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Effects of cow families on production traits in dairy cattle

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Abstract

The components of phenotypic variance attributable to maternal lineage for production traits of the UK Holstein Friesian dairy population were estimated. First lactation production records of 55 230 cows calving between 1996-1998 in the UK Holstein Friesian population were used in the analysis. Maternal pedigree records were traced back to 1960 to establish maternal lineages. The tracing resulted in 36 320 cows being assigned to 11 786 cow families with more than one cow per maternal lineage. Using test day records it was possible to explore aspects of the lactation curve in terms of persistency and different periods of production. The traits analysed were 305-day milk yield and composition traits, the first three milk yield tests of lactation and two measures of persistency. A contemporary record design was used to minimize pair-wise additive direct genetic relationships between cows within a maternal lineage and to remove both the effect of heterogeneous variance over time and the complications of permanent environment effects. No significant component of variance attributable to maternal lineage was found for yield traits. When data were restricted to maternal lineages with five or more records, persistency, as a ratio of cumulative yield in the last third to that in the first third of a 300-day lactation, was estimated to have a 4·4% component due to maternal lineage variance significant at the 5% level. The study also investigated the preferential treatment of cow families. Some evidence of maternal lineage × herd interaction was found.

Keywords: *dairy cows, families, heritability, preferential treatment.*

Introduction

In mammals the mitochondria are almost exclusively inherited from the maternal parent (e.g. Hutchinson *et al.*, 1974) and hence, with the exception of mutational events, all animals of a maternal lineage have identical mtDNA. It is therefore theoretically possible to estimate a component of variance due to maternal lineage, which in turn is assigned to mtDNA. A theoretical experimental design to separate cytoplasmic effects and all interactions was proposed by Beavis *et al.* (1987). In genetic analyses of dairy cattle higher estimates of heritability have been obtained from daughter-dam regression than from paternal half-sib analysis (e.g. Seykora and McDaniel, 1983; Visscher and Thompson, 1992). This suggests that there may be a mechanism of inheritance, in addition to nuclear genetic inheritance, which is not being accounted for in current evaluations. The method of Beavis *et al.* (1987) is not feasible for dairy cattle but it has been shown (Southwood *et al.*, 1989) that with field data the use of an animal model, to account for additive direct genetic and maternal direct genetic contributions, will enable the separation of cytoplasmic inheritance if it is present. Southwood *et al.* (1989) also demonstrated that if additive maternal genetic effects were simulated, and the data analysed using an incorrect model that accounted only for additive and cytoplasmic effects, but not additive maternal genetic effects, then a small cytoplasmic variance component would be detected. Most of the additive maternal genetic variance would be partitioned into additive genetic variance.

Several analyses have estimated the level of phenotypic variance attributable to maternal lineage using an animal model (e.g. Boettcher and Gibson, 1997; Schnitzenlehner and Essl, 1999; Roughsedge *et al.*, 1999). These analyses used the animal model and fitted maternal lineage as a random effect. Schnitzenlehner and Essl (1999) estimated a component of phenotypic variance attributable to maternal lineage of 2% for first lactation milk yield. The study of Roughsedge *et al.* (1999) estimated a significant component of 4% for first lactation fat yield when data were restricted to five or more cows per maternal lineage. Persistency and a herd life trait were also shown to have a significant component of maternal lineage variance (Schnitzenlehner and Essl, 1999). A significant 1·5% component of maternal lineage variance was also estimated for the composite dairy type trait, body (Roughsedge *et al.*, 2000).

The aim of this study was to estimate the components of phenotypic variance of production traits of the UK Holstein Friesian dairy population that are attributable to maternal lineage. Using test day records it is possible to explore aspects of the lactation curve in terms of persistency and different periods of production. Given the hypothesis that mitochondrial DNA is connected with energetic processes it is not unreasonable to speculate that maternal lineage variance is likely to be highest at the time of peak production, i.e. early lactation, and also in the maintenance of production over a lactation, i.e. persistency. The current study also aims to overcome the problem highlighted by the study of Southwood *et al.*, (1989) of attributing additive maternal genetic effects to cytoplasmic inheritance. This is achieved by using a contemporary data set that includes no records of daughter-dam pairs. The study also investigates the preferential treatment of cow families.

Material and methods

A total of 55 230 first lactation Holstein Friesian pedigree cows were available for the analysis. Type records from these cows were used previously to investigate maternal lineage variance (Roughsedge *et al.*, 2000). Two data restrictions based on maternal lineage size were applied. The first restricted maternal lineage size to greater than one and the second to greater than four cows per maternal lineage, which resulted in data sets of 36 320 and 10 596 records available for analysis respectively. All cows calved between 1996 and 1998.

Information on 305 day yields and test day records were available. A summary of the traits analysed is in Table 1.

Traits

The traits were 305-day milk (MLK), fat (FAT) and protein (PRT) yield, fat (FATP) and protein (PRTP) percent. Also analysed were test days one to three for milk (T1-3MLK), fat (T1-3FAT), protein (T1-3PRT) yield and fat (T1-3FATP) and protein (T1-3PRTP) percent.

Table 1 *Trait information for full data set and for restricted data sets*

Trait	Abbreviation	Mean	s.d.	No. of records
Milk (kg)	MLK	6577·4	1374·0	55230
Fat (kg)	FAT	267·0	52·9	55230
Protein (kg)	PRT	215·5	43·7	55230
Fat (%)	FATP	4·1	0·4	55230
Protein (%)	PRTP	3·3	0·2	55230
Milk (kg)	MLK†	6622·2	1387·3	36320
Fat (kg)	FAT†	268·5	53·2	36320
Protein (kg)	PRT†	216·9	44·1	36320
Fat (%)	FATP†	4·1	0·4	36320
Protein (%)	PRTP†	3·3	0·2	36320
Milk (kg)	MLK‡	6765·8	1430·7	10596
Fat (kg)	FAT‡	273·3	54·1	10596
Protein (kg)	PRT‡	221·3	45·3	10596
Fat (%)	FATP‡	4·1	0·4	10596
Protein (%)	PRTP‡	3·3	0·2	10596
Avg. test 1-3 milk (kg)	T1-3MLK†	24·8	5·4	93486
Avg. test 1-3 fat (kg)	T1-3FAT†	1·0	0·2	93486
Avg. test 1-3 protein (kg)	T1-3PRT†	1·0	0·2	93486
Avg. test 1-3 fat (%)	T1-3FATP†	4·0	0·6	93486
Avg. test 1-3 protein (%)	T1-3PRTP†	3·2	0·3	93486
Avg. test 1-3 milk (kg)	T1-3MLK‡	25·3	5·5	28185
Avg. test 1-3 fat (kg)	T1-3FAT‡	1·0	0·2	28185
Avg. test 1-3 protein (kg)	T1-3PRT‡	1·0	0·2	28185
Avg. test 1-3 fat (%)	T1-3FATP‡	4·0	0·6	28185
Avg. test 1-3 protein (%)	T1-3PRTP‡	3·2	0·3	28185
Persistency§	P3†	77·5	17·6	26572
s.d. of milk tests§	SD3†	4·0	1·5	26572
Persistency§	P3‡	77·8	16·7	7241
s.d. of milk tests§	SD3‡	3·9	1·5	7241

† Data set restricted to >1 cow per maternal lineage.
‡ Data set restricted to >4 cows per maternal lineage.
§ Measured over first 300 days of lactation.

Two derived traits of persistency measures were also analysed. The first was the ratio of the last 100 days of production to the first 100 days of production in the first 300 days of milk production (P3) (Sölkner and Fuchs, 1987). The second was standard deviation of test day milk yield over the first 10 test days (SD3), which occur during the first 300 days of lactation, suggested by Sölkner and Fuchs (1987):

$$P3 = \frac{\text{milk yield third 100 days} \times 100}{\text{milk yield first 100 days}}$$

SD3 = standard deviation of first 10 test-day milk yields.

In the calculation of P3 the exponential curve of Wilmink (1987) was used to calculate daily yield.

$$Y_t = a + be^{-kt} + ct \qquad (1)$$

where *Yt* is the yield on day *t* of lactation. Curve parameters *a*, *b* and *c* were estimated for each cow and parameter *k* was fixed at 0·068 (following White *et al.*, 1999). Before the curve was fitted about 5% of the cows with records were rejected for having less than 10 test day records. The Wilmink curve is a four parameter curve but the fourth parameter is generally set to a constant for convenience. It was found to perform better than other three parameter models by Olori *et al.* (1999). The measure P3 was calculated using the fitted values ($\hat{Y}_t$) from equation (1)

$$\mathrm{P3} = \left(\sum_{t=201}^{t=300} \hat{Y}_t \Big/ \sum_{t=1}^{t=100} \hat{Y}_t\right) \times 100 \qquad (2).$$

When test day records were used, in both the derivation of persistency traits and in their direct use as traits of interest, a restriction to the data set was applied to restrict the third test day to the 3rd month of lactation. This was to ensure that animals with missing test days in the first three test days were excluded from the analysis.

Maternal families

Maternal families were established by tracing maternal pedigrees of all cows with records on the Holstein UK and Ireland (HUKI) database. This database holds 5 million pedigree records, going back to 1960. All cows used in the analysis were full pedigree registered cows. No cows used were recent grade-up cows, i.e. all were at least four generations from a non-pedigree dam to avoid small maternal lineages. However of the 55 230 cows with records, about 40% belonged to single cow families, i.e. families with one cow with a record tracing back to one maternal ancestor. The maternal lineage structure is shown in Table 2. Previous studies looking for maternal lineage variance components using field data have made data restriction based on size of maternal lineage, e.g. Boettcher and Gibson (1997) and Schnitzenlehner and Essl (1999) made restrictions of greater than or equal to two and 10 cows per maternal lineage respectively. In the data set used for the current analysis contemporary data were used which limits the number of large maternal lineages but provides benefits in the structure of the data for the detection of true maternal lineage variance effects. With contemporary data most relationships are no closer than maternal cousins, with a common maternal granddam only, sharing 1/16 of nuclear genetic material. However, maternal cousins share 100% of their mtDNA, enabling a better opportunity to separate variance attributable to mtDNA.

Table 2 *Distribution of cows with records by maternal lineage size*

Maternal lineage size	No. of animals with records	No. of families	Average maternal lineage size	Average no. of generations to origin
>1 and <5	25716	10292	2·5	5
>4 and <10	7931	1314	6·0	6
>9 and <15	1331	118	11·5	6
>14 and <20	557	34	16·5	6
>19 and <30	500	21	24·0	7
>29 and <40	139	4	35·0	7
>39 and <50	89	2	44·5	7
>49	57	1	57·0	8

Data analysis

The analysis was performed using REML VCE (Groeneveld, 1996) fitting a univariate animal model. The pedigree used in the model with greater than one record per maternal lineage comprised sire, dam, maternal and paternal grandsire and granddam to give a total of 100 643 animals. The animals with records were all contemporaries; i.e. there were no daughter-dam or daughter-granddam pairs in the data. This contemporary design was used by Roughsedge *et al.* (2000). The use of such a design is intended specifically to remove additional covariance from the data structure that can be attributed to daughter-dam relationships but more generally to reduce the degree of additive direct genetic relationship between individuals within cow families. The additive direct genetic relationship within lineage is reduced but 100% similarity due to mtDNA is retained. In addition to reducing the additive direct genetic relationship and removing the extra covariance structure between daughters and dams, the use of contemporary data reduces the heterogeneity of variance of the traits (Roughsedge *et al.*, 1998).

Three models were fitted for data sets with two or more records per maternal lineage. Model 1 was fitted for 305-day milk, fat and protein yield traits and fat and protein percentage. Model 2 was fitted for the test day yield traits, with a random effect for permanent environment where the first three test days were fitted. Model 3 was fitted to the two persistency traits, SD3 and P3. When data were restricted to five or more records per maternal lineage then model 1 was altered to fit both herd by year as a fixed effect and month of calving as a separate fixed effect to avoid small contemporary groups.

Model 1.

$$Y_{ijkl} = \mathrm{HYS}_i + b_1(\mathrm{age}) + b_2(\mathrm{age}^2) + b_3(\mathrm{holp}) + a_j + f_k + hf_l + e_{ijkl}.$$

Model 2.

$$Y_{abjklm} = \mathrm{H}_a + \mathrm{TD}_b + b_1(\mathrm{age}) + b_2(\mathrm{age}^2) + b_3(\mathrm{dim}) + b_4(\mathrm{dim}^2) + b_5(\mathrm{holp}) + a_j + f_k + hf_l + pe_m + e_{abjklm}.$$

Model 3.

$$Y_{ijkl} = \mathrm{HYS}_i + b_1(\mathrm{age}) + b_2(\mathrm{age}^2) + b_3(\mathrm{holp}) + b_4(\mathrm{milk}) + a_j + f_k + hf_l + e_{ijkl}.$$

where Y_{ijklmn} = trait; HYS_i = fixed effect of herd × year × season of first test day, (i = 1,7170); H_a = fixed effect of herd, (a = 1,2774), season was divided into three 4-month blocks starting with January; TD_b = fixed effect of year × month of test day, (b = 1,29); age = age at classification; b_1(age) = linear regression of Y on age; $b_2(\mathrm{age}^2)$ = quadratic regression of Y on age; holp = percentage Holstein; b_3(holp) = linear regression of Y on holp; dim = number days in milk; b_3(dim) = linear regression of Y on dim; $b_4(\mathrm{dim}^2)$ = quadratic regression of Y on dim; milk = 305-day milk yield; b_4(milk) = linear regression of Y on milk; a_j = additive direct genetic effect of the animal, (j = 1,100640); pe_m = permanent environmental effect of animal; f_k = random effect of maternal lineage, (k = 1,11789); hf_l = random effect of herd × maternal lineage, (l = 1,17475); e_{ijklmn} = residual error. The models were applied to the data with and without the random effect of maternal lineage (f). The models were also applied with a maternal lineage effect (f) with and without a herd × maternal lineage random effect (hf). To test for a significant variance component the model with herd by maternal lineage plus maternal lineage was tested against the model with just maternal lineage and the model with just maternal lineage was tested against the model without maternal lineage.

It is not straightforward to establish the threshold value required for an extra component of variance to be significant in an analysis where several traits are being tested and several components of variance are being fitted. It would appear wise to err on the side of caution in such a situation. It is known when dealing with yield traits that there is a strong correlation structure between them. Persistency traits were estimated to be highly correlated with milk yield by Sölkner and Fuchs (1987) but it was shown that the sign of the correlation depended on the chosen definition of persistency, i.e. SD3 is positively correlated with milk production and P3 is negatively correlated. To accommodate this positive or negative correlation, persistency is regressed on milk yield in the model and is thus independent of yield.

The test statistic used in the analysis was the LRT (log likelihood ratio test). Under the null hypothesis of no variation due to maternal lineage, the asymptotic distribution of the LRT is $1/2\chi^2(0) + 1/2\chi^2(1)$, (e.g. Stram and Lee, 1994). This implies that for a single LRT, the appropriate P value for the test statistic is half of the P value from a $\chi^2(1)$ distribution, or, equivalently, that the threshold for a given type-1 error of α is the threshold from a $\chi^2(1)$ pertaining to 2α. For example, for a single trait univariate estimation the threshold value for an experiment wise error rate of α= 0·05, is 2·7. However more than one independent test is being carried out. The Dunn-Šidák method (Sokal and Rohlf, 1995) determines the probability of a type 1 (α) error given k independent traits are being tested, $(1 - \alpha')^k$. Under a LRT, which is distributed $1/2\chi^2(0) + 1/2\chi^2(1)$ the α' must be further divided by 2 giving $(1 - \alpha'/2)^k$. The experiment wise error rate is then, $\alpha = 1 - (1 - \alpha'/2)^k$. This can then be solved for α = 0·05:

$$\alpha' = 2(1 - (1 - \alpha)^{1/k}).$$

The most extreme case would be to consider that all traits investigated were independent and that the two extra variance components being investigated, i.e., maternal lineage and the maternal lineage × herd interaction were independent. In this scenario five 305-day yield traits, two persistency traits and five test day traits are being tested giving 12 traits and 24 statistical tests. However, given the strong correlation structure between the traits being investigated fewer independent tests are being used. It is not possible to isolate the exact level of the threshold test statistic but to set it too high would seriously reduce the power of detecting a variance component. If k = 12 and α = 0·05 this gives α' = 0·009 requiring a LRT test statistic of 7·03 for a significant additional component of variance. Note that for $k = 1$, $\alpha' = 2\alpha$, as expected.

Results

A summary of the traits analysed can be seen in Table 1. The traits are given with their means and standard deviations. The number of records,

Table 3 *Heritability and variance component estimates (± s.e.) for model 1 with and without maternal lineage fitted*

	Without maternal lineage	With maternal lineage		
Trait	h^2§	h^2§	f^2§	LRT§
MLK	0·436 (0·017)	0·436 (0·015)	0·001 (0·001)	0·04
FAT	0·403 (0·017)	0·399 (0·018)	0·004 (0·003)	0·69
PRT	0·420 (0·017)	0·415 (0·018)	0·002 (0·004)	0·17
FATP	0·644 (0·019)	0·638 (0·020)	0·006 (0·003)	1·49
PRTP	0·655 (0·020)	0·652 (0·018)	0·002 (0·003)	0·10
MLK†	0·443 (0·020)	0·440 (0·019)	0·002 (0·004)	0·20
FAT†	0·382 (0·019)	0·374 (0·018)	0·007 (0·004)	2·60
PRT†	0·415 (0·019)	0·411 (0·019)	0·003 (0·003)	0·42
FATP†	0·655 (0·021)	0·645 (0·021)	0·006 (0·004)	1·95
PRTP†	0·666 (0·021)	0·660 (0·021)	0·004 (0·004)	0·62
P3†	0·119 (0·013)	0·117 (0·013)	0·006 (0·007)	0·49
SD3†	0·160 (0·015)	0·159 (0·016)	0·002 (0·005)	0·09
MLK‡	0·403 (0·032)	0·402 (0·032)	0·002 (0·005)	0·04
FAT‡	0·386 (0·032)	0·374 (0·030)	0·012 (0·006)	2·50
PRT‡	0·387 (0·033)	0·386 (0·028)	0·001 (0·006)	0·02
FATP‡	0·636 (0·035)	0·627 (0·036)	0·008 (0·006)	1·00
PRTP‡	0·608 (0·033)	0·608 (0·033)	0·000 (-)	0·00
P3‡	0·136 (0·030)	0·104 (0·028)	0·044 (0·011)	11·21
SD3‡	0·115 (0·028)	0·110 (0·028)	0·006 (0·014)	0·21

† Data set restricted to >1 cow per maternal lineage.
‡ Data set restricted to >4 cows per maternal lineage.
§ h^2 is the heritability. f^2 is the proportion of phenotypic variance attributable to maternal lineage. LRT is twice the difference in log-likelihood between the two models.

resulting from the various data editing procedures described, are also shown.

Tables 3 and 4 show the results of fitting the random maternal lineage effect. The full, unedited data set was used for 305-day traits to determine that the estimation of heritability was not affected by the data editing procedure. It can be seen that the estimation of heritability was not significantly affected by the maternal lineage data restrictions imposed. Using the full data set no significant component of phenotypic variance attributable to maternal lineage was found (Table 3).

When the data were restricted to families of two or more cows the log likelihood ratio test statistic was larger for fat yield. However, the level of test statistic was not significant at a 5% type 1 error rate using the one independent test threshold value for the LRT of 2·7, and the component was less than 1% of the phenotypic variance. The results from the analysis of 305-day yield data are comparable to those obtained by Boettcher and Gibson (1997) using field data from the Canadian Holstein herd. When the further data restriction of five or more records per maternal lineage were applied to 305-day yield traits no change was seen in the magnitude of the component of variance attributable to maternal lineage.

The persistency traits present a different picture (Table 3). When the data editing allowed records in families of two or more cows in the analysis there was no significant component of variance attributable to maternal lineage. However, when further restrictions were placed on maternal lineage size the P3 trait was estimated to have a 4·4% component of variance attributable to maternal lineage and this component was found to be highly significant. Indeed the LRT value would provide a 5% experiment wise error rate given 125 independent tests. With the assumption that we are undertaking at most 12 independent tests, which is

Table 4 *Heritability and variance component estimates (± s.e.) for model 2 with and without maternal lineage fitted*

	Without maternal lineage		With maternal lineage			
Trait	h^2	p^2§	h^2	p^2§	f^2	LRT
T1-3 MLK†	0·238 (0·012)	0·371 (0·011)	0·233 (0·012)	0·371 (0·011)	0·005 (0·002)	2·30
T1-3 FAT†	0·176 (0·010)	0·270 (0·009)	0·176 (0·010)	0·270 (0·009)	0·000 (0·001)	0·00
T1-3 PRT†	0·189 (0·011)	0·326 (0·010)	0·188 (0·011)	0·326 (0·010)	0·001 (0·002)	0·14
T1-3 FATP†	0·232 (0·010)	0·078 (0·008)	0·231 (0·010)	0·078 (0·008)	0·000 (0·001)	0·02
T1-3 PRTP†	0·246 (0·010)	0·177 (0·008)	0·246 (0·010)	0·177 (0·008)	0·000 (-)	0·00
T1-3 MLK‡	0·226 (0·022)	0·319 (0·020)	0·223 (0·020)	0·319 (0·018)	0·003 (0·004)	0·22
T1-3 FAT‡	0·163 (0·017)	0·284 (0·015)	0·163 (0·017)	0·284 (0·015)	0·000 (-)	0·00
T1-3 PRT‡	0·207 (0·020)	0·316 (0·018)	0·206 (0·019)	0·316 (0·018)	0·001 (0·004)	0·03
T1-3 FATP‡	0·203 (0·017)	0·104 (0·015)	0·203 (0·016)	0·104 (0·013)	0·000 (0·002)	0·00
T1-3 PRTP‡	0·213 (0·018)	0·212 (0·016)	0·212 (0·019)	0·212 (0·017)	0·001 (0·004)	0·07

† Data set restricted to >1 cow per maternal lineage. Note traits are test day one to three of lactation.
‡ Data set restricted to >4 cows per maternal lineage. Note traits are test day one to three of lactation.
§ p^2 is the proportion of phenotypic variance attributable to permanent environment. See Tables 1 and 3 for other abbreviations.

Table 5 *Heritability and variance component estimates (± s.e.) for model 1 with maternal lineage fitted or maternal lineage + herd × maternal lineage fitted*

	With maternal lineage		With maternal lineage + herd × maternal lineage			
Trait	h^2	f^2	h^2	f^2	hf^2§	LRT
MLK	0·436 (0·015)	0·001 (0·001)	0·435 (0·015)	0·000 (-)	0·002 (0·006)	0·03
FAT	0·399 (0·018)	0·004 (0·003)	0·399 (0·017)	0·004 (0·004)	0·000 (-)	0·00
PRT	0·415 (0·018)	0·002 (0·004)	0·415 (0·018)	0·001 (0·001)	0·003 (0·003)	0·08
FATP	0·638 (0·020)	0·006 (0·003)	0·638 (0·019)	0·006 (0·004)	0·000 (-)	0·00
PRTP	0·652 (0·018)	0·002 (0·003)	0·644 (0·019)	0·000 (-)	0·009 (0·004)	2·03
MLK†	0·440 (0·019)	0·002 (0·004)	0·437 (0·017)	0·000 (-)	0·005 (0·005)	0·38
FAT†	0·374 (0·018)	0·007 (0·004)	0·373 (0·016)	0·007 (0·005)	0·001 (0·006)	0·10
PRT†	0·411 (0·019)	0·003 (0·003)	0·408 (0·018)	0·000 (-)	0·006 (0·005)	0·43
FATP†	0·645 (0·021)	0·006 (0·004)	0·645 (0·020)	0·006 (0·003)	0·000 (-)	0·00
PRTP†	0·660 (0·021)	0·004 (0·004)	0·651 (0·022)	0·000 (-)	0·010 (0·004)	2·13
P3†	0·117 (0·013)	0·006 (0·007)	0·117 (0·013)	0·005 (0·008)	0·001 (0·002)	0·00
SD3†	0·159 (0·016)	0·002 (0·005)	0·157 (0·015)	0·000 (-)	0·015 (0·008)	2·00
MLK‡	0·402 (0·032)	0·002 (0·005)	0·394 (0·030)	0·000 (-)	0·010 (0·008)	0·92
FAT‡	0·374 (0·030)	0·012 (0·006)	0·369 (0·031)	0·005 (0·008)	0·013 (0·011)	0·61
PRT‡	0·386 (0·028)	0·001 (0·006)	0·376 (0·030)	0·000 (-)	0·012 (0·008)	1·33
FATP‡	0·627 (0·036)	0·008 (0·006)	0·672 (0·033)	0·008 (0·006)	0·000 (-)	0·00
PRTP‡	0·608 (0·033)	0·000 (-)	0·608 (0·036)	0·000 (-)	0·000 (-)	0·00
P3‡	0·104 (0·028)	0·044 (0·011)	0·102 (0·026)	0·019 (0·017)	0·032 (0·200)	1·18
SD3‡	0·110 (0·028)	0·006 (0·014)	0·110 (0·028)	0·006 (0·014)	0·000 (-)	0·00

† Data set restricted to >1 cow per maternal lineage.

‡ Data set restricted to >4 cows per maternal lineage.

§ hf^2 is the proportion of phenotypic variance attributable to maternal lineage × herd interaction. See Tables 1 and 3 for other abbreviations.

Table 6 *Heritability and variance component estimates (± s.e.) for model 2 with maternal lineage fitted or maternal lineage + herd × maternal lineage fitted*

	With maternal lineage			With maternal lineage + herd × maternal lineage				
Trait	h^2	p^2	f^2	h^2	p^2	f^2	hf^2	LRT
T1-3 MLK†	0·233 (0·012)	0·371 (0·011)	0·005 (0·002)	0·228 (0·012)	0·370 (0·003)	0·000 (-)	0·011 (0·011)	3·56
T1-3 FAT†	0·176 (0·010)	0·270 (0·009)	0·000 (0·001)	0·176 (0·009)	0·270 (0·008)	0·000 (-)	0·000 (0·002)	0·00
T1-3 PRT†	0·188 (0·011)	0·326 (0·010)	0·001 (0·002)	0·184 (0·010)	0·325 (0·009)	0·000 (-)	0·007 (0·003)	2·68
T1-3 FATP†	0·231 (0·010)	0·078 (0·008)	0·000 (0·001)	0·321 (0·010)	0·078 (0·008)	0·000 (-)	0·000 (0·002)	0·00
T1-3 PRTP†	0·246 (0·010)	0·177 (0·008)	0·000 (0·000)	0·245 (0·010)	0·177 (0·009)	0·000 (-)	0·002 (0·002)	0·26
T1-3 MLK‡	0·223 (0·020)	0·319 (0·018)	0·003 (0·004)	0·213 (0·021)	0·318 (0·018)	0·000 (-)	0·015 (0·006)	3·53
T1-3 FAT‡	0·163 (0·017)	0·284 (0·015)	0·000 (0·000)	0·163 (0·015)	0·284 (0·014)	0·000 (-)	0·000 (-)	0·00
T1-3 PRT‡	0·206 (0·019)	0·316 (0·018)	0·001 (0·004)	0·194 (0·020)	0·313 (0·017)	0·000 (-)	0·017 (0·006)	4·86
T1-3 FATP‡	0·203 (0·016)	0·104 (0·013)	0·000 (0·002)	0·203 (0·016)	0·010 (0·014)	0·000 (-)	0·000 (0·002)	0·00
T1-3 PRTP‡	0·212 (0·019)	0·212 (0·017)	0·001 (0·004)	0·211 (0·018)	0·212 (0·016)	0·000 (-)	0·003 (0·004)	0·09

† Data set restricted to >1 cow per maternal lineage. Note traits are test day one to three of lactation.

‡ Data set restricted to >4 cows per maternal lineage. Note traits are test day one to three of lactation.

hf^2 is the sum of the proportion of phenotypic variance attributable to maternal lineage × herd interaction. See Tables 1 and 3 for other abbreviations.

still conservative, then the probability of a type 1 error for the P3 trait is 0·0048. However, a small non-significant maternal lineage component was estimated for the SD3 trait.

Yields from tests one to three, fitted as a repeatability model (Table 4), did not show any significant maternal lineage variance component. These yield records were also individually investigated using a univariate model (results not shown) and again the estimate of the component of variance attributable to maternal lineage was not significant.

The results of fitting the maternal lineage plus the herd × maternal lineage interaction are shown in Tables 5 and 6. To test for the interaction component this model was tested against the model that fitted only animal and maternal lineage effects. For the 305 day yield traits and the persistency traits, whichever data edit was applied, no significant interaction component was detected. However the repeatability model (Table 6) for test days one to three resulted in estimates for components of phenotypic variance attributable to herd by maternal lineage of 1·1% and 0·7% for milk and protein yield, respectively, when greater than one cow per maternal lineage was allowed. The further data restriction of greater than or equal to five cows per maternal lineage increased the estimated components of phenotypic variance detected to 1·5% and 1·7%. Individual test days were analysed with univariate tests. Test day two had consistent estimates of near zero for the interaction component. However, the estimates of the interaction component of variance for test day one were 2·6% and 3·2% of phenotypic variance for milk and protein yield respectively with test statistics of 4·64 and 6·92. The significance of these components however must be questioned. Suppose only five independent tests are carried out, then for a 5% experiment wise error rate ($\alpha = 0{\cdot}05$) a threshold test statistic of 5·41 would be required. All of these test statistics, except for one, are below this level of significance. The interaction component for protein yield for test day one was significant at $\alpha = 0{\cdot}05$ even if as many as 11 independent tests were considered.

Discussion

The hypothesis that the inheritance of mtDNA has an effect on the difference in heritability estimates between daughter-dam and paternal half-sib estimation procedures in yield traits of dairy cattle is dependant on mtDNA having a significant effect on the traits in question. It is known that mitochondria are involved in the respiratory process and indeed are referred to as the 'energy factories' of cells. It has also been established that mitochondria contain a closed loop of 16 338bp of DNA. This mtDNA contains 12 protein-coding genes involved in energy production *via* the electron transport chain (Anderson *et al.*, 1982). Therefore the most likely involvement in production that follows from this is in highly energetic processes and times at which the cow is under metabolic stress. For this reason the yield traits in test days one to three around peak production were investigated. Previous studies have looked at 305 day yield as the trait of interest (e.g. Boettcher and Gibson, 1997; Albuquerque *et al.*, 1998) which is understandable given that national evaluations are based upon this measure. In the present study no significant maternal lineage component of phenotypic variance was estimated for the 305-day yield traits. This is in agreement with similar recent studies utilizing an animal model for the estimation of maternal lineage variance in large Holstein population studies (e.g. Boettcher and Gibson, 1997; Albuquerque *et al.*, 1998). The further investigation of test day yield for test days one to three also resulted in no significant maternal lineage effects.

Persistency is another trait that is connected with energetic processes. It is desirable to have cows with flatter lactation curves to both allow a reduction in the metabolic stress of the cow and also to reduce the cost of feeding the cow (Sölkner and Fuchs, 1987). If the cow has a flatter lactation curve then more production energy can be obtained from roughage in the diet and concentrate costs can be reduced and flatter lactations make other management decisions easier, such as insemination decisions (Dekkers *et al.*, 1998). Sölkner and Fuchs (1987) suggested the use of SD3 due to the fact that it accounts for oscillations in the slope of the curve and is also on the same scale as milk yield. In this study, the estimate of the component of variance due to maternal lineage was not significant for the SD3 trait, which is in contrast to the findings of Schnitzenlehner and Essl (1999). Their study estimated the component to be 3·2% of phenotypic variance for the SD3 measure of persistency in the Austrian Simmental population. However, persistency, as the ratio of milk production in day 201 to 300 of lactation to production in days 1 to 100 of lactation, was estimated to have a highly significant component of variance due to maternal lineage (4·4% of phenotypic variance). This estimate is particularly substantial given that the heritability of this trait was estimated to be 0·104. The component was estimated when the data set was restricted to five or more cows per maternal lineage. Schnitzenlehner and Essl (1999) used a data restriction of 10 or more cows per maternal lineage for this trait. This result suggests that in the Holstein Friesian population maternal lineage has a significant effect on the maintenance of milk yield in the later part of the lactation curve. The data editing procedure also resulted in a significant reduction in the heritability of SD3. The heritability estimates of persistency were both lower than those reported by Sölkner and Fuchs (1987) for the Austrian Simmental population. They estimated heritabilities of SD3 and P3 to be 0·19 and 0·21 respectively for first lactation. However, they are comparable with the heritability estimated in the study of Schnitzenlehner and Essl (1999) for SD3 of 0·12. In this study the estimates for SD3 and P3 were 0·16 and 0·12 respectively when data were restricted to two or more cows per maternal lineage, and 0·12 and 0·14 when the restriction was five or more cows per maternal lineage. It is surprising that a significant component of phenotypic variance attributable to maternal lineage was estimated for the P3 trait in this study and a significant component was not estimated for SD3. These traits were estimated to have an additive genetic correlation of –0·92 but the maternal lineage variance component correlation was –0·34. The difference in the maternal lineage variance estimated in this study and that of Schnitzenlehner and Essl (1999) could be attributed to the different breeds of cattle. If 4% of the phenotypic variance of the P3 trait is attributable to maternal lineage variance for the persistency trait then, given the low heritability of this trait, there may be an impact on EBV of sires. The potential impact of maternal lineage variance on genetic gain in the US dairy industry was investigated by Boettcher *et al.* (1996). A component accounting for as much as 10% of phenotypic variance would have only a minimal effect on genetic progress in milk yield based on a heritability of 0·25. However the estimated heritability for persistency was only 0·14. When maternal lineage was considered the heritability fell to 0·10 with the remaining 0·04 partitioned to maternal lineage variance. It is not unreasonable to hypothesize that when maternal lineage is responsible for such a large component of variance in comparison to additive direct genetic variance there will be overestimation of EBV of sires when using sister and daughter information.

It is not easy to see why the restriction of data size to five or more cows per maternal lineage should have an effect on the estimation of maternal lineage variance for some traits. Small lineages make up the majority of cows that trace back to recent non-pedigree cows that have been graded-up by crossing. Given that these cows cannot be traced back to a distant cytoplasmic origin they may in fact be members of the same maternal lineage. The incorrect assignment of cows to different maternal lineages when they actually belong to the same lineage, would result in a reduction in the estimation of between maternal lineage variance. This consequence can be demonstrated by simulating a number of true maternal families and then estimating between maternal lineage variance with a structure that does not link all true maternal lineage members together. This is the situation that occurs when small maternal families are formed by failing to trace pedigrees back to true cytoplasmic origins and will be explained in a subsequent study.

The current study also attempted to examine preferential treatment (PT) of cow families. A discussion on preferential treatment was presented in Roughsedge *et al.* (2000), which explained that PT of cow families would not be detected using methods which look at within herd standard deviation of yield, and yet could have a significant effect on bull-dam selection. The hypothesis for PT of cow family is that cows coming from known elite maternal lineages will receive PT in some herds. This may occur in some herds, although not in all. In the current study about 3000 cow families were distributed over more than one herd and four families were distributed over more than twenty herds. To investigate PT of cow families a random effect was fitted in the model, which coded the maternal lineage × herd effect. This effect was determined to account for both a maternal lineage and maternal lineage × herd interaction component. The model including this component was tested against the model that fitted maternal lineage. The only significant interaction component (3% of phenotypic variance) was for protein yield for test day one. The fractional component of milk yield for test day one was 2·6%. The test statistic of 4·64 would have been significant at the $\alpha = 0{\cdot}05$ level if three or less independent tests were being carried out. Milk yield in test day one and protein yield in test day one were estimated to have an additive genetic correlation of 0·95 in this study (results not shown). There was also a high correlation between the maternal lineage × herd interaction components of variance for these two traits of 0·96. It is possible to understand how PT could have an effect on first test day milk yield and hence the effect up on protein yield can be explained by the high correlation between the two traits. Such an estimate could however be an artefact of the data structure given that there are many small maternal lineage × herd groups.

The analysis described was designed to provide a relationship structure to estimate maternal lineage variance if present. Contemporary field data were used to avoid the presence of additive maternal genetic effects being incorrectly detected when using a maternal lineage component model. The early part of lactation was also investigated using test day records and no significant maternal lineage variance was estimated for any of the yield traits. A maternal lineage variance component was, however, found for a measure of persistency and this should be considered when persistency is being evaluated.

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