

Heterogeneity of (Co)Variance Components for Jersey Type Traits

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ABSTRACT

Heterogeneity of (co)variances for US Jersey linear and final scores was investigated with data from February 2000 USDA genetic evaluations. (Co)variances were estimated from datasets defined by parity, contemporary group size, and mean final score. First-appraisal scores during first or second parity from records that included all traits were studied. Contemporary groups within each parity were classified by size, based on number of cows in a given parity for that herd appraisal date: 5 to 15, 30 to 55, and ≥ 100 . Groups were further classified as high (above parity-size class mean) or low (below parity-size class mean) for final score. The parity, group size, and final score classifications resulted in 12 datasets, which contained appraisal information from 8111 to 23,692 cows. (Co)variance components were estimated using expectation-maximization REML and canonical transformation. Across all traits and independent of herd size, phenotypic variances tended to be higher for low-scoring contemporary groups and during second parity. Similar or larger heterogeneities existed for genetic variances, but those heterogeneities were not as consistent across trait and contemporary group size class. Associated mean relative differences were defined as the mean of the ratios of the Frobenius norms of the differences between a given matrix and an overall mean matrix to the Frobenius norm of the mean matrix. For variance matrices, covariances were ignored. Mean differences for phenotypic variances were 18% during first and 20% during second parity, and for genetic variances were 26 and 31% for first and second parity, respectively. The different patterns for genetic and phenotypic variances led to significant differences in estimated heritabilities. Mean relative differences for covariances were found to be similarly heterogeneous: 20% for first parity and 23% for second parity, for phenotypic covariance, and 32 and 36% for first and second parities, respectively, for genetic covariance. This heterogeneity resulted more from variance

heterogeneity than from differences among associated correlation matrices (phenotypic: 11% first and 12% second parity; genetic: 20% first and 26% second parity).

(Key words: genetic evaluation, heterogeneous variance, variance estimation)

INTRODUCTION

A single-trait repeatability sire model was used to calculate genetic evaluations for type traits of Jerseys until August 1997. Recent advances have included multitrait analysis and use of animal models ([Gengler et al., 1997a, 1997b, 1999](#)). The computing requirements for multitrait analysis can be reduced greatly with canonical transformation ([Jensen and Mao, 1988](#)), which transforms the initial correlated traits to uncorrelated canonical traits. Since February 1998, this method has been applied to calculate type evaluations for US Jerseys ([Gengler et al., 1999](#)). Multiple diagonalization, which is a generalization of canonical transformation to several random effects rather than only additive genetic effects ([Misztal et al., 1995](#)); an expectation-maximization algorithm that permits the use of this approach even if observations for some traits are missing for some cows ([Ducrocq and Besbes, 1993](#)); and accounting for inbreeding in the construction of the additive genetic relationship matrix ([VanRaden, 1992](#)) are also included.

Although a common assumption of genetic evaluation models is homogeneity of (co)variances, this assumption may be incorrect across time or herds. This has been shown for conformation traits by several authors (e.g., [Koots et al., 1994](#); [Smothers et al., 1993](#); [Sorensen and Kennedy, 1985](#); [Weigel and Lawlor, 1994](#)). A direct consequence of heterogeneous (co)variances is that rankings of animals could be biased. Data can be adjusted to stabilize (co)variances by contemporary group before evaluation, (e.g., [Wiggans and VanRaden, 1991](#)), and this strategy is used for some yield and type evaluations (e.g., [Koots et al., 1994](#); [Weigel and Lawlor, 1994](#)). [Meuwissen et al. \(1996\)](#) have included stabilization of heterogeneous (co)variances simultaneously with the computation of the genetic evaluations. The objective of this study was to investigate heterogeneity of (co)variances for US Jersey linear and final scores due to parity, contemporary group size, and mean final scores.

MATERIAL AND METHODS

Data

Scoring is mandatory during first and second parity for the Jersey breed. At this time, there are 15 linear type traits (stature, strength, dairy form, foot angle, rear legs-side view, body depth, rump angle, thurl width, fore udder attachment, rear udder height, rear udder width, udder depth, udder cleft, front teat placement, and teat length). Scoring for body depth and teat length began during the late 1980s; therefore, many type records prior to 1990 were missing observations for those traits. Linear type traits are scored from 1 to 50. Final scores are computed from the linear type scores.

Data included final scores and scores for the 15 linear type traits, extracted from data used for February 2000 USDA genetic evaluations. Only first-appraisal scores from first or second parity that had scores for all traits were included. The few second scores in a given lactation were eliminated. Data were adjusted before analysis for effect of age at appraisal ([Gengler et al.,](#)

1999). Age groups were defined as <25 mo, 25 to 26 mo, 27 to 28 mo, ..., 37 to 38 mo; for first parity and as <41 mo, 41 to 42 mo, 43 to 44 mo, ..., 53 to 54 mo for second parity. No adjustments were made to mean or standard deviation to standardize for appraiser. The preadjustment was the same as in the routine genetic evaluations, and should only influence the mean, not the variances.

Contemporary groups were defined by parity and herd appraisal date. Within each parity, groups were classified by size, based on number of cows for that herd appraisal date: 5 to 15, 30 to 55, and ≥ 100 . Those classes were chosen to represent small, medium, and large herds. Even though second-lactation contemporary groups are smaller, the same size categories were kept to allow easier comparison of results. Contemporary groups were further classified by mean final score as high (above class average) or low (below average). Final score was used because other studies showed generally negative correlations between phenotypic standard deviation for type traits and herd mean final score (e.g., [Smothers et al., 1991](#)). The resulting 12 datasets were analyzed separately.

Pedigree data were extracted from the Animal Improvement Programs Laboratory database, and ancestors were traced back to 1978. Animals born before 1978 were considered to be the base population.

Estimation of (Co)variance Components

(Co)variance components were computed for each dataset with the procedure developed by [Misztal et al. \(1995\)](#) for Holstein type traits and applied to Jersey type traits by [Gengler et al. \(1997b\)](#). Final score was analyzed as a single trait. A multitrait analysis was applied to the 15 linear type traits using canonical transformation and an expectation-maximization REML algorithm ([Misztal, 1990](#)). Both the single-trait and multitrait analyses used the same general model:

$$\mathbf{y} = \mathbf{Xh} + \mathbf{Hc} + \mathbf{Fd} + \mathbf{Zu} + \mathbf{e}$$

where \mathbf{y} = vector of type records; \mathbf{h} = vector of fixed effects of herd, appraisal date combinations; \mathbf{c} = vector of fixed effects of appraisal age group; \mathbf{d} = vector of fixed effects of lactation stage; \mathbf{u} = vector of random additive genetic effects of animals and genetic groups ($\mathbf{u} = \mathbf{a} + \mathbf{Qg}$, where \mathbf{a} = vector of random additive genetic effects of animals expressed as deviations from group means, \mathbf{g} = vector of fixed effects of genetic groups, and \mathbf{Q} = incidence matrix that links \mathbf{g} with \mathbf{u}); \mathbf{X} , \mathbf{H} , \mathbf{F} , and \mathbf{Z} = incidence matrices that associate \mathbf{h} , \mathbf{c} , \mathbf{d} , and \mathbf{u} , respectively, with \mathbf{y} ; and \mathbf{e} = vector of random residual effects. This model contains no appraiser effect and is very similar to the model used in the official genetic evaluation.

To account for differences in mean genetic merit of unknown ancestors, over time, common genetic groups for sires and dams were included as proposed by [Westell et al. \(1988\)](#). Nine genetic groups were defined based on birth year (<1979, 1979 to 1980, 1981 to 1982, ..., 1991 to 1992, >1992).

Comparison of (Co)variance Components

Absolute (co)variance components are not reported, because they are difficult to interpret as type trait scales are somewhat arbitrary. Instead, (co)variances were compared with mean (co)variances across datasets.

Comparison of matrices used the concept of the Frobenius norm defined as:

$$\|\mathbf{M}\|_F = \sqrt{\sum_{ij} m_{ij}^2}$$

where m_{ij} is the element of row i and column j of matrix \mathbf{M} . The Frobenius norm is useful in comparing (co)variance matrices if there are no dominant elements in the diagonal. In this case, variances were always of similar magnitude. For the comparison of a matrix \mathbf{M} to the average matrix $\overline{\mathbf{M}}$, the ratio $\|\mathbf{M} - \overline{\mathbf{M}}\|_F / \|\overline{\mathbf{M}}\|_F$ was computed which provides the relative mean difference of the elements in \mathbf{M} to the elements in $\overline{\mathbf{M}}$.

Overall differences among variances for data sets were computed using diagonal matrices obtained by ignoring covariances in (co)variance matrices \mathbf{C} . The ratios $\|\text{diag}(\mathbf{C} - \overline{\mathbf{C}})\|_F / \|\text{diag}(\overline{\mathbf{C}})\|_F$ were computed, where $\overline{\mathbf{C}}$ is the mean (co)variance matrix. In a second step, overall differences of the whole (co)variance matrices were determined by computing $\|\mathbf{C} - \overline{\mathbf{C}}\|_F / \|\overline{\mathbf{C}}\|_F$. Correlation matrices were compared to the mean correlation matrix using $\|\mathbf{C}_r - \overline{\mathbf{C}}_r\|_F / \|\overline{\mathbf{C}}_r\|_F$.

Comparison of Heritabilities

Heritability estimates were obtained for each dataset to determine whether observed differences might be the result of sampling error. The sampling errors of the heritabilities were approximated for each trait and dataset with the formula of [Swiger et al. \(1964\)](#). This formula is based on the estimation of variance of the intraclass correlation of progeny groups for a sire model. The approximation enables simple statistical tests of maximum relative differences. Sampling error for a given data set is obtained from

$$\sigma_{h^2} = 4 \sqrt{\frac{2(N-1)(1-0.25h^2)^2 [1+(k-1)0.25h^2]^2}{k^2(N-s)(s-1)}}$$

$$k = \frac{1}{s-1} \left(N - \frac{\sum n_i^2}{N} \right),$$

where N = total number of observations, s = number of half-sib groups, and n_i = number of daughters of sire i .

For every trait and parity, the largest relative differences were computed as the difference between heritability divided by the joint sampling error of the estimates:

$$u_{ij} = \frac{|h_i^2 - h_j^2|}{\sqrt{(\sigma_{h^2}^2)_i + (\sigma_{h^2}^2)_j}},$$

where $\sqrt{(\sigma_{h^2}^2)_i + (\sigma_{h^2}^2)_j}$ is the joint sampling error of heritability estimates i and j . Then u_{ij} was tested against theoretical values at significance levels of 10, 5, 1, and 0.1%.

This method, however, does not account for fixed effects. More complicated approaches (i.e., based on the inverse of the information matrix) were not available for our computations.

RESULTS AND DISCUSSION

Descriptive Statistics

The numbers of records, contemporary groups, and animals in the relationship matrix in the 12 datasets are presented in [Table 1](#). An interesting finding was that the relationship matrix was smaller for larger herds. This is attributed to the use of relatively fewer sires and the tendency of pedigrees to be less complete.

Table 1. Numbers of records, numbers of contemporary groups, mean numbers and mean final scores of contemporary groups, numbers of animals in the relationship matrix (**A**), and numbers of sires of daughters.

	Number of animals per contemporary group					
	5 to 15		30 to 55		≥ 100	
	Low final score	High final score	Low final score	High final score	Low final score	High final score
			First parity			
Records, no.	21,666	23,692	21,024	21,457	22,901	22,141
Contemporary groups, no.	2334	2544	526	543	140	138
Records per group, \bar{x}	9.28	9.31	39.97	39.52	163.58	160.44
Final score per group, \bar{x}	74.27	79.64	74.62	78.79	74.05	77.66
Animals in A , no.	46,089	50,528	41,251	43,631	44,327	44,722
Sires of daughters with records,	2293	2250	1950	2002	1767	1452

no.

			Second parity			
Records, no.	18,835	19,760	12,209	11,441	8111	8789
Contemporary groups, no.	2119	2302	308	294	57	65
Records per group, \bar{x}	8.89	8.58	39.64	38.91	142.30	135.22
Final score per group, \bar{x}	76.77	82.07	76.01	80.41	75.09	79.02
Animals in A , no.	38,096	41,127	24,033	24,368	16,967	20,022
Sires of daughters with records, no.	2123	2065	1534	1455	976	786

In [Table 2](#), means and standard deviations are presented of adjusted final and linear scores used in this study. As expected, differences in final scores were found across datasets. Differences were also found for other linear traits. An important finding was that standard deviations were not constant. Contemporary groups with higher final scores always had lower standard deviations than the corresponding groups with lower final scores. This finding was also reported for US Holsteins by [Smothers et al. \(1991\)](#), who found a negative correlation of -0.59 between intraherd standard deviation and mean final score of the herd. They also found significant negative regression coefficients for the other linear traits, except fore udder attachment. The most likely explanation could be that the scales are not infinite and, therefore, in high scoring herds less variation is possible.

It is somewhat surprising that mean scores were different across parity despite additive age adjustments, but equal means are not required in the current genetic evaluation model because contemporary groups are separated by parity. Current age adjustments are, therefore, only required to standardize within a parity. The more important finding was that standard deviations were not constant across parity. This was not surprising because the preadjustment does not attempt to stabilize the variances. It was, however, surprising to see that standard deviation tended to increase from first to second parity. This could indicate that type is not necessarily an important culling reason in Jersey and that classifiers may exploit larger ranges of the scales in second lactation appraisals.

Table 2. Means and standard deviations of final score and linear traits in the 12 datasets.

Number of animals per contemporary group		
5 to 15	30 to 55	≥ 100

Trait	Low final score		High final score		Low final score		High final score		Low final score		High final score	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	First parity											
Final score	74.3	6.4	79.6	4.9	74.6	6.5	78.8	5.4	74.0	6.8	77.7	5.7
Stature	21.9	7.0	25.2	6.2	22.0	6.9	24.4	6.0	22.4	6.8	24.5	5.9
Strength	21.5	6.7	24.9	5.9	22.4	6.7	24.8	6.0	23.1	6.6	25.1	5.9
Dairy form	25.0	7.7	30.3	6.2	25.8	7.9	29.8	6.5	25.7	7.7	28.8	6.5
Foot angle	21.3	7.2	23.5	6.6	22.0	7.2	24.0	6.7	21.9	7.0	23.3	6.2
Rear legs (side view)	26.8	7.7	26.5	6.3	27.2	7.4	27.0	6.2	26.9	7.2	26.7	6.1
Body depth	24.0	6.7	27.3	5.7	24.7	6.7	27.4	5.8	25.2	6.6	27.2	5.6
Rump angle	25.9	7.3	26.2	6.3	26.2	7.2	26.1	6.4	26.0	7.3	26.0	6.4
Thurl width	21.9	6.4	25.3	5.2	22.6	6.4	25.1	5.3	23.0	6.3	24.9	5.4
Fore udder attachment	27.2	8.2	28.5	6.8	26.2	8.3	27.5	6.9	25.2	8.0	26.2	6.6
Rear udder height	27.5	6.7	31.2	5.9	27.6	6.9	30.4	6.1	26.2	7.1	28.7	6.4
Rear udder width	25.3	6.6	30.2	5.7	25.9	6.7	29.9	5.9	25.2	6.8	28.4	6.2
Udder depth	33.2	8.3	31.6	6.8	31.5	8.2	29.9	7.1	28.3	8.6	27.8	7.6
Udder cleft	26.7	5.7	28.4	5.1	26.7	5.8	27.7	5.4	25.8	6.2	26.9	5.4
Teat placement	23.2	7.0	25.9	6.2	22.4	7.1	25.0	6.5	22.1	7.1	24.4	6.3
Teat length	19.6	6.2	21.7	5.7	19.6	6.3	21.4	5.9	19.3	6.4	21.1	5.8
	Second parity											
Final score	76.8	6.8	82.0	5.0	76.0	7.2	80.4	6.0	75.1	7.3	79.0	6.3
Stature	26.6	6.6	28.5	6.0	26.3	6.6	27.8	6.0	26.2	6.9	27.1	5.7
Strength	26.8	6.6	28.8	5.7	27.6	6.7	28.9	6.0	27.6	6.8	28.3	5.8
Dairy form	29.3	7.4	33.7	6.1	29.3	7.6	32.5	6.6	28.0	7.6	31.2	6.3
Foot angle	20.5	7.3	23.0	6.7	20.1	7.4	23.0	7.2	20.8	7.6	23.3	6.9
Rear legs (side view)	27.9	7.6	27.3	6.2	28.4	7.7	27.8	6.6	27.4	8.0	27.0	6.0
Body depth	29.1	6.2	31.1	5.5	29.9	6.4	31.2	5.7	29.8	6.5	30.3	5.5
Rump angle	25.4	7.3	25.0	6.4	26.1	7.6	25.4	6.7	25.6	7.9	25.3	6.4
Thurl width	26.7	6.3	28.4	5.3	27.2	6.5	28.1	5.6	27.1	6.7	27.2	5.8
Fore udder attachment	24.7	8.5	28.1	7.0	23.3	8.6	26.8	7.5	23.3	8.7	25.7	6.9
Rear udder	29.0	7.2	33.3	6.3	28.6	7.7	31.6	6.9	27.5	7.7	29.3	7.2

height													
Rear udder width	28.9	6.6	33.2	5.9	29.0	6.9	32.2	6.5	27.7	7.0	30.5	6.9	
Udder depth	23.4	9.1	25.2	7.3	19.9	8.9	23.2	7.7	19.7	8.8	20.8	7.1	
Udder cleft	26.4	7.0	28.7	5.8	26.3	7.2	27.7	6.3	25.8	7.3	26.7	6.2	
Teat placement	22.7	7.8	26.0	6.6	22.3	7.8	25.2	7.1	22.7	8.0	25.1	6.9	
Teat length	23.0	6.7	23.9	5.8	22.2	6.7	23.1	6.1	21.8	6.9	22.5	6.2	

Variations

Tables 3 and 4 show the genetic and phenotypic variances, respectively, for each dataset relative to the mean variance across datasets. The mean variance across datasets was chosen instead of redoing a random sampling because it allowed an estimate of the overall population variance, taking the studied sources of heterogeneity into account. Previous computations of variance components ignored those sources and were based on data from larger herds (Gengler et al., 1999).

The averages of the six datasets of a given parity also were reported. Simple averages were used because estimation of population (co)variance components based on sampling also used simple averages. Average first-parity genetic variances were less than one, except for dairy form and rear udder width, indicating below average variances. For most traits, medium-sized contemporary groups had the highest genetic variances in first parity. In second parity, large contemporary groups often showed the largest genetic variance. For both parities, contemporary groups with higher average final scores usually had lower genetic variance than the corresponding low final score groups. For phenotypic variances, larger contemporary groups with lower mean final scores generally showed the highest variances, while small contemporary groups with high final scores had the lowest variances. Sorensen and Kennedy (1985) found similar results for US Holsteins and report the same pattern for genetic variances. The pattern of genetic variances is less clear in the current study.

Table 3. Genetic variances relative to the mean genetic variances by trait.

Trait	Number of animals per contemporary group						Average of parity
	5 to 15		30 to 55		≥ 100		
	Low final score	High final score	Low final score	High final score	Low final score	High final score	
	First parity						
Final score	1.05	0.57	1.42	0.75	1.22	0.71	0.95
Stature	0.72	0.88	1.17	1.02	1.08	0.72	0.93
Strength	0.75	0.80	1.33	0.85	1.13	0.74	0.93

Dairy form	0.86	0.65	1.76	0.94	1.24	0.86	1.05
Foot angle	0.68	0.68	1.38	1.10	1.07	0.67	0.93
Rear legs (side view)	0.68	0.85	1.38	0.86	1.43	0.67	0.98
Body depth	0.75	0.70	1.32	0.92	1.32	0.74	0.96
Rump angle	0.86	0.65	1.21	0.72	1.15	0.87	0.91
Thurl width	0.63	0.69	1.42	0.81	1.24	0.62	0.90
Fore udder attachment	0.71	0.86	1.05	0.88	1.24	0.71	0.91
Rear udder height	0.74	0.62	1.09	0.75	1.28	0.74	0.87
Rear udder width	0.82	0.74	1.49	0.87	1.34	0.82	1.01
Udder depth	0.78	0.70	1.00	0.66	1.25	0.78	0.86
Udder cleft	0.54	0.53	1.02	0.49	1.03	0.53	0.69
Teat placement	0.73	0.85	1.19	0.78	0.99	0.73	0.88
Teat length	0.76	0.72	1.43	0.96	1.07	0.75	0.95
All traits, \bar{x}	0.75	0.72	1.29	0.83	1.19	0.73	0.92

			Second parity				
Final score	1.19	0.57	1.17	1.00	1.48	0.88	1.05
Stature	1.14	1.02	1.15	0.93	1.31	0.87	1.07
Strength	0.93	0.89	1.35	0.97	1.30	0.96	1.07
Dairy form	1.17	0.69	1.17	0.99	1.17	0.51	0.95
Foot angle	1.11	0.63	1.34	1.50	1.36	0.47	1.07
Rear legs (side view)	1.23	0.86	1.34	0.83	1.61	0.26	1.02
Body depth	1.07	0.74	1.47	1.01	1.25	0.71	1.04
Rump angle	1.12	0.76	1.35	0.89	1.66	0.77	1.09
Thurl width	1.33	0.75	1.42	1.05	1.19	0.87	1.10
Fore udder attachment	1.15	0.80	1.29	1.00	1.41	0.90	1.09
Rear udder height	1.03	0.76	1.02	1.18	1.60	1.19	1.13
Rear udder width	1.05	0.73	0.88	0.96	1.37	0.91	0.99
Udder depth	1.28	0.69	1.58	0.91	1.80	0.56	1.14
Udder cleft	1.50	0.85	1.74	0.80	2.22	0.75	1.31
Teat placement	1.32	0.91	1.33	0.93	1.42	0.81	1.12
Teat length	1.50	0.81	1.58	0.93	0.82	0.65	1.05

All traits, \bar{x}	1.19	0.78	1.32	0.99	1.44	0.76	1.08
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Table 4. Phenotypic variances relative to the mean phenotypic variances by trait.

Trait	Number of animals per contemporary group						Average of parity
	5 to 15		30 to 55		≥ 100		
	Low final score	High final score	Low final score	High final score	Low final score	High final score	
	First parity						
Final score	1.07	0.59	1.11	0.73	1.19	0.82	0.92
Stature	0.86	0.89	1.17	0.91	1.18	0.86	0.98
Strength	0.90	0.84	1.14	0.90	1.17	0.90	0.97
Dairy form	0.89	0.77	1.34	0.88	1.25	0.89	1.00
Foot angle	0.82	0.83	1.08	0.92	1.08	0.82	0.92
Rear legs (side view)	0.80	0.82	1.15	0.81	1.16	0.80	0.92
Body depth	0.91	0.85	1.24	0.91	1.24	0.91	1.01
Rump angle	0.87	0.79	1.09	0.85	1.15	0.87	0.94
Thurl width	0.86	0.75	1.15	0.81	1.20	0.86	0.94
Fore udder attachment	0.77	0.78	1.17	0.82	1.15	0.77	0.91
Rear udder height	0.88	0.71	1.00	0.79	1.11	0.88	0.89
Rear udder width	0.92	0.73	1.07	0.81	1.15	0.92	0.93
Udder depth	0.87	0.67	1.03	0.75	1.24	0.87	0.90
Udder cleft	0.75	0.66	0.89	0.72	1.02	0.75	0.80
Teat placement	0.82	0.77	0.99	0.83	1.05	0.82	0.88
Teat length	0.90	0.81	1.07	0.87	1.09	0.90	0.94
All traits, \bar{x}	0.87	0.77	1.11	0.83	1.15	0.85	0.93
	Second parity						
Final score	1.25	0.64	1.32	0.91	1.37	1.01	1.08
Stature	1.09	0.89	1.12	0.91	1.28	0.84	1.02
Strength	1.07	0.81	1.18	0.91	1.29	0.89	1.03

Dairy form	1.14	0.72	1.21	0.87	1.24	0.80	1.00
Foot angle	1.07	0.86	1.20	1.07	1.27	1.00	1.08
Rear legs (side view)	1.21	0.79	1.35	0.91	1.45	0.74	1.08
Body depth	1.03	0.78	1.15	0.89	1.23	0.86	0.99
Rump angle	1.11	0.82	1.25	0.95	1.37	0.88	1.06
Thurl width	1.11	0.75	1.21	0.88	1.40	1.03	1.06
Fore udder attachment	1.25	0.82	1.30	0.95	1.38	0.84	1.09
Rear udder height	1.15	0.84	1.24	1.00	1.30	1.09	1.11
Rear udder weight	1.07	0.80	1.13	0.99	1.24	1.17	1.07
Udder depth	1.27	0.81	1.33	0.90	1.47	0.80	1.10
Udder cleft	1.36	0.89	1.41	1.04	1.49	1.03	1.20
Teat placement	1.24	0.87	1.26	0.98	1.35	1.01	1.12
Teat length	1.16	0.83	1.20	0.95	1.19	1.02	1.06
All traits, \bar{X}	1.16	0.81	1.24	0.95	1.33	0.94	1.07

Table 5 shows the relative mean difference of variances from every data set, computed as the ratio of the Frobenius norm of the difference to the Frobenius norm of the mean

$\|\text{diag}(\mathbf{C} - \bar{\mathbf{C}})\|_{\mathbb{F}} / \|\text{diag}(\bar{\mathbf{C}})\|_{\mathbb{F}}$ where \mathbf{C} is the (co)variance matrix, and average variances by parity.

The differences in genetic variances were larger than the differences in phenotypic variances.

This could be due to larger sampling errors for estimated genetic (co)variance matrices.

Table 5. Relative mean difference of variances from every data set, computed as the ratio of the Frobenius norm of the difference to the Frobenius norm of the mean

$\|\text{diag}(\mathbf{C} - \bar{\mathbf{C}})\|_{\mathbb{F}} / \|\text{diag}(\bar{\mathbf{C}})\|_{\mathbb{F}}$ where \mathbf{C} is the (co)variance matrix, and average variances by parity.

(Co)variance matrix	Number of animals per contemporary group						Average of parity
	5 to 15		30 to 55		≥ 100		
	Low final score	High final score	Low final score	High final score	Low final score	High final score	
	First parity						
Genetic	0.24	0.29	0.32	0.23	0.22	0.25	0.26
Residual	0.14	0.24	0.12	0.18	0.15	0.14	0.16
Phenotypic	0.16	0.25	0.15	0.18	0.17	0.16	0.18

			Second parity				
Genetic	0.23	0.24	0.39	0.11	0.55	0.32	0.31
Residual	0.19	0.19	0.25	0.09	0.32	0.12	0.19
Phenotypic	0.19	0.20	0.26	0.08	0.35	0.14	0.20

Covariances and Correlations

[Table 6](#) shows the relative mean difference of covariances from every dataset, computed as ratios of the Frobenius norm of the difference to the Frobenius norm of the mean $\|\mathbf{C} - \bar{\mathbf{C}}\|_{\text{F}} / \|\bar{\mathbf{C}}\|_{\text{F}}$, where \mathbf{C} is the covariance matrix, and average covariance by parity. The results were very close to those of the variances shown in [Table 5](#), suggesting that heterogeneity of variances and covariances were of similar amplitude. As with variances, genetic covariance differences tended to be larger than phenotypic ones.

Table 6. Relative mean difference of covariances from every dataset, computed as ratios of the Frobenius norm of the difference to the Frobenius norm of the mean $\|\mathbf{C} - \bar{\mathbf{C}}\|_{\text{F}} / \|\bar{\mathbf{C}}\|_{\text{F}}$ where \mathbf{C} is the covariance matrix, and average covariances by parity.

Covariance matrix	Number of animals per contemporary group						Average of parity
	5 to 15		30 to 55		≥ 100		
	Low final score	High final score	Low final score	High final score	Low final score	High final score	
			First parity				
Genetic	0.27	0.31	0.46	0.24	0.34	0.27	0.31
Residual	0.14	0.27	0.17	0.19	0.19	0.14	0.18
Phenotypic	0.15	0.27	0.22	0.19	0.21	0.15	0.20
			Second parity				
Genetic	0.26	0.27	0.44	0.27	0.56	0.38	0.36
Residual	0.22	0.22	0.26	0.13	0.31	0.26	0.23
Phenotypic	0.20	0.22	0.25	0.11	0.34	0.26	0.23

To test whether the pattern of covariances was the same as the pattern of variances, the (co) variance matrices were transformed into correlation matrices which excluded the influence of heterogeneous variances. [Table 7](#) reports the relative mean difference of correlations from every dataset, computed as ratios of the Frobenius norm of the difference to the Frobenius norm of the mean $\|\mathbf{C}_r - \bar{\mathbf{C}}_r\|_{\text{F}} / \|\bar{\mathbf{C}}_r\|_{\text{F}}$, where \mathbf{C}_r is the correlation matrix, and average correlation by parity.

The results show that for phenotypic and, to a lesser extent, for genetic (co)variance matrices, the differences observed in covariances come primarily from variances and only marginally from correlations. This finding is useful because it allows consideration of the joint correction for variance and covariance heterogeneity under the assumption that correlations across datasets are stable. This result could also be an indication that, at least in a limited time frame excluding the influence from selection, genetic correlations are stable biological parameters.

Table 7. Relative mean difference of correlations from every dataset, computed as ratios of the Frobenius norm of the difference to the Frobenius norm of the mean $\|C_r - \bar{C}_r\|_F / \|\bar{C}_r\|_F$, where C_r is the correlation matrix, and average correlations by parity.

Correlation matrix	Number of animals per contemporary group						Average of parity
	5 to 15		30 to 55		≥ 100		
	Low final score	High final score	Low final score	High final score	Low final score	High final score	
	First parity						
Genetic	0.18	0.21	0.26	0.18	0.21	0.18	0.20
Residual	0.13	0.10	0.13	0.09	0.10	0.13	0.11
Phenotypic	0.11	0.09	0.15	0.08	0.11	0.11	0.11
	Second parity						
Genetic	0.17	0.22	0.21	0.29	0.29	0.40	0.26
Residual	0.12	0.10	0.15	0.10	0.13	0.22	0.14
Phenotypic	0.09	0.08	0.11	0.09	0.13	0.24	0.12

Heritabilities

[Table 8](#) shows the heritabilities obtained for the 12 datasets. For most traits, the estimates were different from those reported by [Gengler et al. \(1998\)](#), which are currently in use, and reported as official in [Table 8](#). Differences from the official heritabilities may result from the use of a different sample and the use of repeated observations in a repeatability model.

Observed differences in variances among datasets, especially the different patterns among genetic and phenotypic variances, were responsible for the appearance of differences in heritabilities. Heterogeneity of heritability for each trait was tested within parity by using the two datasets with the maximum difference in heritability estimate. In first parity, the maximum relative difference was significant for most traits. In second parity, sampling errors were larger because datasets were smaller and, therefore, fewer traits were above the significance threshold. These results, shown in [Table 8](#), seem to indicate that because heterogeneity in phenotypic and genetic variances is not totally proportional, heritability differences result. The significant

difference in heritabilities for final score is different from the findings of [Sorensen and Kennedy \(1985\)](#), [Koots et al. \(1994\)](#) and [Weigel and Lawlor \(1994\)](#) who assumed homogeneous heritabilities. [Smothers et al. \(1993\)](#), however, found heterogeneous heritabilities not only for final score, but also for other linear type traits.

Table 8. Heritabilities (h^2) and approximate SE by trait and dataset.

Trait	Official ¹ h^2	Number of animals per contemporary group												Maximum relative difference	
		5 to 15				30 to 55				≥ 100					
		Low final score		High final score		Low final score		High final score		Low final score		High final score			
h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE	h^2	SE		
		First parity													
Final score	0.23	0.18	0.02	0.17	0.02	0.23	0.02	0.19	0.02	0.19	0.02	0.16	0.02	3.085	**
Stature	0.39	0.31	0.02	0.37	0.02	0.37	0.02	0.41	0.02	0.34	0.02	0.31	0.02	3.415	***
Strength	0.25	0.17	0.02	0.19	0.02	0.24	0.02	0.19	0.02	0.20	0.02	0.17	0.02	2.842	**
Dairy form	0.23	0.22	0.02	0.20	0.02	0.31	0.02	0.25	0.02	0.23	0.02	0.22	0.02	4.094	***
Foot angle	0.10	0.09	0.02	0.09	0.01	0.14	0.02	0.13	0.02	0.11	0.01	0.09	0.01	2.428	*
Rear legs (side view)	0.10	0.10	0.02	0.12	0.02	0.14	0.02	0.12	0.02	0.14	0.02	0.10	0.01	2.287	*
Body depth	0.25	0.20	0.02	0.20	0.02	0.25	0.02	0.24	0.02	0.25	0.02	0.19	0.02	2.440	*
Rump angle	0.31	0.26	0.02	0.21	0.02	0.29	0.02	0.22	0.02	0.26	0.02	0.26	0.02	2.897	**
Thurl width	0.20	0.11	0.02	0.14	0.02	0.19	0.02	0.16	0.02	0.16	0.02	0.11	0.01	3.526	***
Fore udder attachment	0.22	0.17	0.02	0.20	0.02	0.17	0.02	0.20	0.02	0.20	0.02	0.17	0.02	1.505	NS
Rear udder height	0.26	0.16	0.02	0.17	0.02	0.21	0.02	0.18	0.02	0.22	0.02	0.16	0.02	2.532	*
Rear udder width	0.23	0.16	0.02	0.19	0.02	0.25	0.02	0.19	0.02	0.21	0.02	0.16	0.02	3.710	***
Udder	0.38	0.30	0.02	0.35	0.02	0.32	0.02	0.29	0.02	0.34	0.02	0.30	0.02	1.954	†

depth														
Udder cleft	0.20	0.11	0.02	0.12	0.02	0.17	0.02	0.10	0.02	0.15	0.02	0.10	0.01	3.027 **
Teat placement	0.24	0.18	0.02	0.22	0.02	0.24	0.02	0.19	0.02	0.19	0.02	0.18	0.02	2.458 *
Teat length	0.26	0.20	0.02	0.21	0.02	0.31	0.02	0.26	0.02	0.23	0.02	0.20	0.02	4.465 ***
						Second parity								
Final score	0.23	0.17	0.02	0.16	0.02	0.16	0.02	0.20	0.03	0.20	0.03	0.16	0.03	1.204 NS
Stature	0.39	0.39	0.02	0.42	0.02	0.38	0.03	0.38	0.03	0.38	0.04	0.38	0.03	1.168 NS
Strength	0.25	0.18	0.02	0.22	0.02	0.23	0.03	0.22	0.03	0.20	0.03	0.22	0.03	1.711 †
Dairy form	0.23	0.24	0.02	0.22	0.02	0.23	0.03	0.27	0.03	0.22	0.03	0.15	0.03	3.142 **
Foot angle	0.10	0.12	0.02	0.08	0.02	0.12	0.02	0.16	0.03	0.12	0.03	0.05	0.02	3.102 **
Rear legs (side view)	0.10	0.12	0.02	0.13	0.02	0.12	0.02	0.11	0.02	0.13	0.03	0.04	0.02	3.130 **
Body depth	0.25	0.24	0.02	0.22	0.02	0.30	0.03	0.27	0.03	0.24	0.03	0.20	0.03	2.729 **
Rump angle	0.31	0.26	0.02	0.24	0.02	0.28	0.03	0.24	0.03	0.31	0.03	0.23	0.03	1.945 †
Thurl width	0.20	0.19	0.02	0.16	0.02	0.18	0.03	0.19	0.03	0.13	0.03	0.13	0.03	1.748 †
Fore udder attachment	0.22	0.17	0.02	0.18	0.02	0.18	0.03	0.19	0.03	0.19	0.03	0.20	0.03	0.811 NS
Rear udder height	0.26	0.17	0.02	0.17	0.02	0.16	0.02	0.22	0.03	0.23	0.03	0.21	0.03	1.926 †
Rear udder width	0.23	0.18	0.02	0.17	0.02	0.14	0.02	0.18	0.03	0.20	0.03	0.14	0.03	1.585 NS
Udder depth	0.38	0.34	0.02	0.29	0.02	0.39	0.03	0.34	0.03	0.41	0.04	0.23	0.03	3.903 ***
Udder cleft	0.20	0.16	0.02	0.14	0.02	0.18	0.03	0.11	0.02	0.22	0.03	0.11	0.02	2.845 **
Teat placement	0.24	0.21	0.02	0.21	0.02	0.21	0.03	0.19	0.03	0.21	0.03	0.16	0.03	1.565 NS
Teat length	0.26	0.30	0.02	0.23	0.02	0.31	0.03	0.23	0.03	0.16	0.03	0.15	0.03	4.519 ***

¹ [Gengler et al. \(1998\)](#).

† $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

CONCLUSIONS

Based on expectation-maximization REML estimates from samples of the data, genetic and phenotypic variances in Jersey final score and linear traits were heterogeneous. This heterogeneity was also found for covariances and to a much lesser extent in correlations. The effects contributing to heterogeneity in this study were parity and mean final score and size of contemporary group. The heterogeneity of correlations was extremely low for phenotypic correlations, indicating that correction of variances would also correct most of the heterogeneity of covariances. The heterogeneity of (co)variances found in this study contributed to significant differences among heritabilities. This suggests that adjustment for heterogeneous genotypic and phenotypic (co)variances could improve the current genetic evaluation model, however heritability differences might also be random or due to sampling errors. Although we attempted to estimate the degree of significance, the lack of precise sampling errors made our tests unreliable. Our results showed statistically significant differences in heritabilities, which is contrary to most literature which reports no or insignificant heritability differences.

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