WEANING WEIGHT REVISITED : ESTIMATES OF GENETIC PARAMETERS FITTING A REGRESSION ON MATERNAL PHENOTYPE

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SUMMARY

Restricted maximum likelihood estimates of genetic parameters for weaning weight were obtained fitting a regression on maternal phenotype to account for direct-maternal environmental covariances. For Herefords there was a substantial negative regression on dam's phenotype (up to -0.2), accompanied by small, negative estimates of the direct-maternal genetic covariance. For Angus and Limousin, the direct-maternal genetic covariance was clearly more important than its environmental counterpart, i.e. an estimate of the direct-maternal genetic correlation of about -0.5 could not be attributed to a negative environmental relationship not taken into account. Fitting a sire × herd-year interaction as an additional random effect reduced estimates of the direct-maternal genetic covariance for these breeds, resulting in corresponding correlation estimates of -0.3 to -0.2.

Keywords: Beef Cattle, weaning weight, maternal effects, genetic parameters

INTRODUCTION

Numerous studies of preweaning growth of beef cattle and also sheep, have found an antagonistic correlation between direct and maternal genetic effects, often in the range of -0.5 to -0.7. While a slightly adverse genetic relationship between direct and maternal effects has been considered plausible, such estimates have been met with justified scepticism. Repeatedly this has been attributed to a negative direct-maternal environmental covariance which is expected to bias the estimate of the direct-maternal genetic covariance (σ_{AM}) and correlation (e.g. Koch, 1972). Falconer (1965) modeled maternal effects on litter size in mice by fitting a regression on maternal phenotype. This accounted for direct-maternal environmental covariances. This paper reports analyses of weaning weight records for beef cattle, fitting a regression on maternal phenotype in addition to genetic and permanent environmental maternal effects, i.e. an 'integrated Falconer-Willham' model (Koerhuis and Thompson, 1996).

MATERIAL AND METHODS

Data. Data consisted of records for Australian Polled Herefords, Herefords and Limousin, respectively, extracted from the National Beef Recording data base. Basic edits included consistency and range checks for birth and weighing dates and weights. Weights within the range of 80 to 300 days allowed by (GROUP)BREEDPLAN closest to to target weaning age of 200 days were selected. For Herefords and Polled Herefords only calves born from 1980 onwards were considered, and only herds with 200 or more calves with maternal phenotype known were included. In addition, subsets of data for Australian (AUS) and New Zealand (NZ) Angus, analysed previously assuming $\sigma_{AM} = 0$ (Meyer, 1995) were obtained, extracting records for herds contributing at least 200 (AUS) and 100 (NZ) weights with dams' records available. Characteristics of the data structure are summarised in Table 1.

Analyses Analyses were carried out by Restricted Maximum Likelihood (REML) using a derivative-free algorithm. For Limousins all pedigree information available was used while only one (Herefords)

Table 1. Characteristics of the data structure for weaning weight

		Polled H.	Hereford	Angus AUS	Angus NZ	Limousin
No. of records		61,787	79,434	87,389	57,375	16,635
… with dam's rec.		23,234	33,426	46,274	29,319	3926
No. of animals[a]		84,520	107,154	109,841	69,817	28,236
No. of sires[b]		2089	2689	2589	1819	1086
No. of dams[b]		23,967	30,866	31,272	19,456	8502
No. of contemp. groups		6224	6551	6903	2553	4304
No. of S×HY[c]		7337	7837	7719	3776	3291
Weight (kg)	$\bar{x}$[d]	221.9	219.0	232.9	216.6	232.3
	sd[e]	50.4	55.7	47.3	50.5	49.4
Age (days)	$\bar{x}$	218.2	214.1	214.6	201.8	215.4
	sd	42.0	39.1	32.6	39.8	40.1
Dam age (years)	$\bar{x}$	5.33	4.91	4.88	5.41	–
	sd	2.30	2.38	2.29	2.57	–

[a] in the analysis, including parents without records
[b] with progeny in the data
[c] sire × herd-year interaction effects
[d] mean
[e] standard deviation

or two (Angus) passes through the pedigree were performed to locate parental identities for the other data sets to restrict the total number of animals in the analysis.

Random effects. An animal model including maternal genetic as well as permanent environmental effects in addition to animals' direct additive genetic effects was fitted throughout. Ignoring maternal phenotype, analyses were carried out under Models 5 (assuming $\sigma_{AM} = 0$; M5) and 6 (allowing $\sigma_{AM} \neq 0$; M6) of previous analyses (e.g. Meyer, 1993). Furthermore, Model 7 (M7) was like M6 but fitted a sire × herd-year interaction with assumed covariance matrix $\sigma^2_H \mathbf{I}$ as an uncorrelated, additional random effect. All three models were augmented by fitting a regression on maternal phenotype (β) in addition as described by Meyer (1996), yielding models 5^{β} (M5^{β}), 6^{β} (M6^{β}) and 7^{β} (M7^{β}), respectively.

Fixed effects. Analyses were carried within contemporary groups, defined as herd-year-management group-sex subclasses, with an "age slicing" of 45 days, i.e. subclasses were divided further, so that only calves born not more than 45 days apart were directly compared with each other. Additional differences in age at weighing were taken into account by fitting a linear regression on age within sex. Age of dam was fitted as a linear and quadratic covariable. Age status of dam (heifers : 28 month or less at calving *vs.* cows : older than 28 months), the so-called "heifer factor" and birth type (single *vs.* twin) were fitted as crossclassified, fixed effects. For the Hereford and Angus data sets, a small proportion of dam ages were missing and, for the purpose of analysis, replaced by the mean dam age. For Limousins, insufficient dam ages were available, and the regression on age of dam and the "heifer factor" were omitted from the model of analysis.

RESULTS AND DISCUSSION

Estimates of genetic parameters and corresponding error and phenotypic variances are given in Table

2. The most parameterised model (M7$^{\beta}$) fitted best in all cases, but there were distinct differences in the relative importance of genetic and environmental correlations between dams and offspring.

Herefords. Results for Polled Herefords and Herefords followed the same pattern. Estimates of β were negative, -0.16 to -0.20. Koch (1972) speculated that its magnitude was -0.1 to -0.2 for preweaning growth of beef calves. Ignoring β but allowing for a non-zero σ_{AM} (M6) resulted in substantial, negative estimates for σ_{AM}. Likelihoods for M5$^{\beta}$ were markedly higher than for M6, indicating that the negative dam-offspring covariance was environmental rather than genetic. In line with this, estimates of β under M6$^{\beta}$ were only slightly reduced (in absolute value) compared to those under M5$^{\beta}$, while estimates of σ_{AM} though negative, amounted to only 5 to 8% of the phenotypic variance. Allowing for a direct-maternal covariance (either kind), increased estimates of both the direct (h^2) and maternal (m^2) heritability (M5$^{\beta}$, M6 and M6$^{\beta}$ *vs.* M5), while fitting a regression on maternal phenotype tended to reduce the estimate of the maternal environmental variance. Including a sire × herd-year 'interaction' (M7 and M7$^{\beta}$) gave estimates of σ^2_H amounting to about 4% of σ^2_P and substantially increased likelihoods, while reducing estimates of h^2, m^2 and σ_{AM} (absolute value) compared to M6 and M6$^{\beta}$. In contrast, estimates of the permanent environmental maternal effects (c^2) and β were virtually unchanged.

Angus and Limousin. Maternal phenotypes proved to be considerably less important for these breeds, with M6 fitting the data better than M5$^{\beta}$. Again, there was some cross-substitution between parameters, i.e fitting β and not σ_{AM} (M5$^{\beta}$) resulted in sizable, negative estimates for β, while fitting β over and above σ_{AM} (M6$^{\beta}$ *vs.* M6) gave small, negative estimates for β (-0.03 to -0.04). Augmenting the model of analysis by a sire × herd-year effect resulted in a dramatic increase in $\log \mathcal{L}$ for these data sets, substantially more than due to allowing for a non-zero σ_{AM} or β. Estimates of σ^2_H were 4% to 9 % of σ^2_P. Considering 5 Angus (AUS) herds, Robinson (1996) obtained estimates of σ^2_H of 11% (of σ^2_P), and of h^2, $m^2$and r_{AM} of 0.11, 0.25 and 0.014, respectively, compared to estimates of 0.29 (h^2), 0.14 (m^2) and -0.52 (r_{AM}) under M6.

CONCLUSIONS

Results identified clear breed differences in maternal effects. For Herefords, there appears to be a substantial direct-maternal environmental covariance, so that fitting a regression on maternal phenotype alleviated the problem of inexplicably large (absolute value), negative estimates of σ_{AM} to a large extent. Fitting a sire × herd-year interaction as an additional effect dramatically increase $\log \mathcal{L}$ in all cases. This was accompanied by reduced estimates of σ_{AM} (absolute value), h^2 and m^2, suggesting that inflated values of σ_{AM} might have been caused by unaccounted sources of variation, such as paddocks or management groups, particularly if confounded with paternal half-sib groups.

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Table 2. Estimates of genetic parameters[a]

Model	β	h^2	m^2	c_{AM}	r_{AM}	c^2	s^2	σ^2_E	σ^2_P	$\log \mathcal{L}$
Polled Herefords										
5		0.155	0.112			0.266		327.6	701.8	-360.41
5^{β}	-0.171	0.192	0.142			0.218		270.2	736.8	-196.22
6		0.251	0.225	-0.153	-0.642	0.263		291.4	703.7	-247.43
6^{β}	-0.157	0.240	0.193	-0.077	-0.357	0.223		262.7	728.5	-155.85
7		0.163	0.190	-0.102	-0.582	0.265	0.040	311.9	701.1	-92.89
7^{β}	-0.155	0.162	0.168	-0.038	-0.230	0.224	0.038	281.9	725.8	0
Herefords										
5		0.165	0.105			0.232		358.0	718.2	-564.66
5^{β}	-0.195	0.228	0.138			0.170		279.6	772.8	-268.39
6		0.283	0.210	-0.159	-0.650	0.231		313.0	720.0	-419.95
6^{β}	-0.186	0.272	0.168	-0.051	-0.241	0.173		268.8	767.6	-249.04
7		0.176	0.170	-0.098	-0.564	0.233	0.045	338.2	717.2	-182.79
7^{β}	-0.188	0.172	0.138	-0.003	-0.022	0.175	0.045	294.3	763.8	0
Angus - Australia										
5		0.239	0.092			0.148		272.5	523.1	-673.31
5^{β}	-0.089	0.272	0.102			0.125		250.4	543.2	-598.30
6		0.387	0.181	-0.165	-0.625	0.154		232.8	525.5	-496.52
6^{β}	-0.035	0.384	0.171	-0.144	-0.562	0.146		230.5	529.9	-490.18
7		0.220	0.130	-0.077	-0.456	0.156	0.071	262.2	523.7	-7.83
7^{β}	-0.037	0.222	0.123	-0.059	-0.359	0.147	0.070	258.6	528.7	0
Angus - New Zealand										
5		0.180	0.082			0.144		333.9	561.9	-168.48
5^{β}	-0.076	0.207	0.095			0.125		315.1	577.6	-139.51
6		0.256	0.145	-0.100	-0.519	0.147		311.1	563.2	-114.25
6^{β}	-0.032	0.256	0.138	-0.084	-0.445	0.139		308.5	567.2	-111.57
7		0.144	0.111	-0.042	-0.329	0.150	0.038	335.7	560.3	-3.23
7^{β}	-0.033	0.147	0.109	-0.029	-0.230	0.140	0.037	332.5	564.6	0
Limousin										
5		0.252	0.117			0.159		290.7	615.5	-74.53
5^{β}	-0.130	0.286	0.131			0.132		243.3	635.4	-57.57
6		0.400	0.264	-0.210	-0.647	0.160		241.4	624.1	-47.72
6^{β}	-0.093	0.392	0.231	-0.153	-0.509	0.141		226.9	632.5	-43.19
7		0.225	0.201	-0.113	-0.532	0.159	0.086	280.2	632.6	-5.07
7^{β}	-0.099	0.224	0.172	-0.060	-0.304	0.137	0.085	262.3	642.7	0

[a] β : regression on maternal phenotype, h^2: direct heritability, m^2: maternal heritability, c_{AM}: direct-maternal genetic covariance as proportion of the phenotypic variance, c^2: permanent environmental maternal variance as proportion of the phenotypic variance, s^2: variance due to sire × year effects as proportion of the phenotypic variance, σ^2_E: residual variance, σ^2_P: phenotypic variance, and $\log \mathcal{L}$: log likelihood, as deviation from model 7^{β}