. Records were selected from the databases of the Australian Angus and Hereford Societies. Complete herds with long histories of recording ultrasonic measures of carcass traits were extracted. The numbers of animals in the pedigree and records for each trait are shown in Table 1 together with raw means and standard deviations.

Model. The complete model used to analyse these data was: $y=Xb+Z_1a+Z_2g_s+Z_3g_d+e$, where y is a vector of observations, b a vector of fixed effects, a, g_s and g_d are vectors of breeding values for additive, sire gametic and dam gametic effects respectively, e is a vector of residuals and X, Z_1, Z_2 and Z_3 are incidence matrices assigning observations to effects. Covariances among random effects were modeled as $A\sigma_a^2$, $G\sigma_{gs}^2$, $G\sigma_{gd}^2$ and $I\sigma_e^2$, where A is the numerator relationship matrix, G is the gametic relationship matrix, I is an identity matrix and σ_a^2, σ_{gs}^2 and σ_{gd}^2 are the variances due to the breeding values and sire and dam gametic effects respectively, and σ_e^2 is the residual variance. The vector b included age of calf (AOC) and AOC^2, age of dam (AOD) and AOD^2 and contemporary groups consisting of herd, year, date of measurement and management group class.

For each trait four basic models were examined. These were the animal model (Model 1) without gametic effects, an animal model with a paternal gametic effect (Model 2), an animal model with a maternal gametic effect (Model 3) and an animal model with both, uncorrelated, gametic effects (Model 4). Animal models with either cytoplasmic or Y-chromosomal effects were also tested. As a result of analyzing the traits within sex, there were too few dams with multiple offspring in each data set to test for permanent environmental effects of the dam. WOMBAT (Meyer 2007) was used to find the maximum likelihood for each model and dataset. The likelihood profile for the effect of maternally inherited alleles was determined for EMA in Hereford heifers.

Correlations between estimated genetic merit provided by models 1 and 4 were examined for EBVs for EMA in Herefords born in 2008. With model 4, EBVs for the next generation were

Table 1 Basic statistics of ultrasonically measured Angus and Hereford Bulls and Heifers for eye muscle area (EMA, cm^2), P8 fat (mm) and Rib fat (mm)

| Trait	Angus		Mean	σ	Hereford		Mean	σ
	N				N			
	Pedigree	Records			Pedigree	Records		
				Bulls				
EMA	130026	64828	79.3	13.0	166234	65739	82.3	14.2
P8 fat	128815	64633	4.27	2.01	167069	65868	5.23	2.48
Rib fat	127351	63298	3.33	1.41	166583	65680	3.80	1.57
				Heifers				
EMA	96823	59103	61.1	9.33	96575	43028	59.2	10.7
P8 fat	94824	58221	6.61	3.24	99706	44101	6.73	3.36
Rib fat	96863	59191	5.10	2.34	96380	42771	4.74	2.12

Table 2 Phenotypic variances and component ratios and approximate standard errors (s.e.) for direct genetic (h^2: heritiability) and gametic effects (g_s^2 and g_m^2: proportion of variance due to paternal and maternal effects) for Angus and Hereford Bulls and Heifers (and Steers) for three carcass traits – Eye muscle area (EMA, cm^2), P8 Fat (mm) and Rib Fat (mm)

Trait	σ_p^2	s.e.(σ_p^2)	h^2	s.e.(h^2)	g_s^2	s.e.(g_s^2)	g_m^2	s.e.(g_m^2)
Angus bulls								
EMA	42.4	0.29	0.21	0.016	0.03	0.010	0.06	0.009
P8 fat	1.78	0.013	0.24	0.018	0.05	0.010	0.06	0.011
Rib fat	0.80	0.006	0.22	0.016	0.03	0.009	0.04	0.010
Angus heifers								
EMA	28.6	0.21	0.30	0.011	0.04	0.008	-	-
P8 fat	4.10	0.034	0.40	0.017	0.05	0.011	0.04	0.012
Rib fat	2.04	0.017	0.35	0.017	0.06	0.011	0.03	0.012
Hereford bulls								
EMA	38.7	0.25	0.18	0.016	0.04	0.009	0.08	0.011
P8 fat	2.45	0.017	0.26	0.016	0.03	0.009	0.04	0.010
Rib fat	0.96	0.006	0.20	0.015	0.03	0.008	0.05	0.010
Hereford heifers								
EMA	27.4	0.22	0.17	0.018	0.05	0.011	0.09	0.014
P8 fat	4.02	0.035	0.37	0.018	0.04	0.011	0.05	0.013
Rib fat	1.66	0.014	0.30	0.018	0.02	0.010	0.06	0.013

calculated as the sum of the direct genetic effect and the two appropriate gametic effects (paternal for bulls, maternal for heifers) and for subsequent generations as the sum of all 5 genetic effects.

RESULTS

Estimated phenotypic variances and variance ratios, together with their approximate standard errors, from the best model for each of the breed-sex-trait combinations are shown in Table 2. The effect of imprinted loci is found for all combinations, and generally includes imprinting of both paternally and maternally inherited genes. The one exception to this is EMA in Angus heifers, where maternally inherited genes appear to have no independent effect. The proportion of variance due to imprinted effects varied across traits and populations. For EMA of Hereford heifers, imprinting accounted for nearly half the variation due to genetic effects. The steepness of the profile log likelihood (Figure 1) shows there is plenty of information to estimate the parameter. Imprinted loci had their least effect – about 12% of the total genetic variation – in EMA of Angus Heifers.
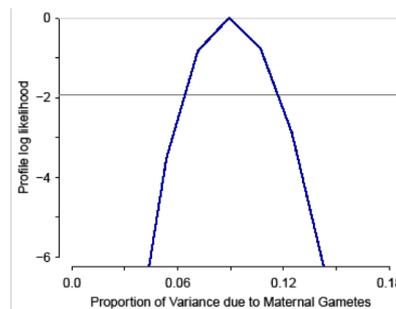
Figure 1. Profile log likelihood for the proportion of variance due to maternal gametic effects for EMA of Hereford Heifers

Estimates of variance due to paternally and maternally inherited gametes were consistent between models with one gametic or both gametic effects (results not shown). Estimates of total genetic variation are consistent with previous published reports (Meyer 2005). Neither cytoplasmic nor Y-chromosomal effects were significant when included with gametic effects.

The variances of the measures of genetic merit for EMA of Herefords born in 2008 are shown in Table 3. Compared to Model 1, there is less variation for next generation EBVs from Model 4

but more for subsequent generations for both bulls and heifers. The correlations between EBVs from model 1 with total genetic merit for the next and subsequent generations derived from model 4 were all greater than 0.98. The lowest correlation of 0.93 was that between genetic merit for the next and subsequent generations for heifers (N=2484); the corresponding result for bulls was 0.96 (N=3654).

Table 3 Standard deviation (cm^2) of EBVs for EMA of Herefords born in 2008.

	Bulls	Heifers
M1	1.9	1.7
Next	1.7	1.6
Subsequent	2.2	1.9

M1: EBvs from model 1; Next: sum of direct and appropriate gametic effects (model 4); Subsequent: sum of all genetic effects (model 4).

DISCUSSION

This study suggests that both paternally and maternally imprinted genes show substantial and ubiquitous effects in ultrasonically measured carcass traits. The effects of both types of imprinting are found for all traits but EMA in Angus Heifers, where no independent effect of maternally inherited gametes was found. The variance due to maternally inherited gametes was generally larger than that due to paternally inherited gametes, but not in any trait of the Angus Heifers. This could be due in part to inestimable maternal effects.

For both breeds and most traits, a significant proportion of variation can be ascribed to the effect of parent-of-origin. At 45% of the variation due to genetic effects, this is largest for EMA in Hereford heifers. It is a minimum of 12% in one case but averages around one-fifth to one-quarter of the genetic variation for most breed-traits. For EMA in Herefords, the correlations between EBVs from models with and without gametic effects are high. This suggests that similar groups of individuals will be selected at any given selection intensity. However, the consistency of gametic effects across traits and breeds suggests that the question regarding the importance of including or ignoring parent-of-origin effects should be examined further. It would be worthwhile to examine the level of imprinting effects required to justify separate parental lines.

Analysing carcass traits within sex reflects the differences between the body compositions of young male and female calves, and corresponds to the predictive models used in BREEPDLAN (Graser *et al.* 2005) and has been used here as an initial, exploratory step. Bivariate analysis, where the data from both heifer and bull calves are analysed jointly but as separate, correlated traits is a natural next step as the pairs of traits across gender are highly genetically correlated. It is probably prudent to analyse other, non-carcass traits.

CONCLUSION

Parent-of-origin effects account for a large amount (12-45%) of the genetic variation of ultrasonic measures of body composition in Australian Angus and Hereford cattle. Their inclusion in routine analyses will improve the efficacy of selection.

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