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Lack of Evidence of Cytoplasmic Inheritance in Milk Production Traits of Dairy Cattle

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ABSTRACT

Heritability estimates, by year of freshening of daughter, were obtained from daughter-dam and granddaughter-granddam regressions using 61,482 triply matched first lactations of artificially sired Holstein cows obtained from the Northeast Dairy Records Processing Laboratory. After adjusting for herd-year-season effects, residual effects may include additive and other genetic effects of the animal, maternal effects, cytoplasmic effects, and other environmental effects. Analysis of residuals showed that cytoplasmic effects accounted for no variation in milk and fat yield and fat percent. Weighted yearly heritability estimates and standard errors from daughter on dam regressions were $.35 \pm .01$ for milk yield, $.30 \pm .01$ for milk fat yield, and $.63 \pm .01$ for milk fat percent and from daughter on granddam regressions were $.34 \pm .03$ for milk production, $.28 \pm .03$ for milk fat production, and $.55 \pm .03$ for milk fat percent. The differences between daughter-dam and daughter-granddam heritability estimates, which estimate twice the fraction of variance due to cytoplasmic effects, were negative and not statistically significant for milk fat yield and also were negative but highly significant for milk fat percent.

INTRODUCTION

Bell et al. (2) suggested that cytoplasmic inheritance may influence milk production traits of dairy cattle. They estimated that cytoplasmic effects accounted for 2.0, 1.8, 1.8, and

3.5% of total variation in milk yield, milk fat yield, 3.7% fat-corrected milk yield, and milk fat percent in first lactation records of Holsteins from herds of the North Carolina Department of Agriculture and the North Carolina State University. Huizinga et al. (3) reported that cytoplasmic origin is associated with significant effects on energy yield (protein plus fat) based on analysis of first lactation production of 290 cows tracing in two and three generations to 66 and 39 cytoplasmic lines, respectively. Kennedy (7), however, has shown by simulation that such results may be due to genetic drift. Cytoplasmic effects may be one reason for the consistently higher estimates of heritability from daughter-dam regressions as compared with paternal half-sib correlations for milk production (12, 13).

Cytoplasmic inheritance occurs quite regularly in eukaryotes as well as some prokaryotes. A major problem is that cytoplasmic factors are invisible or unidentifiable, which leads to difficulty in studying them (10).

A potential route for these cytoplasmic effects is in mitochondrial deoxyribonucleic acid (mtDNA), which carries the genetic information essential to mitochondrial function (4). In contrast to the chromosomal genome, which is inherited from both sire and dam, Hutchison et al. (4) and Avise et al. (1) found that the mitochondrial genome is inherited solely from the maternal side.

Mayer et al. (8) determined that resistance to certain diseases may be transmitted by maternal mtDNA. In addition, mitochondria function in the glycolytic pathway and provide energy for the cell via oxidative phosphorylation (5).

Because mtDNA varies between animals of the same species, and mitochondria are involved in lactation (6, 11), it would seem logical that extranuclear variation in mitochondria may play a role in the total variation of milk produc-

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tion. Cytoplasmic inheritance would place emphasis on the maternal line of the pedigree in the selection and production of cows. Cytoplasmic inheritance, in addition to nuclear inheritance, could be important in selection of cows to produce embryos for transfer and splitting.

The objective of this study was to determine if there is evidence that cytoplasmic inheritance affects milk yield, milk fat yield, or milk fat percent in dairy cattle.

MATERIALS AND METHODS

Data were first lactation production records of 63,034 daughter-dam-granddam trios of AI Holsteins from the Northeast Dairy Records Processing Laboratory (DRPL). Analyses were done separately by year of first freshening of the daughter for 1966 to 1982. A dam or granddam could have daughters or granddaughters in more than 1 yr but not more than one in a year. Estimates for years having less than 200 residual df are not reported. A total of 61,482 trios of records were used from 1969 through 1982. Analyses also were initially done by production based on rolling herd averages for a given year (9), but the estimates were highly variable due to small sample sizes and therefore only estimates of overall production are reported.

The statistical model used for the analysis was:

Daughter record = herd-season effect of daughter + effect of sire of daughter + residual effect of daughter;

Dam record = effect corresponding to herd-season of daughter + dummy effect corresponding to sire of daughter + residual effect of dam;

Granddam record = effect corresponding to herd-season of daughter + dummy effect corresponding to sire of daughter + residual effect of granddam.

This model allowed estimation of residual covariances from analyses of sums such as daughter record plus granddam record. Programs developed by Mirande and Van Vleck (9) were used to obtain variances and covariances of residuals. The model for a residual for a record of the y^{th} animal was assumed to be:

$$P_y = g_y + m_x + c_b + e_y$$

where:

P_y = residual for milk yield, milk fat yield, or milk fat percent of animal y ;

g_y = direct additive genetic value of animal y or fraction of the additive genetic value when the sire effect is removed;

m_x = maternal additive genetic value of animal x , the dam of animal y ;

c_b = cytoplasmic effect of ancestral base female b ; and

e_y = other environmental effects on a record of animal y .

This model assumes that the residual of an animal's production record is determined only by the animal's additive genetic effects, its dam's maternal additive genetic effects, some cytoplasmic effect passed on by females from one generation to the next, and other environmental effects. The expected covariances of the residuals between each pair of animals can be obtained from this model. Given the simple pedigree where Z is the foundation female contributing cytoplasm to W , X , and Y :

$$Z \rightarrow W \rightarrow X \rightarrow Y$$

it follows that:

$$\text{Cov}(P_Y, P_X) = .5\sigma_a^2 + .5\sigma_m^2 + \sigma_c^2$$

and:

$$\text{Cov}(P_Y, P_W) = .25\sigma_a^2 + .25\sigma_m^2 + \sigma_c^2$$

where:

σ_a^2 = direct additive genetic variance,
 σ_m^2 = maternal additive genetic variance,
 σ_c^2 = cytoplasmic variance,
 σ_e^2 = other residual variance, and
 $\sigma_p^2 = \sigma_a^2 + \sigma_m^2 + \sigma_c^2 + \sigma_e^2$.

Only additive direct genetic effects and additive maternal genetic effects are assumed. The variance of cytoplasmic effects (minus small fractions of variances due to possible additive by additive direct and maternal genetic effects and higher order genetic effects) is:

$$\sigma_c^2 = 2[\text{Cov}(P_Y, P_W)] - \text{Cov}(P_Y, P_X)$$

Regression coefficients can be used instead of covariances to account for selection. Regression coefficients were calculated from the residual covariances and variances. Using heritability estimates (doubled regression of daughter on dam and quadrupled regression of daughter on granddam), the proportion of variance due to cytoplasmic effects to total variance can be estimated from the difference between $2b_{YX}$, with expected value:

$$[\sigma_a^2 + \sigma_m^2 + 2\sigma_c^2]/\sigma_p^2,$$

and $4b_{YW}$, with expected value:

$$(\sigma_a^2 + \sigma_m^2 + 4\sigma_c^2)/\sigma_p^2.$$

The expected value of the difference, $4b_{YW} - 2b_{YX}$, is $2\sigma_c^2/\sigma_p^2$. The variance of maternal effects and of additive effects drops out of the difference. Although variance due to additive by additive genetic effects and higher order genetic effects may account for some of the total variance in milk production traits, they would enter the difference as negative values due to the signs of the coefficients in the difference. Dominance genetic effects may or may not be important. Dominance variance, however, does not contribute to the covariance between daughter and dam or daughter and granddam.

RESULTS

Weighted heritability estimates for milk yield, milk fat yield, and milk fat percent are in Table 1. Estimates by year are in Table 2.

Heritability estimates over years were weighted by the inverses of the variances of the estimates. The differences between daughter-dam heritability estimates and daughter-granddam heritability estimates are not significant ($P > .05$) for milk yield or milk fat yield. The difference between daughter-dam and daughter-granddam heritability for milk fat percent is also negative but is highly significant ($P < .005$).

Data in Table 1 provide no evidence for cytoplasmic inheritance for the traits studied. The percentages of total variation due to cytoplasmic effects for milk yield, milk fat yield, and milk fat percent are estimated to be negative: -0.35% , -1.33% , and -3.65% .

DISCUSSION AND CONCLUSION

Results indicate that maternally transmitted cellular components do not have any significant effect on production traits in dairy cattle. Estimates of heritability from daughter-dam and daughter-granddam regression are expected to be equal if there are no cytoplasmic effects. The daughter-granddam heritability estimates would have to be greater than the daughter-dam heritability estimate to provide evidence that cytoplasmic inheritance affects milk production traits. As shown in Table 1, the daughter-dam and daughter-granddam heritability estimates for milk yield and milk fat yield are not statistically different. In the case of the heritability estimate for milk fat percent, the daughter-dam estimate is greater than the daughter-granddam estimate. The reason for negative differences between four times the granddaughter-granddam and daughter-dam regressions is not ob-

TABLE 1. Weighted estimates of heritability from daughter-dam (DD) and daughter-granddam (DG) regressions for milk yield, milk fat yield, and milk fat percent. Estimates are pooled over years of daughter freshening from 1969 through 1982.

Trait	Heritability (h^2) estimates				Estimated fraction of variance due to cytoplasmic effects ¹
	DD		DG		
	h^2	SE	h^2	SE	
Milk yield	.3474	.0120	.3405	.0253	-.0035
Milk fat yield	.3046	.0118	.2780	.0250	-.0133
Milk fat percent	.6261	.0111	.5532	.0252	-.0365

¹ Assumes no variation due to additive by additive effects or higher order genetic effects.

TABLE 2. Estimates of heritability and standard errors by year of daughter freshening.¹

Year	df	Milk			Fat			Fat %					
		DD	SE	DG	DD	SE	DG	DD	SE	DG			
		SE	SE	SE	SE	SE	SE	SE	SE	SE			
1969	277	.22	.14	.45	.28	.14	.64	.28	.11	.64	.54	.11	.64
1970	476	.29	.10	.21	.19	.10	.16	.19	.09	.82	.51	.09	.82
1971	735	.25	.08	.21	.17	.08	.16	.16	.06	.44	.55	.06	.44
1972	972	.30	.06	.40	.13	.06	.40	.13	.06	.35	.70	.06	.35
1973	1183	.32	.06	.17	.12	.06	.19	.11	.05	.56	.59	.05	.56
1974	1589	.25	.05	.34	.10	.05	.21	.10	.04	.38	.53	.04	.38
1975	1835	.38	.05	.43	.10	.05	.24	.10	.04	.42	.54	.04	.42
1976	2409	.38	.04	.41	.09	.04	.24	.09	.04	.67	.69	.04	.67
1977	2943	.45	.04	.43	.08	.04	.36	.08	.04	.49	.65	.04	.49
1978	3192	.30	.04	.42	.08	.04	.32	.09	.04	.65	.69	.04	.65
1979	4216	.37	.04	.39	.08	.03	.32	.07	.03	.45	.61	.03	.45
1980	5054	.30	.03	.24	.07	.03	.21	.07	.03	.57	.66	.03	.57
1981	5969	.42	.03	.29	.06	.03	.26	.06	.03	.72	.67	.03	.72
1982	3007	.30	.04	.32	.08	.04	.36	.08	.04	.53	.55	.04	.53

¹ DD = Daughter on dam estimate, DG = daughter on granddam estimate.

vious. Possible reasons include variance due to additive by additive genetic effects, failure to account adequately for management effects as well in granddam records as in dam records, and changes in variance over time. For all three traits, the differences in heritability estimates lead to negative estimates of variance due to cytoplasmic effects corresponding almost exactly to the positive estimates of Bell et al. (2). Kennedy (7) simulated the design of Bell et al. (2) with no cytoplasmic effects. Analysis of the simulated data resulted in estimates of variance due to cytoplasmic origin that were comparable to those of Bell et al. (2). Maternal cytoplasmic inheritance appears to have no important effect on milk yield, milk fat yield, or milk fat percent.

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