

Estimates of repeatability and heritability of productive and reproductive traits in a herd of Jersey cattle*

R.M. Roman¹, C.J. Wilcox² and F.G. Martin³

Abstract

Estimates of the repeatability and heritability of 19 measures of performance in Jersey cows were obtained using an animal model with a relationship matrix and a derivative-free restricted maximum likelihood algorithm. The data consisted of 935 records for 374 cows by 69 sires over the period 1969-1987. The estimates were similar to those obtained by ordinary least squares methods reported for the same data set and in other studies, but had smaller error variances. A likelihood ratio test showed agreement between these heritability estimates and those in the literature. The heritability estimates of milk, fat, protein, lactose-mineral, solids-not-fat, and total solids yields were about 0.25; for the corresponding percentages, and for the protein to fat and solids-not-fat to fat ratios, the estimates were 0.50. Heritability estimates were 0.10 or less for the time from parturition to first breeding and for three measures of somatic cell counts. These estimates of heritability in a dairy cattle population in a subtropical environment were not different from those of populations in temperate climates.

INTRODUCTION

Knowledge of genetic and phenotypic parameters is required for planning efficient breeding programs in animal husbandry. Two of these parameters are heritability and repeatability. The first explains the extent to which observed differences between individuals are associated with additive genetic variance (the variance of the breeding values). With knowledge of this parameter, animal geneticists can determine whether or not a particular trait can be improved by selection, by improvement of management practices, or both. The second is defined as the correlation between measurements made on the same animal or plant over time or space (Lush, 1937).

Unequal numbers of observations per subclass are frequent in animal breeding data. Notable changes in estimation procedures occurred after the introduction of Henderson's methods for variance component estimation (Henderson, 1953), which were based on equating analogous mean squares to their expectations. In recent years, estimation methods have used Henderson's mixed model equations to obtain restricted maximum likelihood (REML) estimates. This is now possible because of the discovery of an algorithm for finding the inverse of the relationship matrix (Henderson, 1975), as well as the development of new algorithms such as the derivative-free restricted maximum likelihood or DFREML (Graser *et al.*, 1987; Meyer, 1993), the availability of computer programs (Meyer, 1993), and advances in computer capabilities.

Many estimates of heritability are available for milk

yield and composition traits in dairy cattle populations. Table I shows several such estimates for Jersey cattle. In general, heritability estimates are higher for composition traits than for yields. Differences in the estimates are expected as a result of differences in populations, in estimation methods, in the mathematical models employed and because of sampling errors.

Dong *et al.* (1988) investigated the effect of the degree of completeness of the relationships in models which considered relationships among animals and found that heritability estimates from REML were lower if the relationships were from sires only, compared with those from more complete pedigrees. They also found that full relationships with REML from ancestors of about two generations resulted in slightly higher estimates than when relationships were from only one generation.

Some researchers have observed that estimates of heritability were higher for first lactation records than for later lactations (Deb *et al.*, 1974; Rothschild and Henderson, 1979; Powell *et al.*, 1981; Meyer, 1984; Sigurdsson, 1993; Albuquerque *et al.*, 1996). However, Butcher and Freeman (1968) reported that even when heritability estimates for the first lactation were higher than for the second lactation, these differences were not statistically significant; however, they suggested that weighting the first and second lactations separately would increase the progress from selection. On the other hand, Tong *et al.* (1979) found that estimates due to sire effects were relatively constant across lactations for yield traits but increased for percentages. Estimates of error variance increased steadily with lacta-

*Florida Agricultural Experiment Station Journal Series No. R-06252. ¹Faculty of Agronomy, University of Zulia, Maracaibo, Venezuela. Departments of ²Dairy and Poultry Sciences, and ³Statistics, University of Florida, Gainesville, FL 32611, USA. Send correspondence to C.J.W. Fax: +1-352-392-5595, E-mail: cjwgenetic@aol.com

Table I - Several heritability estimates for the yield and composition of milk from Jersey cattle.

Trait	Gacula <i>et al.</i> (1968)	Wilcox <i>et al.</i> (1971)	Benya <i>et al.</i> (1976)	Sharma <i>et al.</i> (1983)	Moya <i>et al.</i> (1985)
Milk yield	0.38	0.25	0.26	0.26	0.31
Fat yield	0.31	0.20	0.41	0.27	0.48
Protein yield	0.34	0.21	0.46	0.26	0.36
LM yield	-	0.28	<0	0.23	0.37
SNF yield	0.36	0.25	0.33	0.24	0.36
TS yield	0.33	0.22	0.35	0.24	0.42
Fat %	0.72	0.71	0.52	0.53	0.38
% Protein	0.57	0.56	0.34	0.50	0.47
Lactose-mineral %	-	-	0.64	0.18	0.11
SNF %	0.59	0.63	0.41	0.46	0.42
TS %	0.58	0.69	0.25	0.59	0.47
Protein/fat ratio	-	0.52	0.24	0.28	0.31
SNF/fat ratio	-	0.72	0.50	0.39	0.31

LM = Lactose-mineral, SNF = solids-not-fat, and TS = total solid yields.

tion number for yields but did not change appreciably for percentages.

Table II shows several repeatability estimates from the literature for milk, fat and protein yields and fat and protein percentages, which perhaps are the traits most extensively studied in dairy cattle. As a whole, repeatability estimates are higher than heritability estimates because the former include variation attributable to total genetic differences as well as permanent environmental sources of variation. Evidence of variable relationships between pairs of lactations was reported by Butcher and Freeman (1968), based on the milk and fat yields of two separate data sets. These authors reported that the repeatability of consecutive lactations increased gradually as the animals got older whereas that of nonconsecutive lactations decreased gradually as the lactations became more separated in time.

Some researchers have argued that the assumptions made for estimating repeatabilities are not realistic and have therefore analyzed milk and fat yields of different lactations as separate traits in order to account for the bias in

later lactations due to selection, and for the bias due to violation of the assumption that milk yield is determined by the same genes in each lactation. High genetic correlations between consecutive lactations were reported by Meyer (1984, 1985). However, Albuquerque *et al.* (1996) provided evidence that genetic correlations differed from 1.0 even though they were high. Nevertheless, estimates of the phenotypic correlations were in the range normally accepted for these traits (Meyer, 1984, 1985; Sigurdsson, 1993; Albuquerque *et al.*, 1996).

The relative importance of environmental differences is considerably higher for reproductive traits than for milk yield and composition (Raheja *et al.*, 1989; Weller, 1989; Campos *et al.*, 1994). This means that even with selection the changes in these traits would be expected to be nil (or small) and that efforts should therefore be devoted to improving management practices.

Based on measures of somatic cells (SC) in milk, most results suggest that the amount of additive genetic variance is small. Thus, changes resulting from selection could be obtained only over a long period of time. Heritability estimates of somatic cell scores (SCS) are generally less than 0.15 (Schutz *et al.*, 1990; Detilleux *et al.*, 1995). However, the latter study found an estimate as high as 0.50 in second lactation cows. Another measure of cell count frequently used is somatic cell counts (SCC) for which heritability estimates are considerably lower than for SCS (Monardes *et al.*, 1983; Coffey *et al.*, 1985; Emanuelson *et al.*, 1988). Genetic evaluations based on either of these measures have been proposed in the USA and Canada (Boettcher *et al.*, 1992; Shook and Schutz, 1994; Zhang *et al.*, 1994).

The objectives of this study were to estimate the heritability and repeatability for milk yield and composition traits, for the time from parturition to first breeding period, and for somatic cells, in an experimental herd of Jersey cattle using animal models with a DFREML algorithm.

Table II - Repeatability estimates for milk, fat and protein yields and for fat and protein percentages in dairy cattle.

Trait					Reference
M	F	P	F %	P %	
0.53	0.56	-	0.75	-	Wilcox (1962)
0.47	0.44	-	-	-	Bereskin and Freeman (1965)
0.38	0.31	0.34	0.72	0.57	Gacula <i>et al.</i> (1968)
0.39	0.38	0.31	0.67	0.61	Moya (1977)
0.47	0.44	-	-	-	Oltenacu <i>et al.</i> (1979)
0.32	0.24	0.28	0.68	0.63	Sharma <i>et al.</i> (1983)
0.40	0.34	0.40	0.37	0.40	Sigurdsson (1993)

M = Milk, F = fat, and P = protein yields. F% and P%, fat and protein percentages, respectively.

MATERIAL AND METHODS

Experimental material

The data were from an experimental herd of Jersey cattle maintained at the Dairy Research Unit of the University of Florida (UF). This herd was founded in 1901, but for this analysis only records pertaining to a selection project initiated in July, 1968 (Wilcox and Head, 1969) were included. The project involved a selection group for which the only criteria for selection was milk yield, and a random mating control group. In the analyses only records from the years 1969 through 1987 were included. There were 374 first lactation records and a combined data set of 935 records consisting of the first and succeeding lactations.

Data sets were constructed from 10,076 monthly totals recorded on a daily basis for milk (M), and from monthly tests for fat (F) and protein (P). The lactose-minerals (LM), solids-not-fat (SNF), and total solids (TS) yields were calculated from measurements of fat percent and specific gravity and the corresponding percentages determined for F, P, L, SNF and TS. In addition, the ratios P/F and SNF/F were included as dependent variables. Details of the chemical analyses have been given by Benya *et al.* (1976), Sharma *et al.* (1983), and Moya *et al.* (1985). Three measures of somatic cells in milk were examined: the arithmetic average of the SCS taken during lactation, the arithmetic average of the SCC, and the SCS weighed for monthly milk yield (WSCS). In addition, the time from parturition to first breeding (PAFBR) was studied. The data sets were edited according to the guidelines published by the S-49 Technical Project Committee (Wilcox *et al.*, 1972). Records longer than 305 days were truncated at 305 days and those less than 90 days were excluded.

Statistical analyses

Univariate analyses to estimate additive genetic as well as permanent and temporary environmental variance components were done using an animal model and the DFREML program developed by Meyer (1993).

Two basic models were fitted to the data. Model I was used for measurements on first parity cows. This model included the fixed effects of selection group, year (continuous up to a third degree polynomial) and month of calving, the interaction of selection group by year, a second degree polynomial for the duration of lactation and the linear covariate for age at parturition. The random portion of the model represented additive genetic effects attributable to differences among individuals. The model is represented in matrix form as: $y = Xb + Zu + e$, where y is the data vector with size 374 (the number of animals), X is a matrix of 0's and 1's relating records and fixed effects, and Z is an incidence matrix relating records and random effects. The Z matrix was augmented with columns of zeros for ani-

mals without records. The vectors b and u represent unknown vectors of the fixed and random effects.

The distributional properties of the terms in the above model were assumed to be

$$E[y] = [Xb], \text{ and } V \begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix}$$

where E and V represent the expectation and variance operators, and y , X and b are defined as before. A is the numerator relationship matrix among all animals in the pedigree, I is an identity matrix, and σ_a^2 and σ_e^2 are the additive genetic and environmental variances, respectively.

Model II was used for the analyses including all records. This model was a single trait, simple repeatability animal model and was similar to model I but with the effects of age fitted to the cubic order. A second random effect representing permanent effects associated with animals having repeated records was included. This effect, assumed to be uncorrelated with additive genetic effects, allowed for the partitioning of environmental variance into permanent and temporary components.

The model represented in matrix form is: $y = Xb + Z_1u + Z_2p + e$, where the terms y , X , Z , u and b are defined as before, Z_1 is a matrix associating permanent environmental effects to y with order $N \times q_p$, where N is the number of records and q_p is the number of animals with records; p is a vector representing the unknown permanent effects.

The distributional properties were assumed to be as follows:

$$E[y] = [Xb], \text{ and } V \begin{bmatrix} p \\ u \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 \\ 0 & I_c\sigma_p^2 & 0 \\ 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

A full relationship matrix was included and was found by including connections between animals back to 1955 based on the pedigree files of the herd. This was possible because of the long history of the UF Jersey herd (Wilcox and Head, 1969). Source programs of DFREML version 2.1, initially written to work in UNIX environments, were adapted to run on an MS DOS-based PC. The programs were compiled with a Lahey's Extended Memory Fortran Compiler.

After running the data preparation program (DFPREP), the first estimation step was carried out using the simplex method with the convergence criterion (the variance of log likelihoods) set to 1×10^{-5} ; a maximum of 500 iterations was run. This step was followed by a restart by lowering the convergence criteria to 1×10^{-6} , and finally a run to check for convergence to a global maximum was performed with the convergence criteria lowered to 1×10^{-8} , and the step size set to 1%. Likelihood ratio tests (LRT) were performed to test two hypotheses of interest: the first was to test heritability estimates against 0 and the

Table III - Estimates of additive genetic and environmental variance components, and heritability estimates (with their approximate standard errors) for first parity Jerseys.

Trait	Estimate			SE
	$\hat{\sigma}_A^2$	$\hat{\sigma}_E^2$	h^2	
M	71500.14	204585.61	0.26	0.11
F	182.50	402.67	0.31	0.10
P	61.30	310.05	0.17	0.09
LM	314.17	527.85	0.37	0.12
SNF	588.36	1584.49	0.27	0.11
TS	987.85	3262.45	0.23	0.10
F%	0.1296	0.1167	0.53	0.13
P%	0.0375	0.0334	0.53	0.12
LM%	0.0155	0.0322	0.33	0.11
SNF%	0.0179	0.0190	0.49	0.13
TS%	0.0989	0.0707	0.58	0.12
P/F ratio	0.0034	0.0048	0.42	0.13
SNF/F ratio	0.0206	0.0186	0.53	0.12
CL%	0.000017	0.000103	0.14	0.09
AC%	0.00014	0.00028	0.33	0.09

$\hat{\sigma}_A^2$ = Additive genetic variance component. $\hat{\sigma}_E^2$ = environmental variance component. h^2 = heritability estimate. M = milk, F = fat, P = protein, LM = lactose-mineral, SNF = solids-not-fat and TS = total solid yields. AC% and CL%, percentage acidity and chloride, respectively.

other to test whether each parameter was different from the normally accepted values in dairy cattle populations. For this purpose, θ , representing heritability, was set to 0.25 for yields, 0.50 for percentages and ratios (Wilcox, 1992), and 0.10 for measures of SC and PAFBR (Boettcher *et al.*, 1992). The sampling distribution of minus twice the difference between logs of the two likelihoods has a χ^2 distribution with degrees of freedom equal of the number of parameters being tested (Johnson and Wichern, 1992; Meyer, 1993).

RESULTS AND DISCUSSION

Estimates of additive genetic and environmental variances for M in first lactation cows were obtained for a grid of values within the permissible values for heritability and for each of the three estimation steps of the DFREML program (Meyer, 1993). Different starting values of h^2 between 0.05 and 0.95 had no effect on final estimates.

Additive genetic and environmental variance estimates for milk yield and composition along with their respective standard errors for first parity cows are given in Table III. Heritabilities ranged from 0.17 to 0.37 for yield traits. These estimates were only slightly higher than previous reports based on comparable data sets (Gaunt, 1973; Benya *et al.*, 1976), the former being for this same herd without using the relationship matrix. However, in terms of overall precision, the estimates with the animal model had smaller standard errors. Dong *et al.* (1988) found that REML heritability estimates were higher as the degree of completeness in the relationship used increased. In this study, ancestors were traced back to 1955 so it was expected that estimates would be higher than

those from other estimation methods. Nevertheless, our estimates were less than estimates for first lactations with animal models in other studies (Dong *et al.*, 1988; Misztal *et al.*, 1992; Campos *et al.*, 1994). This discrepancy may reflect variations in the models, breeds, populations, and sampling errors. The standard errors for heritability data ranged from 0.09 to 0.13 and reflected the small size of the data set.

Heritability estimates for composition traits ranged from 0.33 to 0.58, with most above 0.40, which agrees with the pattern normally found for these traits (Gaunt, 1973; Jairath *et al.*, 1995). This finding suggests that the influences of environmental sources of variation on milk composition traits are relatively less than on yields.

Table IV summarizes the results of the LRT for both hypotheses. In the first case, the results supported the null hypothesis only for CL%; hence, all parameter estimates were considered different from zero ($P < 0.01$). For the second hypothesis, the likelihood ratio test for most traits did not provide evidence that these animal model estimates were different from the average of estimates of other studies which used different estimation methods and assumptions. The parameter estimates can be used as estimated, or, if necessary, a constant can be added to them to perform the LRT.

The estimates of the additive genetic, permanent environmental, and temporary environmental variances for milk yield and composition traits from the simple repeatability animal model are shown in Table V. Estimates of the additive genetic variances for yield traits were dramatically smaller than the converged estimates from the simple animal model applied to first parity cows. As a result, heritability estimates for yield traits with repeated records were less. Most studies suggest that heritability estimates for first lactation cows are higher than estimates for subsequent lactations (Deb *et al.*, 1974; Rothschild and Henderson, 1979; Meyer, 1984). However, some authors have found only slight changes in the heritabilities of first, second and third lactations (Butcher and Freeman, 1968; Sölkner, 1989). Conversely, changes in the additive genetic variances for the percentage traits for all records were small compared to those of the simple animal model. Apparently, Jersey cows are able to systematically maintain milk composition throughout their lives.

The differences in yield traits between animals attributable to permanent environmental variance ranged from 17 to 25% of the total variability; fat and protein were the traits most affected. For the percentage traits, non-genetic differences contributing to the resemblance among successive records for the same animal were small compared to the relative importance of additive genetic differences. The exception was LM% for which this source of variation accounted for 21% of the total variance. For the remaining traits, permanent environmental effects accounted for 5-13% of the total variability with the parameter estimates frequently close to their standard errors.

Table IV - Likelihood ratio tests for testing the difference of heritability estimates from zero or average literature values (θ) for traits measured in the first lactation of Jersey cows.

Trait	Likelihood function		Likelihood ratio test		
	$\hat{h}^2 = 0$	$\hat{h}^2 = \theta$	$L(\Omega_0)$	$-2 [L(\Omega)] - L(\Omega_0)$	
	$L(\Omega_0)$	$L(\Omega_0)$		$\hat{h}^2 = 0$	$\hat{h}^2 = \theta$
M	-2674.6676	-2669.9088	-2669.9062	9.52 **	0.01
F	-1595.3950	-1584.0953	-1583.9046	16.98**	1.46
P	-1511.7226	-1510.3736	-1509.9830	239.63**	0.78
LM	-1653.6049	-1645.3816	-1664.7815	17.65**	1.20
SNF	-1822.1307	-1816.7405	-1816.7213	10.82**	0.04
TS	-1940.7810	-1936.4731	-1936.4586	8.64**	0.03
F%	-216.2642	-203.1491	-2013.1282	26.27**	1.04
P%	-0.4597	16.2405	16.2693	33.46**	0.06
LM%	66.1584	72.5991	73.1212	15.13**	2.24
SNF%	117.0936	128.0390	128.0453	21.90**	0.01
TS%	-150.8086	-133.5088	-133.2818	35.05**	0.45
P/F ratio	381.0301	387.7226	387.9746	13.89**	0.42
SNF/F ratio	107.8366	120.6162	120.6375	25.60**	0.04
CL%	1117.3553	1113.7126	1119.2046	3.70 †	10.98**
AC%	893.7989	904.7792	906.2740	24.95**	2.99

$L(\Omega_0)$ = Likelihood function evaluated for the null hypothesis; average literature values were 0.25 for yields and 0.50 for percentages and ratios. For abbreviations see legend to Table III. Yields are in kilograms. ** ($P < 0.01$). † ($P < 0.10$)

Table V - Estimates of additive genetic, permanent and temporary environmental variance components, heritabilities, repeatabilities and standard errors from a simple repeatability animal model for Jersey cattle.

Trait	Variance component			Parameter estimate				
	$\hat{\sigma}_A^2$	$\hat{\sigma}_{EP}^2$	$\hat{\sigma}_{ET}^2$	\hat{h}^2	SE	\hat{p}^2	SE	r
M	44282.	38986.	158323.	0.18	0.06	0.16	0.06	0.34
F	69.24	103.79	317.25	0.14	0.07	0.25	0.07	0.35
P	28.92	58.34	209.69	0.10	0.06	0.20	0.06	0.29
LM	141.89	134.29	509.55	0.18	0.06	0.17	0.06	0.35
SNF	263.66	344.58	1254.86	0.14	0.06	0.18	0.06	0.33
TS	442.03	673.55	2417.53	0.13	0.05	0.19	0.06	0.32
F%	0.1330	0.0004	0.0906	0.59	0.08	0	-	0.60
P%	0.0289	0.0074	0.0296	0.46	0.08	0.12	0.07	0.55
LM%	0.0117	0.0174	0.0529	0.14	0.07	0.21	0.07	0.35
SNF%	0.0180	0.0077	0.0330	0.31	0.08	0.13	0.08	0.44
TS%	0.0818	0.0135	0.0675	0.50	0.08	0.08	0.07	0.59
P/F ratio	0.0029	0.0004	0.0038	0.41	0.10	0.06	0.08	0.46
SNF/F ratio	0.0186	0.0018	0.0179	0.49	0.08	0.05	0.07	0.53
CL%	0.000066	0.00012	0.000226	0.14	0.08	0.19	0.09	0.26
AC%	0.000017	0.000023	0.00078	0.22	0.06	0.04	0.05	0.34

$\hat{\sigma}_A^2$ = Additive genetic variance component. $\hat{\sigma}_{EP}^2$ and $\hat{\sigma}_{ET}^2$, permanent and temporary environmental variance components, respectively; \hat{h}^2 = heritability estimate; \hat{p}^2 = permanent environmental variance and r = repeatability. For other abbreviations see legend to Table III.

One of the assumptions behind the use of repeatability models in the present study is that all lactations are genetically the same trait. This implies that the same set of genes exerts a common influence on the phenotypic expression of the first and later lactations. This assumption is supported by observations that the genetic correlations among records are close to unity (Tong *et al.*, 1979; Meyer, 1984, 1985). However, some authors have claimed that each lactation should be considered as

a separate trait because genetically they may be different entities. For this reason, they suggest the use of multivariate analysis (Alburqueque *et al.*, 1996).

Repeatabilities for yields ranged from 0.29 to 0.35. These estimates were either less than (Wilcox *et al.*, 1962; Bereskin and Freeman, 1965; Susuki and Van Vleck, 1994) or comparable to (Gacula *et al.*, 1968; Moya, 1977; Oltenacu *et al.*, 1979) other estimates. As with first lactation records, composition traits tended to have higher es-

Table VI - Estimates of additive genetic and environmental variance components and heritability for time from parturition to first breeding and for measures of somatic cells for first parity Jerseys and likelihood ratio tests of differences of heritability estimates from zero and from average estimates from previous studies.

Trait	Variance component		Likelihood ratio test			
	$\hat{\sigma}_A^2$	$\hat{\sigma}_E^2$	$-2 [L(\Omega)] - L(\Omega_0)$			
			h^2	SE	$h^2=0$	$h^2=\theta$
PAFBR	135.35	504.82	0.21	0.11	5.85	1.19
WSCS	0.2370	0.4884	0.33	0.13	9.64**	3.85*
SCS	0.1730	0.4163	0.29	0.12	8.39**	2.94
SCC	4897.65	43240.67	0.10	0.11	0.14	0

$\hat{\sigma}_A^2$ = Additive genetic variance, and $\hat{\sigma}_E^2$ = environmental variance; average estimates of heritability from previous studies were 0.16 from PAFBR, WSCS, SCS and SCC. PAFBR = Parturition to first breeding period; SCS = somatic cell score; SCC = somatic cell count; WSCS = weighted somatic cell score. ** P < 0.01.

estimates within the range normally accepted for dairy cattle (Gacula *et al.*, 1968; Moya, 1977; Wilcox *et al.*, 1962). In addition, the relative importance of permanent environmental variances for these traits was small and frequently negligible.

Table VI summarizes estimates of the variance components and heritabilities (and standard errors), as well as likelihood ratio tests for the time from parturition to first breeding and for measures of SC for first parity cows. Although the heritability estimates agreed with previous results, the SCC was not significantly different from zero (Coffey *et al.*, 1985; Monardes *et al.*, 1983; Emanuelson *et al.*, 1988). Both estimates of measures of SCS were significantly different from zero (P < 0.01). However, the likelihood test suggested that the estimate for SCS was similar to 0.10; for WSCS, the null hypothesis was rejected at the 5% level. The results of the analyses of all records are in Table VII. The estimates for SC suggest that little genetic progress can be made by selection for these traits. The es-

timates for SCS were only slightly higher than those for SCC. The additive genetic variances and permanent environmental variances were similar in magnitude. In addition, the correlation between records for the same animal was low. For this reason, the use of multiple records may be of interest for these traits. With regard to PAFBR, all analyses confirmed the importance of environmental differences in determining the phenotypic values of this trait.

CONCLUSIONS

Estimates of heritability with an animal model for yield traits of first lactation records were in the range normally accepted for dairy cattle populations in temperate climates. Heritability estimates for first parity composition traits were higher than those for yields. Variance due to permanent environmental effects was an important source of variation. Heritability estimates for yields using repeatability animal models were lower than those for first lactation cows but agreed with least squares estimates. Composition traits tended to be less affected by permanent or temporal environmental fluctuations. Additive genetic variances for the time from parturition to first breeding and for measures of somatic cells were low compared to the environmental variance. Thus, the possibility of changing these traits through selection is small.

RESUMO

Estimativas da repetibilidade e da herdabilidade de 19 medidas de desempenho de vacas da raça Jersey foram obtidas usando-se um modelo animal com uma matriz de relação e um algoritmo de máxima verossimilhança. Os dados consistiram em 935 registros de 374 vacas e 69 touros no período de 1969 a 1987. As estimativas foram semelhantes às obtidas pelo método de quadrados mínimos relatadas para o mesmo conjunto de dados e em outros estudos, mas tiveram menores erros de variação. Um teste de verossimilhança mostrou concordância entre estas estimativas de herdabilidade e as da literatura. As estimativas de herdabilidade de produção de leite, gordura,

Table VII - Estimates of additive genetic, permanent and temporary environmental variance components, heritabilities (h^2), repeatabilities (r) and standard errors (SE) from a simple repeatability animal model for the time from parturition to first breeding and for somatic cell measurements of Jersey cows.

Trait	Variance component			Estimate				
	$\hat{\sigma}_A^2$	$\hat{\sigma}_{EP}^2$	$\hat{\sigma}_{ET}^2$	h^2	SE	p^2	SE	r
PAFBR	23.43	30.93	603.40	0.04	0.04	0.05	0.04	0.08
WSCS	0.0811	0.0520	0.7532	0.09	0.06	0.06	0.06	0.15
SCS	0.0509	0.0533	0.6047	0.07	0.06	0.08	0.06	0.15
SCC	8662.34	6281.77	101577.77	0.07	0.04	0.05	0.04	0.13

$\hat{\sigma}_A^2$ = Additive genetic variance. $\hat{\sigma}_{EP}^2$ and $\hat{\sigma}_{ET}^2$ permanent and temporary environmental effects, respectively; p^2 = permanent environmental variance and r = repeatability. PAFBR = Parturition to first breeding period; SCS = somatic cell score; SCC = somatic cell count; WSCS = weighted somatic cell score.

proteína, lactose-mineral, sólidos não-gordura e sólidos totais foram de cerca de 0,25; para as porcentagens correspondentes e para as relações proteína/gordura e sólidos não-gordura/gordura, as estimativas foram de 0,50. As estimativas de herdabilidade foram 0,10 ou menos para o período desde o parto até a primeira cria e para três medidas de contagem de células somáticas. Estas estimativas de herdabilidade em uma população de gado leiteiro num ambiente subtropical não foram diferentes das de populações em clima temperado.

REFERENCES

- Albuquerque, L.G., Keown, J.F. and Van Vleck, L.D.** (1996). Genetic parameters of milk, fat and protein yields in the first three lactations, using an animal model and restricted maximum likelihood. *Braz. J. Genet.* 19: 79-86.
- Benya, E.G., Wilcox, C.J., Martin, F.G., Adkinson, R.W., Krienke, W.A. and Franke, D.E.** (1976). Parametros geneticos para peso corporal, composicion y produccion de leche de un rebano localizado en Florida. *Asoc. Latinoam. Prod. Anim. Men.* 11: 163-169.
- Bereskin, B. and Freeman, A.E.** (1965). Genetic and environmental factors in dairy sire evaluation. I. Effects of herds, months, and year-seasons on variance among lactation records; repeatability and heritability. *J. Dairy Sci.* 48: 347-351.
- Boettcher, P.J., Hansen, L.B., VanRaden, P.M. and Ernst, C.A.** (1992). Genetic evaluation of Holstein bulls for somatic cells in milk of daughters. *J. Dairy Sci.* 75: 1127-1137.
- Butcher, D.F. and Freeman, A.E.** (1968). Heritabilities and repeatabilities of milk and milk fat production by lactations. *J. Dairy Sci.* 51: 1387-1391.
- Campos, M.S., Wilcox, C.J., Becerril, C.M. and Diz, A.** (1994). Genetic parameters for yield and reproductive traits of Holstein and Jersey cattle in Florida. *J. Dairy Sci.* 77: 867-873.
- Coffey, E.M., Vinson, W.E. and Pearson, R.E.** (1985). Heritabilities for lactation average of somatic cell counts in first, second, and third or later parities. *J. Dairy Sci.* 68: 3360-3362.
- Deb, R.N., Gobble, J.L., Hargrove, G.L. and Thoele, H.W.** (1974). Lactation records of Jersey cattle in Pennsylvania: season of calving, phenotypic trend, heritability, and genetic trend. *J. Dairy Sci.* 57: 884-888.
- Detilleux, J.C., Kehrl Jr., M.E., Freeman, A.E., Fox, L.K. and Kelley, D.H.** (1995). Mastitis of periparturient Holstein cattle: A phenotypic and genetic study. *J. Dairy Sci.* 78: 2285-2293.
- Dong, M.C., Van Vleck, L.D. and Wiggans, G.R.** (1988). Effect of relationships on estimation of variance components with an animal model and restricted maximum likelihood. *J. Dairy Sci.* 71: 3047-3052.
- Emanuelson, U., Danell, B. and Philipsson, J.** (1988). Genetic parameters for clinical mastitis, somatic cell counts, and milk production estimated by multiple-trait restricted maximum likelihood. *J. Dairy Sci.* 71: 467-476.
- Gacula Jr., M.C., Gaunt, S.N. and Damon Jr., R.A.** (1968). Genetic and environmental parameters of milk constituents for five breeds. II. Some genetic parameters. *J. Dairy Sci.* 51: 438-444.
- Gaunt, S.N.** (1973). Genetic and environmental changes possible in milk composition. *J. Dairy Sci.* 56: 270-278.
- Graser, H.U., Smith, S.P. and Tier, B.** (1987). A derivative-free approach for estimating variance components in animal models by restricted maximum likelihood. *J. Anim. Sci.* 64: 1362-1370.
- Henderson, C.R.** (1953). Estimation of variance and covariance components. *Biometrics* 9: 226-252.
- Henderson, C.R.** (1975). Use of all relatives in intraherd prediction of breeding values and producing abilities. *J. Dairy Sci.* 58: 1910-1916.
- Jairath, L.K., Hayes, J.F. and Cue, R.I.** (1995). Correlations between first lactation and lifetime performance traits of Canadian Holsteins. *J. Dairy Sci.* 78: 438-448.
- Johnson, R.A. and Wichern, D.W.** (1992). *Applied Multivariate Statistical Analysis*. 3rd edn. Prentice Hall, Englewood Cliffs.
- Lush, J.L.** (1937). *Animal Breeding Plans*. Collegiate Press, Inc., Ames.
- Meyer, K.** (1984). Estimates of genetic parameters for milk and fat yield for the first three lactations in British Friesian cows. *Anim. Prod.* 38: 313-332.
- Meyer, K.** (1985). Genetic parameters for dairy production of Australian black and white cows. *Livest. Prod. Sci.* 12: 205-219.
- Meyer, K.** (1993). *DFREML. User notes. Version 2.1. Animal Genetics and Breeding Unit*. Univ. New England, Armidate, Australia (Mimeo).
- Misztal, I., Lawlor, T.J., Short, T.H. and Van Raden, P.M.** (1992). Multiple-trait estimation of variance components of yield and type traits using an animal model. *J. Dairy Sci.* 75: 544-551.
- Monardes, H.G., Kennedy, B.W. and Moxley, J.E.** (1983). Heritabilities of measures of somatic cell count per lactation. *J. Dairy Sci.* 66: 1707-1713.
- Moya, J.** (1977). Maximum likelihood estimation of genetic trends in milk yield and composition in the Florida experiment station dairy herd. Master's thesis, University of Florida, Gainesville, FL, USA.
- Moya, J., Wilcox, C.J., Bachman, K.C. and Martin, F.G.** (1985). Genetic trends in milk yield and composition in a subtropical dairy herd. *Rev. Bras. Genét.* VIII: 509-521.
- Oltenacu, P.A., Olson, C.C. and Young, C.W.** (1979). Repeatability of milk and fat yield for cows with changed environments. *J. Dairy Sci.* 62: 310-315.
- Powell, R.L., Norman, H.D. and Elliot, R.M.** (1981). Different lactations for estimating genetic merit of dairy cows. *J. Dairy Sci.* 64: 321-330.
- Raheja, K.L., Burnside, E.B. and Schaeffer, L.R.** (1989). Relationships between fertility and production in Holstein dairy cattle in different lactations. *J. Dairy Sci.* 72: 2670-2678.
- Rothschild, M.F. and Henderson, C.R.** (1979). Maximum likelihood estimates of parameters of first and second lactation milk records. *J. Dairy Sci.* 62: 990-995.
- Schutz, M.M., Hansen, L.B., Steuernagel, G.R., Reneau, J.K. and Kuck, A.L.** (1990). Genetic parameters for somatic cells, protein and fat in milk of Holsteins. *J. Dairy Sci.* 73: 494-502.
- Sharma, A.K., Rodriguez, L.A., Mekonnen, G., Wilcox, C.J., Bachman, K.C. and Collier, R.J.** (1983). Climatological and genetic effects on milk composition and yield. *J. Dairy Sci.* 66: 119-126.
- Shook, G.E. and Schutz, M.M.** (1994). Selection on somatic cell score to improve resistance to mastitis in the United States. *J. Dairy Sci.* 77: 648-658.
- Sigurdsson, A.** (1993). Estimation of genetic and phenotypic parameters for production traits of Icelandic dairy cattle. *Acta Agric. Scand.* 43: 81-86.
- Sölkner, J.** (1989). Genetic relationships between level of production in different lactations, rate of maturity and longevity in a dual purpose cattle production. *Livest. Prod. Sci.* 23: 33-45.
- Susuki, M. and Van Vleck, L.D.** (1994). Heritability and repeatability for milk production traits of Japanese Holsteins from an animal model. *J. Dairy Sci.* 77: 583-588.
- Tong, A.K.W., Kennedy, B.W. and Moxley, J.E.** (1979). Heritabilities and genetic correlations for the first three lactations from records subject to culling. *J. Dairy Sci.* 62: 1784-1790.
- Weller, J.L.** (1989). Genetic analysis of fertility traits in Israeli dairy cattle. *J. Dairy Sci.* 72: 2644-2650.
- Wilcox, C.J.** (1992). Genetics: basic concepts. In: *Large Dairy Herd Management* (Van Horn, H.H. and Wilcox, C.J., eds.). American Dairy Science Association, Champaign.
- Wilcox, C.J. and Head, H.H.** (1969). Selection for milk yield in Jerseys. Annual report. In: *Genetic Methods of Improving Dairy Cattle for the South*. S-49 Project. Minutes of the Annual Meeting of the Southern Regional Tech. Comm. Virginia Polytechnic Institute, Blacksburg, VA, USA, p. 34.
- Wilcox, C.J., Pfau, K.O., Mather, R.E., Gabriel, R.F. and Bartlett, J.W.** (1962). Phenotypic, genetic, and environmental relationships of milk production and type ratings of Holstein cows. *J. Dairy Sci.* 45: 223-232.
- Wilcox, C.J., Miller, L.H., White, J.M. and Rakes, J.M.** (1972). Methods and procedures. In: *Genetic Methods of Improving Dairy Cattle for the South*. Minutes of the Annual Meeting of the Southern Regional Tech. Comm. Agricultural Library, Betsville, MD, USA, pp. 7-10.
- Zhang, W.C., Dekkers, J.C.M., Banos, G. and Burnside, E.B.** (1994). Adjustment factors and genetic evaluation for somatic cell score and relationships with other traits of Canadian Holsteins. *J. Dairy Sci.* 77: 659-665.

