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Estimation of variance of maternal lineage effects at the Langhill dairy herd

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Abstract

Evidence to support the existence of a maternal lineage variance component for production and food intake traits at the Langhill experimental dairy herd was investigated. Maternal pedigree records of the herd were traced back to the points of cytoplasmic origin using herd book records. Cytoplasmic origin was defined as the earliest maternal ancestor of a cow and used to assign cows to maternal lineages. This was either a grade-up cow or an ancestor traced back to 1920. The tracing resulted in the cows being assigned to 56 maternal lineages, ranging in size from one to 72 cows. A total of 1118 records of 517 cows, all with a first lactation record, were used in the analysis. Traits analysed were daily milk, fat and protein yield, fat %, protein %, food dry-matter intake, net energy of milk production, a measure of milk production efficiency, average condition, and calving condition, all averaged over the first 26 weeks of lactation. The analysis was performed using a residual maximum likelihood animal model with and without a random component for maternal lineage. Possible bias, due to the fact that the sires were a select sample from the population, was also examined. No significant effect was found in the analysis of the full data set that could be assigned to maternal lineage. Fat yield was the only trait to show a variance component approaching a 5% significance level with a magnitude of 4% of phenotypic variance. However, when maternal lineages of at least five cows were considered, a significant 4% maternal lineage component of phenotypic variance was found for fat yield. The power of the analysis to detect a variance component of less than 4% was shown to be poor. No evidence was found for a maternal lineage component of food intake traits or condition score. Treating sire as a fixed effect or regressing data on sire EBV made little difference to the maternal lineage component.

Keywords: *cytoplasmic inheritance, dairy cows, heritability, maternal effects, milk yield.*

Introduction

Over recent years it has been hypothesized that a component of the phenotypic variance of economically important traits in dairy cattle is inherited exclusively through the maternal line (e.g. Bell *et al.*, 1985; Schutz *et al.*, 1992). This component of inheritance is of cytoplasmic rather than nuclear origin. It is a long held belief by cattle breeders that some cow families are more important in breeding terms than others, and cows from these families will be used as breeding animals in preference to other cows with similar breeding values. There is also evidence to show that estimates of heritability from daughter dam regressions are higher than those estimates from paternal half-sib analysis (e.g. Seykora and McDaniel, 1983; Visscher and Thompson, 1992). This may suggest that there is a mechanism of inheritance, in addition to nuclear genetic inheritance, that is being transmitted through the female line, which is not being accounted for by current evaluations. A possible explanation for this is the almost exclusively maternal transmission of mitochondrial DNA (mtDNA) in mammalian species (Hutchinson *et al.*, 1974).

Although mtDNA encodes only about 0·05% of all the nuclear plus cytoplasmic genes it is the nature of the potential contribution to phenotypic variation that makes it important. The mitochondria are the energy factories of the cell, and mtDNA codes 13 of

the 60 proteins involved in the respiratory chain. For this reason mtDNA may be responsible for a significant component of the phenotypic variation of energy dependent production traits, such as the production of milk.

Early attempts to estimate the magnitude of phenotypic variance attributable to cytoplasmic inheritance treated maternal lineage as a fixed effect in a least-squares model of analysis (Bell *et al.*, 1985; Huizinga *et al.*, 1986). These early analyses have been criticized for detecting lineage components that could be explained by sampling variance and residual additive genetic correlations among members of a lineage, not being correctly accounted for by the model applied (Kennedy, 1986). In a more recent study, Boettcher *et al.* (1996a) investigated what the most appropriate method of analysis was and concluded that considering cytoplasmic lineage as a fixed or a random effect in an animal model produced very similar results. Boettcher *et al.* (1996a) simulated data which included a maternal lineage (ML) effect and compared the impact of treating ML as fixed or random in the estimation of breeding values. Their results demonstrated a higher correlation of EBV (estimated breeding value) with TBV (true breeding value) if ML was fitted as a random effect in the model. It can be argued that in the commercial situation a large number of small maternal lineages will be encountered, and their treatment as random effects is therefore more appropriate. Further, the mtDNA genomes represented in the study are only a sample from the base population.

The aim of this study was to estimate the magnitude of the maternal lineage component of milk production traits and other measures of efficiency. The Langhill dairy herd is involved in a long-term selection experiment that has been running since 1973. Extensive recording of production traits, food intake and animal condition has been undertaken, thereby allowing a more in-depth analysis of the traits highly dependent on energetic mechanisms, for which estimates of the ML component has not been previously undertaken. Given the strong link between energy metabolism, food intake and the efficiency of production these traits may be significantly influenced by a ML component. Due to the nature of the experimental herd, environmental randomization has occurred and management of all cows is well recorded and can be accounted for, which should eliminate any effects due to preferential treatment of individual cow families. A second aim of the study was to investigate what bias was being introduced into the estimation of a maternal lineage variance component by using sire half-sib relationships in the relationship matrix of the animal model. The sires used at the Langhill herd have been selected within the national population and an anticipated reduction in between-sire variance will not be accounted for when using Langhill data, even when an animal model is used for analysis. The bias caused by selection of sires outside of the data set has not been accounted for in previous investigations that have estimated the magnitude of the variance of the maternal lineage component using an animal model (e.g. Boettcher *et al.*, 1996b).

Material and methods

Data description

A total of 1118 records of 517 cows calving between 1982 and 1997, all with a first lactation record, were extracted from the Langhill database.

The traits investigated were all taken from the first 26 weeks of lactation. The methodology of the data collection and the treatment of missing records were outlined in detail by Veerkamp *et al.* (1994). The traits used in the analysis were average daily yield of milk (MLK), fat (FAT), protein (PRT) and average fat and protein percentage (FATP and PRTP). In addition, average daily food dry-matter intake (DMI), net energy of milk production (NE), defined as NE = (0·376 × FATP + 0·209 × PRTP + 0·9480) × MLK, and a raw measure of efficiency (EFF), defined as EFF = NE/DMI, were analysed. EFF is the average daily energy content of the milk yield (MJ), as calculated by Simm *et al.* (1991), divided by the average DMI (kg) of the cow.

In addition the condition score, on a scale of 1 for lean to 5 for fat, of the cows recorded 48 h post calving (CC) and the average weekly condition score of the cows over the first 26 weeks of lactation (AC), were also analysed.

All cows were traced back to founder ancestors in the Langhill herd. These founder ancestors were then traced using the United Kingdom (UK) registration records of the Holstein Friesian Society to either the first point of registration of a founder female or to a cut off point of the year 1920, given that no further convergence looked probable. The earliest cows traced were taken as being the points of cytoplasmic origin for the Langhill herd. This tracing resulted in 517 cows being assigned to 56 cytoplasmic lineages, which define the maternal lineages. The largest ML contained 72 cows with records within a structure that comprised 49 daughter dam pairs and 38 maternal half-sibs. Nine MLs had only one cow with records. Cows were traced up to 16 generations in the establishment of all the points of cytoplasmic origin in the herd and 13% of the records were allocated to MLs of less than five cows with records.

Data analysis

Data were analysed with REML VCE (Groeneveld, 1996) using a univariate animal model. Three approaches were taken. The first fitted a full animal model with the pedigree fitted including sire, dam, paternal grandsire and granddam, and maternal grandsire and granddam, to give a total of 1212 animals. The second and third approaches were designed to investigate the effect of national sire selection on the variance components, and fitted two alternative animal models, both having a reduced pedigree structure with only daughters, dams and granddams present, a total of 834 animals. In these two models sires were treated as unknown parents in the calculation of A inverse. In the second model, sire was fitted as a fixed effect, and in the third each trait was regressed on the sire's estimated breeding value (EBV) for that trait where possible. For the food and condition traits, where sires EBVs were not available, the data were regressed on the sire fat yield EBV. All three models were fitted with and without a random component to account for maternal lineage. In summary:

model 1

$$Y_{ijklmn} = L_i + F_j + YS_k + AL_l + a_m + p_m + c_n + e_{ijklmn}$$

model 2

$$Y_{ijklmno} = L_i + F_j + YS_k + AL_l + S_o + a_m + p_m + c_n + e_{ijklmno}$$

model 3

$$Y_{ijklmn} = L_i + F_j + YS_k + AL_l + a_m + p_m + c_n + b_1 (\text{sirePTA}) + e_{ijklmn}$$

where $Y_{ijklmn(o)}$ = trait; L_i = fixed effect of line, (i = 1, 2 representing selection or control line); F_j = fixed effect of food type, (j = 1, 2 representing high or low concentrate food); YS_k = fixed effect of year-season of calving, (season was divided into two 6-month periods from June to November and December to May); AL_l = fixed effect of age at calving within lactation (l = 1, 8); a_m = additive genetic effect of the animal (m = 1,517); p_m = permanent environmental effect of animal; c_n = random effect of maternal lineage (n = 1, 56); S_o = fixed effect of sire (o = 1, 77); b_1 (sirePTA) = linear regression of Y on sire estimated breeding value ; $e_{ijklmn(o)}$ = residual error. The model was applied to the data with and without the random effect of ML. The ML groups were distributed evenly across the selection and control lines and also across the food types. A subset of the data containing only first lactation records was also analysed using the above models, fitting age at calving as a linear and quadratic covariable.

In order to investigate whether or not very small lineages were causing confounding between nuclear genetic effects and cytoplasmic effects, the traits that approached a significant component of variance attributable to ML in the first analysis, i.e. FAT, NE and EFF, were reanalysed using two reduced data sets. The first included only MLs that had five or more cows with records, which resulted in 448 cows with 973 records in 27 MLs. The second data set had cows with 10 or more cows per lineage, which resulted in 374 cows with 812 records in 16 MLs.

Results

Overall means and standard deviations of the traits used in the analysis are presented in Table 1. The results of the analyses of production traits are in Tables 2, 3 and 4. Estimates of repeatabilities of all the yield traits, using the full pedigree (Table 2), were about 10% lower than recent estimates from data of the UK-based Dairy Information System (DAISY) (Pryce *et al.*, 1998). The heritability estimates were higher by 9%, 22% and 16% respectively for milk, fat and protein yield, than in this study but the heritabilities obtained were very similar to those obtained by Pander *et al.* (1992) in a study of the UK national population. The results of all of the analyses of production traits of the full data set failed to demonstrate any significantly detectable component of variance attributable to ML at the 5% threshold (Tables 2, 3 and 4). This was demonstrated by either the standard errors (from VCE) or taking the log-likelihood ratio test as the test statistic (LRT). Fat yield gave an LRT very close to significance at the 5% level when analysed using model 3, which fitted a maternal pedigree within the animal model and regressed the data on the sire EBV, with a 4% variance component attributable to ML. The inclusion of a ML random component in the model resulted in a repartitioning of the variance

Table 1 *Trait information for 1118 records and a subset of first lactation records of 517 cows in 56 maternal lineages*

		First lacatation		All records	
Trait	Abbreviations	Mean	s.d.	Mean	s.d.
Milk (kg/day)	MLK	23	4·8	27	6·4
Fat (kg/day)	FAT	0·96	0·19	1·1	0·25
Protein (kg/day)	PRT	0·73	0·15	0·84	0·20
Fat (%)	FATP	4·2	0·49	4·1	0·51
Protein (%)	PRTP	3·2	0·23	3·2	0·23
Dry-matter intake (kg/day)	DMI	15	2·1	16	2·8
Efficiency (MJ/kg)	EFF	5·0	0·77	5·1	0·78
Net energy (MJ)	NE	73	14	84	19
Average condition	AC	2·6	0·31	2·4	0·42
Calving condition	CC	2·7	0·22	2·6	0·35

Table 2 *Heritability (±s.e.) estimates etc. for the repeatability model, model 1, with and without maternal lineage fitted*†

	Without maternal lineage				With maternal lineage						
Trait†	h^2		p^2		h^2		p^2		c^2		LRT
MLK	0·42	(0·05)	0·13	(0·04)	0·40	(0·06)	0·14	(0·04)	0·02	(0·02)	0·28
FAT	0·49	(0·05)	0·09	(0·04)	0·42	(0·05)	0·11	(0·05)	0·04	(0·02)	2·44
PRT	0·43	(0·05)	0·11	(0·04)	0·40	(0·06)	0·12	(0·05)	0·02	(0·02)	0·43
FATP	0·65	(0·05)	0·16	(0·05)	0·65	(0·05)	0·16	(0·05)	0·00	(0·00)	0·00
PRTP	0·62	(0·05)	0·12	(0·05)	0·62	(0·06)	0·12	(0·05)	0·00	(0·00)	0·00
DMI	0·37	(0·05)	0·22	(0·05)	0·37	(0·06)	0·22	(0·05)	0·00	(0·00)	0·00
EFF	0·38	(0·05)	0·11	(0·04)	0·33	(0·06)	0·13	(0·04)	0·03	(0·02)	1·18
NE	0·45	(0·05)	0·09	(0·04)	0·39	(0·05)	0·11	(0·04)	0·04	(0·02)	1·88
AC	0·38	(0·05)	0·17	(0·04)	0·38	(0·05)	0·17	(0·04)	0·00	(0·00)	0·00
CC	0·25	(0·04)	0·09	(0·04)	0·25	(0·04)	0·09	(0·04)	0·002	(0·01)	0·06

† See Table 1 for abbreviations.
h^2 is the heritability. p^2 is the proportion of phenotypic variance attributable to permanent environment. c^2 is the proportion of phenotypic variance attributable to maternal lineage. LRT is twice the difference in log-likelihood between the two models.

components for fat yield, increasing the permanent environment component from 9% to 13% and reducing the additive variance from 42% to 34% of the total variance. The repeatability estimate for all models did not differ significantly if an ML component was fitted, indicating that no repartitioning of the residual error variance occurred. Boettcher *et al.* (1996b), performing an analysis using an animal model and treating ML as random, reported ML variance components of 0·38, 0·71 and 2·90% respectively for milk yield, fat yield and fat concentration. The data of Schutz *et al.* (1992), when re-analysed using an animal model, as reported by Boettcher *et al.* (1996a), gave ML variance components of zero for yield traits and 5·6% for the fat concentration trait. This is in contrast to the present study, which found a higher variance component for the fat yield trait and no significant component for fat concentration.

When the energy traits were analysed DMI was not found to have any component of variance attributable to maternal lineage, (Tables 2, 3, and 4). NE did however have a 4% component of variance estimated for maternal lineage, though this was not significant (Table 2). The efficiency trait, a combination of both intake and NE, had an ML variance component of 3% of phenotypic variance but this was not significant at the 5% level. A similar result was obtained for the two different approaches adopted to account for sire effects (Tables 3 and 4).

No significant ML component was found for condition scores of the cows, whether as a single

Table 3 *Heritability (±s.e.) estimates for the repeatability model, model 2, with and without maternal lineage fitted. Sire fitted as a fixed effect*†

	Without maternal lineage				With maternal lineage						
Trait	h^2		p^2		h^2		p^2		c^2		LRT
MLK	0·24	(0·07)	0·23	(0·07)	0·24	(0·07)	0·23	(0·07)	0·00	(0·00)	0·00
FAT	0·40	(0·06)	0·10	(0·06)	0·33	(0·08)	0·14	(0·07)	0·03	(0·02)	1·30
PRT	0·32	(0·07)	0·14	(0·06)	0·32	(0·06)	0·14	(0·06)	0·00	(0·00)	0·00
FATP	0·61	(0·08)	0·17	(0·07)	0·59	(0·09)	0·18	(0·07)	0·01	(0·03)	0·02
PRTP	0·55	(0·08)	0·13	(0·07)	0·55	(0·08)	0·13	(0·07)	0·00	(0·00)	0·00
DMI	0·42	(0·07)	0·12	(0·06)	0·42	(0·07)	0·12	(0·06)	0·00	(0·00)	0·00
EFF	0·24	(0·06)	0·19	(0·06)	0·20	(0·07)	0·21	(0·06)	0·02	(0·02)	0·56
NE	0·32	(0·07)	0·13	(0·06)	0·29	(0·07)	0·15	(0·07)	0·01	(0·02)	0·30
AC	0·32	(0·06)	0·17	(0·06)	0·31	(0·07)	0·17	(0·06)	0·003	(0·01)	0·03
CC	0·24	(0·05)	0·06	(0·05)	0·22	(0·06)	0·07	(0·05)	0·01	(0·01)	0·60

† See Tables 1 and 2 for abbreviations.

Table 4 *Heritability (±s.e.) estimates for the repeatability model, model 3, with and without maternal lineage fitted. Trait regressed on sire PTA*†

Trait	Without maternal lineage				With maternal lineage						
	h^2		p^2		h^2		p^2		c^2		LRT
MLK	0·25	(0·06)	0·23	(0·06)	0·25	(0·07)	0·23	(0·06)	0·00	(0·00)	0·00
FAT	0·42	(0·05)	0·09	(0·05)	0·34	(0·07)	0·13	(0·05)	0·04	(0·02)	2·65
PRT	0·33	(0·06)	0·14	(0·05)	0·30	(0·07)	0·15	(0·06)	0·02	(0·02)	0·34
FATP	0·64	(0·06)	0·14	(0·05)	0·62	(0·08)	0·16	(0·06)	0·01	(0·03)	0·08
PRTP	0·58	(0·07)	0·12	(0·07)	0·58	(0·07)	0·12	(0·06)	0·00	(0·00)	0·00
DMI	0·31	(0·06)	0·26	(0·06)	0·31	(0·06)	0·26	(0·06)	0·00	(0·00)	0·00
EFF	0·27	(0·05)	0·17	(0·05)	0·20	(0·06)	0·20	(0·06)	0·03	(0·02)	1·43
NE	0·38	(0·06)	0·10	(0·05)	0·31	(0·07)	0·13	(0·06)	0·03	(0·02)	1·58
AC	0·34	(0·06)	0·16	(0·05)	0·34	(0·05)	0·16	(0·05)	0·00	(0·00)	0·00
CC	0·21	(0·05)	0·11	(0·05)	0·20	(0·04)	0·11	(0·04)	0·002	(0·01)	0·06

† See Tables 1 and 2 for abbreviations.

measure taken 48 h after calving or as an average weekly score over the 26 weeks of recording and indeed when the data was analysed with the ML component model little or no variance was partitioned into ML.

The results from first lactation records alone are not shown here as they provided similar results. Very low or zero LRT values were obtained from the comparison of models with and without an ML component. The fat yield trait had a 2% component of variance partitioned into ML but the s.d. associated with this was greater in magnitude than the component, indicating a similar trend to the full data set. The power of detection of a ML component for this reduced data set was lower than that of the repeatability model for the same cows.

When ML size was restricted to five or more cows per lineage, using model 1, a significant 4% ML variance component was estimated for fat yield and a 4% component approaching significance was estimated for NE (Table 5). With maternal lineage restricted to 10 or more cows per lineage both the NE and fat yield traits were found to have a significant component of variance attributable to maternal lineage of 5% and 6% respectively (Table 5).

Discussion

Given the nature of mitochondria it would be expected that highly energy dependent traits such as milk and fat yield would be more likely to have a component of phenotypic variance attributable to ML than, for example, protein yield. Previous investigations have tended to provide evidence to reinforce the hypothesis that if the trait is highly energy dependent then a significant ML component can be detected (Boettcher *et al.*, 1996b). The aim of this study was to investigate further the hypothesis that energy dependent traits have a component of phenotypic variance attributable to ML. This was undertaken by analysing food intake data, recorded at Langhill, and also combining recorded yield and

Table 5 *Heritability (±s.e.) estimates for the repeatability model, model 1, with and without maternal lineage fitted. Maternal lineage greater than or equal to five or 10 cows*†

Trait	Without maternal lineage				With maternal lineage						
	h^2		p^2		h^2		p^2		c^2		LRT
FAT (5)	0·44	(0·05)	0·12	(0·04)	0·37	(0·06)	0·14	(0·05)	0·04	(0·02)	3·27
FAT (10)	0·42	(0·05)	0·10	(0·04)	0·34	(0·06)	0·13	(0·05)	0·06	(0·03)	4·18
EFF (5)	0·36	(0·05)	0·12	(0·04)	0·31	(0·06)	0·14	(0·04)	0·03	(0·02)	1·43
EFF (10)	0·42	(0·05)	0·08	(0·04)	0·36	(0·06)	0·10	(0·05)	0·04	(0·03)	2·09
NE (5)	0·41	(0·05)	0·12	(0·04)	0·35	(0·06)	0·14	(0·05)	0·04	(0·02)	2·58
NE (10)	0·40	(0·05)	0·09	(0·05)	0·33	(0·06)	0·11	(0·05)	0·05	(0·03)	3·09

† See Tables 1 and 2 for abbrevations.

intake information into a measure of efficiency. The efficiency trait that was used is a crude measure, since DMI was used instead of MJ energy intake, and the ratio of these varies across years, between treatments, and between early and late lactation. However, the model fitted a food effect to account for high and low concentrate feeding, and also a year-season effect, which accounted in some way for between year variation in food quality. These effects are expected to account for most of the dietary energy variability.

The results of the investigation of net energy, efficiency and DMI traits failed to provide evidence to support the energetic relationship hypothesis using the full data set. For the intake trait all three models failed to detect a component of phenotypic variance attributable to ML. The LRT for these models were zero. Under the null hypothesis of no variation due to maternal lineage, the asymptotic distribution of the log likelihood ratio test is $1/2\chi^2(0) + 1/2\chi^2(1)$, giving a 5% significance threshold of 2·7 (e.g. Stram and Lee, 1994). It may be the case that the power is too low to detect a small ML effect. In order to investigate the power of detecting a component of variance of the magnitude expected due to maternal lineage a one-way random effect ANOVA was considered. Given a balanced data structure of 500 cows, a similar magnitude to the data set used in this analysis, the power of detection of various maternal lineage variance components was investigated using the F ratio power test (e.g. Lynch and Walsh, 1998). It was shown that 3%, 4% and 5% variance components would be detected with, respectively, powers of 25 to 70%, 30 to 80% and 50 to 90%. This test places an upper limit on the detection of a 3% maternal lineage variance component of 70% power which re-enforces the suggestion that the power of this analysis was too low to detect a small ML variance component. The energy trait however approached significance with a component of about 4% in magnitude. Previous analyses by Schutz *et al.* (1992) demonstrated a significant effect of maternal lineage on milk energy concentration treating lineage as a fixed effect but in the present study yield traits were found to show a stronger relationship with maternal lineage than energy concentration traits.

When the data were edited to include only maternal lineages of greater than, or equal to, either five or 10 cows per lineage, the LRT was significant at the 5% level for fat yield and NE. A possible explanation is that with few cows with records in a lineage the maternal lineage variance is confounded with the additive nuclear variance. Given the low number of records available, the small lineages were used in the analysis to provide a better estimate of the additive variance. The loss in power that would appear to be the result of the inclusion of these lineages was not expected.

The three different models were fitted to quantify, in some way, what effect selected sires were having on the detection of an ML component. The reduction in variance due to sire selection is not accounted for when the full animal model is fitted because not all of the data on which selection was based is present in the analysis. However in treating sires separately from the pedigree, heterogeneous variance between sire and dam estimates is removed from the animal model. By regressing the data on the sire EBV the sire variance is accounted for, if the EBVs are estimated accurately and only a single degree of freedom is lost. Information is lost from the estimation of additive nuclear variance. The theoretical expectation of the estimate of heritability using an animal model with only maternal relationships and removing the variation due to sires is of the magnitude $h^2/(1 - h^2/4)$, where h^2 is the heritability estimate of the full pedigree animal model. This represents the loss of residual variance due to fitting the sires as a fixed effect in the model. However it was found that the heritabilities obtained from this model were lower than expected (Tables 3 and 4). When model 1 was run accounting only for paternal relationships or maternal relationships in the relationship matrix, a higher estimate was obtained for heritability from the paternal model. For milk yield this was 0·62 compared with a maternal model estimate of 0·43 (results not shown in Tables). This difference in heritability estimates was caused by a higher estimate of additive variance from the paternal relationship model. This may be explained by a genetic trend inflating the variance of a group of selected sires used over a period of 15 years. This trend was not accounted for in our models. It is apparent from the results that treating sire as a fixed effect and excluding sires from the pedigree (Table 3) did not improve the detection of a maternal lineage component. By regressing the data on sire EBV (Table 4) the significance of the detection of a component of variance attributable to ML for fat yield increased to a level that was very nearly significant but the magnitude of the component was unchanged from the full pedigree estimate. The regression approach was expected to be superior, as only one degree of freedom was lost. Indeed the results indicated this to be the case. Fitting a linear regression on sire PTA in the model actually increased the LRT for fat yield but still failed to provide a criterion for rejection of the null hypothesis at the 5% level of significance. Given the magnitude of the components of ML variance detected it is difficult to draw any conclusions as to whether or not this alternative treatment of sires in the model provides a better method of estimation.

Another concern was the use of data collected over 15 years during which time the mean milk yield has increased leading to an associated change in variance. In a preliminary investigation log transformations were applied to the yield data in order to correct for the heterogeneous variance over time due to an increase in mean yield. The analysis of this transformed data provided similar results to the untransformed data and it was concluded that analysing records that were not contemporaries did not adversely affect the results (Roughsedge *et al.*, 1998).

Although the analysis of one herd provided limited numbers of records, the maternal pedigree used to assign ML was extensive, in that it provided all known links since 1920. This structure ranged from grade up cows, with only daughters present in the herd, to contemporary animals with 16 generations to their cytoplasmic origin. This assignment of ML is necessary with a small data set but is vulnerable to a reduction in power due to pedigree errors. The effect of pedigree errors occurring in the assignment of lineage has the effect of downward biasing the estimation of a ML component. Gibson *et al.* (1997) proposed that, given knowledge of the pedigree structure and the pedigree error rate, a correction factor could be calculated to account for the bias. Given knowledge of the error rate and of the information obtained by tracing further generations in the maternal lineage, an optimum number of generations could be calculated for the assignment of ML.

Given the detection of a component of variance for ML in production traits then several implications can be considered. Boettcher *et al.* (1996a) using simulated data investigated the impact of such a component on both the ranking of animals and the selection of bull-dams for progeny testing schemes. They found that there was a greater impact on ranking of cows than bulls but the greatest immediate impact would be on bull-dam selection. Of potentially greater importance is the identification of superior individuals in MOET nucleus schemes where information from full- and half-sibs is used in the evaluation of donor cows and nucleus bulls. Looking to the future the process of cloning by nuclear transfer (Wilmut *et al.*, 1997) will require the identification of superior cytoplasmic lines as the recipients of nuclear material.

In order to increase the power of estimation for maternal lineage variance analysis of larger data sets of contemporary records is necessary; although these analyses will be restricted to milk yield traits. We plan to perform such an analysis on a national UK data set in a further study.

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References

Bell, B. R., McDaniel, B. T. and Robinson, O. W. 1985. Effects of cytoplasmic inheritance on production traits of dairy cattle. *Journal of Dairy Science* **68:** 2038-2051.

Boettcher, P. J., Kuhn, M. T. and Freeman, A. E. 1996a. Impacts of cytoplasmic inheritance on genetic evaluations. *Journal of Dairy Science* **79:** 663-675.

Boettcher, P. J., Steverink, D. W. B., Beitz, D. C., Freeman, A. E. and McDaniel, B. T. 1996b. Multiple herd evaluation of the effects of maternal lineage on yield traits of Holstein cattle. *Journal of Dairy Science* **79:** 655-662.

Gibson, J. P., Freeman, A. E. and Boettcher, P. J. 1997. Cytoplasmic and mitochondrial inheritance of economic traits in cattle. *Livestock Production Science* **47:** 115-124.

Groeneveld, E. 1996. *REML VCE a multivariate multi model restricted maximum likelihood (co)variance component estimation package version 3.2 user's guide*. Federal Research Center of Agriculture, Mariensee, Germany.

Huizinga, H. A., Korver, S., McDaniel, B. T. and Politiek, R. D. 1986. Maternal effects due to cytoplasmic inheritance in dairy cattle. Influence on milk production and reproduction traits. *Livestock Production Science* **15:** 11-25.

Hutchinson, C. A., Newbold, J. E., Potter, S. S. and Edgell, M. H. 1974. Maternal inheritance of mammalian mitochondrial DNA. *Nature* **251:** 536-538.

Kennedy, B. W. 1986. A further look at evidence for cytoplasmic inheritance of production traits in dairy cattle. *Journal of Dairy Science* **69:** 3100-3105.

Lynch, M. and Walsh, B. 1998. *Genetics and analysis of quantitative traits*. Sinauer Associates, Inc., Sunderland, Mass.

Pander, B. L., Hill, W. G. and Thompson, R. 1992. Genetic parameters of test day records of British Holstein-Friesian heifers. *Animal Production* **55:** 11-21.

Pryce, J. E., Esslemont, R. J., Thompson, R., Veerkamp, R. F., Kossaibati, M. A. and Simm, G. 1998. Estimation of genetic parameters using health, fertility and production data from a management recording system for dairy cattle. *Animal Science* **66:** 577-584.

Roughsedge, T., Brotherstone, S. and Visscher, P. M. 1998. Lack of evidence for cytoplasmic inheritance for milk production traits at the Langhill dairy herd. *Proceedings of the sixth world congress on genetics applied to livestock production, Armidale, vol. 23,* pp. 351-354.

Schutz, M. M., Freeman, A. E., Beitz, D. C. and Mayfield, J. E. 1992. The importance of maternal lineage on milk yield traits of dairy cattle. *Journal of Dairy Science* **75:** 1331-1341.

Seykora, A. J. and McDaniel, B. T. 1983. Heritabilities and correlations of lactation yields and fertility for Holsteins. *Journal of Dairy Science* **66:** 1486-1493.

Simm, G., Persaud, P., Neilson, D. R., Parkinson, H. and McGuirk, B. J. 1991. Predicting food intake in dairy heifers from early lactation records. *Animal Production* **52:** 421-434.

Stram, D. O. and Lee, J. W. 1994. Variance-components testing in the longitudinal mixed effects model. *Biometrics* **50:** 1171-1177.

Veerkamp, R. F., Simm, G. and Oldham, J. D. 1994. Effect of interaction between genotype and feeding system on milk production, feed intake, efficiency and body tissue mobilization in dairy cows. *Livestock Production Science* **39:** 229-241.

Visscher, P. M. and Thompson, R. 1992. Comparisons between genetic variances estimated from different types of relatives in dairy cattle. *Animal Production* **55:** 315-320.

Wilmut, I., Schnieke, A. E., McWhir, J., Kind, A. J. and Campbell, K. H. S. 1997. Viable offspring derived from fetal and adult mammalian cells. *Nature* **385:** 810-813.

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