

## GENETICS AND BREEDING

### Multiple-Trait Estimation of Variance Components of Yield and Type Traits Using an Animal Model

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#### ABSTRACT

Genetic relationships between yield and type traits were investigated using multiple-trait REML procedures with an animal model. Computing strategies were developed to deal with large populations and numbers of traits. Data consisted of records for 3 production and 15 type traits for 20,836 primiparous cows from 1982 to 1988. The model included 2358 herd management effects, 28,749 animal effects, and 23 groups for unknown parents. (Co)variance components were estimated using a canonical transformation with an accelerated expectation-maximization REML algorithm. Direct inversion of the coefficient matrix and solution to the transformed single-trait equations were by a sparse matrix solver.

Heritabilities for milk, fat, and protein yield were .44, .42, and .40, respectively. Heritabilities for type traits ranged from .10 to .42; the largest was for stature. Dairy form had the largest genetic correlations with yield traits, which ranged from .59 with milk to .68 with fat. Genetic correlations between all yield and most type traits were positive (from .01 to .68); exceptions were fore udder attachment, udder depth, and front teat placement (-.01 to -.44). Selection

solely for increased milk yield would cause some udder characteristics to deteriorate. Restricted selection for milk yield while holding udder traits constant would decrease response in milk yield by 15%.

(Key words: restricted maximum likelihood, multivariate analysis, animal model)

Abbreviation key: AM = animal model, CPU = central processing unit, EM = expectation-maximization, HYMC = herd-year-month-classification, HYS = herd-year-season, SM = sire model.

#### INTRODUCTION

The primary emphasis in dairy cattle selection is for yield traits because highest producing cows usually are more profitable (1). In general, profitability will be even higher if cows produce large quantities of milk in routinely initiated lactations while also remaining functionally sound. Selection on yield traits alone could decrease merit for other traits. Selection emphasis on type traits associated with increased herd life may be beneficial to decrease involuntary culling and increase profitability (16). One of the primary reasons for collecting and utilizing information on type is to aid breeders in selecting profitable, functional cows so that early culling for causes unrelated to yield (involuntary culling) can be avoided.

Since 1983, the Holstein Association has collected data on 14 type traits scored on a linear scale (18) as well as overall conforma-

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tion (final score). Emphasis placed on each of these traits in a selection program including yield traits depends partly on their genetic correlations with yield. In particular, selection criteria should include traits that change in the undesired direction if selection is for yield traits only.

Information on genetic relationships between yield traits and linearly scored type traits is limited. Meyer et al. (11) reported genetic correlations ranging from  $-.52$  to  $.24$  between linear type scores and milk yield in primiparous British Friesians. Udder depth and fore udder attachment had largest antagonistic correlations with yield ( $-.52$  and  $-.37$ , respectively). Corresponding phenotypic correlations were smaller in magnitude and ranged from  $-.27$  to  $.21$ . Genetic correlation between milk yield and final score in first parity was  $-.14$ .

Foster et al. (4) obtained genetic correlations between first lactation herdmate deviation for milk and fat and linear type traits for Holsteins. For linear traits similar to those used by the Holstein Association, the largest negative genetic correlation with deviation for milk was  $-.12$  for udder depth.

Norman et al. (14) calculated genetic correlations between first lactation yields and linear type traits for Guernseys and Jerseys. Largest negative genetic correlations with yield were  $-.59$  and  $-.56$  for udder depth and fore udder attachment in Jerseys and  $-.29$  and  $-.25$  for foot angle and thurl width in Guernseys. For both breeds, largest positive correlations with yield were for dairy character. Genetic correlations between milk yield and final score were  $.25$  for Guernseys and  $.21$  for Jerseys.

These analyses used the sire model (SM), which neglects all female relationships. Studies using the animal model (AM), which considers all known relationships, indicate that it results in higher estimates of heritability than SM (12, 21, 22). Visscher and Thompson (22) state that SM accounts for the male genetic variation, whereas AM takes both male and female genetic variation into account. If selection intensity for males were greater than for females, the male genetic variance would be smaller. Subsequently, SM might underestimate genetic variability and, thus, lead to poor estimates of genetic parameters, even with large data files.

The AM estimates of genetic parameters also could be useful in genetic evaluation sys-

tems. Many genetic evaluation programs, inside and outside the US, have changed or are changing from SM to AM. It appears desirable that the parameters for these evaluations be derived from the same model as that used in the evaluation, i.e., AM.

Estimates of genetic correlations between yield and type traits by an AM were not available, and current computing algorithms for multitrait REML were inadequate to process the large numbers of animals needed to estimate these parameters with sufficient accuracy. Objectives of this study were to develop an efficient algorithm to estimate genetic parameters with an AM and to apply this algorithm to multitrait yield and type data.

## MATERIALS AND METHODS

### Data

Data were from primiparous Holstein cows in every third herd enrolled continuously between 1982 and 1988 in the Dairy Herd Improvement Registry program. Each animal's record contained 15 type traits and 3 production traits. Type scores and lactation information were collected between 1982 and 1988. Type scores included 14 linearly evaluated traits (scored on a 50-point scale) preadjusted for age of cow and stage of lactation. Final scores were preadjusted for age of cow; low scores also were preadjusted upward to eliminate skewness. Yield records were 305-d twice daily mature equivalent first lactation yields. Only cows with both yield and type information were included. Cows must have been classified before 43 mo of age and, at most, 9 mo after calving. After edits, the data set contained 20,836 cows. Additionally, the pedigree file contained 5502 dams without records and 2441 sires, for a total of 28,779 animals. Unknown parents were assigned to 23 groups. Records for type traits were distributed in 1616 herd-year-month-classification (HYMC) subclasses. Records for production traits were distributed in 2358 herd-year-seasons (HYS) for which seasons were defined as May to October and November to April. Because of the requirements of the computational procedure of an identical model for all traits, HYS were selected as the contemporary groups for yield and type traits. The bias caused by inappropri-

ate contemporary groups for type traits was small because of a high level of overlapping: 74% HYS subclasses contained only a single HYMC subclass; the remaining 26% contained 2 HYMC subclasses. Means and standard deviations for the 18 traits are given in Table 1.

#### Model

The linear mixed model used was

$$y = Hh + Zu + e \quad [1]$$

where  $y$  is a  $20,836 \times 18$  matrix of records;  $h$  is a  $2358 \times 18$  matrix of fixed contemporary groups;  $u = a + Qg$  is a  $28,779 \times 18$  random matrix of total genetic merit effects;  $a$  is a  $28,779 \times 18$  matrix of additive genetic animal effect;  $g$  is a  $23 \times 18$  matrix of unknown parent groups;  $e$  is a  $20,836 \times 18$  random matrix of residual effects;  $H$  and  $Z$  are incidence matrices relating  $h$  and  $u$  to  $y$ , respectively; and  $Q$  is an incidence matrix relating animals to unknown parent groups. Animal and residual effects were treated as random with variances  $G \otimes A$  and  $E \otimes I$ , respectively;  $G$  and  $E$  denote covariance matrices among the 18 traits for the animal and residual effects, respectively;  $A$  denotes additive genetic relationship among the animals; and  $\otimes$  denotes Kronecker product.

#### Computational Strategy

The estimates of  $G$  and  $R$  were obtained by multiple-trait REML using a canonical transformation (6). After the transformation, single-trait estimates were obtained using a sparse matrix solver modified for the efficient use of the supercomputer (12). Standard errors of the estimates of variance components were approximated as in VanRaden (19); however, the accuracy of this approximation for AM has not been determined.

Three techniques were used to reduce the cost of computations approximately 500-fold, which made the computations feasible. First, the trace function was tabulated from relatively few points, to avoid inverting the coefficient matrix many times. Subsequent references to that function were by interpolation or extrapolation. Second, to reduce the inversion central processing unit (CPU) time, columns of the

TABLE 1. Means and standard deviations for the 3 yield traits (kilograms) and 15 type traits (points).

Trait	$\bar{X}$	SD
Milk	9239.3	1771.5
Fat	333.8	63.7
Protein	294.3	53.1
Final score	81.6	4.0
Stature	32.2	8.5
Strength	30.0	7.6
Body depth	32.0	7.7
Dairy form	30.6	7.5
Rump angle	25.1	5.1
Thurl width	28.5	7.3
Rear leg set	27.2	6.7
Foot angle	24.5	6.3
Fore udder attachment	25.5	7.2
Udder height	27.3	7.4
Udder width	27.2	7.3
Udder cleft	27.2	5.6
Udder depth	24.0	4.6
Front teat placement	24.8	6.1

inverse corresponding to animals without records were not computed because their contribution to the trace function is known and equals  $1/\alpha$  per animal (13), where  $\alpha$  is the variance ratio. Finally, to obtain better convergence rate, the expectation-maximization (EM) REML algorithm was replaced by the procedure described by VanRaden (19).

*Interpolation of the Trace Function.* Inversion of the mixed model coefficient matrix would have to be performed too many times to be computationally feasible. Assuming that 100 rounds of iteration provided adequate convergence, the EM-type algorithm would require  $100 \text{ rounds} \times 18 \text{ traits} = 1800$  matrix inversions or evaluations of the trace function

$$t(\alpha) = \text{trace}[A^{-1}C^{uu}(\alpha)] \quad [2]$$

where  $C^{uu}$  is the submatrix of the inverse of the mixed model equations corresponding to equations for animal effects. The trace function is equivalent to a simpler form after diagonalizing the system of equations (6):

$$t(\alpha) = \sum_{i=1}^n 1/(d_i + \alpha) \quad [3]$$

with  $d_i$  an element of  $d$ . Calculating  $d$  explicitly involves dense matrix algorithms and

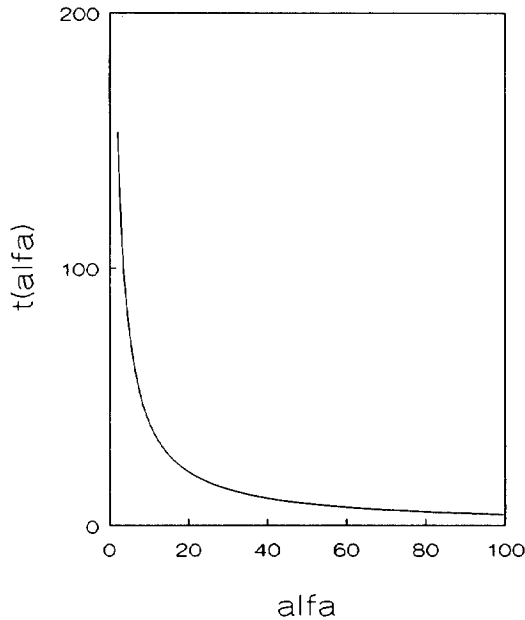


Figure 1. Shape of the trace function obtained from a test data set.

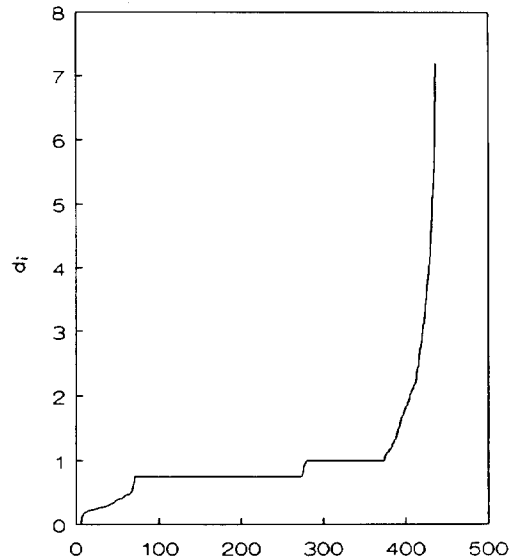


Figure 2. The distribution of the diagonal elements  $d$  in the diagonalized mixed model equations obtained from a test data set.

is prohibitively CPU expensive for matrices of order greater than 5000, even on supercomputers. Figure 1 presents a typical shape of  $t(\alpha)$  for different values of  $\alpha$ , and Figure 2 shows the distribution of  $d$ , both obtained from a data set with 430 animals.

Because the trace function is continuous and smooth, it can be interpolated or extrapolated from a small set of points, which can be computed explicitly. High accuracy of the approximated trace is important because even small errors in the value of the trace can cause large differences in the value of the REML estimates. For example, in this study, differences in approximated traces on the fourth significant digit caused differences in estimates of variance components on the second significant digit. The spline functions did not produce adequate accuracy for the interpolation or extrapolation. Much higher accuracy was obtained using the function that resembles [3]

$$t(\alpha) \approx n \sum_{i=1}^m w_i / (\delta_i + \alpha), \quad \sum w_i = 1 \quad [4]$$

where  $\delta_i$  were estimated separately for each  $\alpha$  from  $m$  closest points, and  $w_i$  are arbitrary weights. For  $m = n$  and  $w_i = 1/n$ , formulas [4] and [3] are the same. For  $m = 1$ , the weight  $w_1$  is 1, and  $\delta$  is approximately an average of all elements  $d$ . An example of estimating parameters  $\delta$  in function [4] for  $m = 1$  and  $m = 2$  is given in the Appendix. Formula [4] with  $m > 2$  was not used because of difficulties in estimating the parameters  $\delta_i$ . In this study, the value of  $t(\alpha)$  was computed explicitly only for 33 points:  $\alpha = .4, .4 \times 1.2, .4 \times 1.2^2, \dots, .4 \times 1.2^{32}$  using the inversion and subsequent references to  $t(\alpha)$  used this function with  $m = 2, w_1 = .2$ , and  $w_2 = .8$ .

*EM-Type Formulas.* In our experiments, the EM REML formula (2) was very slow and did not converge in 500 rounds. The formula by VanRaden (19)

$$\hat{\sigma}_a^2 = \frac{\hat{a}'A^{-1}\hat{a} - \hat{\sigma}_a^2\beta [n - \alpha t(\alpha)]}{[n - \alpha t(\alpha)] (1 - \beta)}, \quad [5]$$

where  $a$  is a single-trait direct genetic animal effect and  $-\infty < \beta < 1$ , converged up to 20 times faster but was dependent on the choice

TABLE 2. Estimates (Est) of residual and genetic variances (Var), heritabilities, and approximate standard errors for the 18 traits.

Trait	Residual		Genetic		Heritability	
	Var	SE	Var	SE	Est	SE
Milk <sup>1</sup>	10.6	.1	8.4	.4	.44	.01
Fat <sup>2</sup>	14.3	.1	10.5	.5	.42	.01
Protein <sup>2</sup>	9.8	.1	6.5	1.3	.40	.01
Final score	9.6	.1	3.8	.3	.29	.02
Stature	33.7	.4	24.5	1.3	.42	.01
Strength	33.2	.4	13.6	1.1	.29	.02
Body depth	31.1	.3	17.0	1.1	.35	.02
Dairy form	34.4	.4	13.5	1.1	.28	.02
Rump angle	17.2	.2	6.8	.6	.28	.02
Thurl width	32.8	.3	11.7	1.0	.26	.02
Rear leg set	33.9	.4	6.2	1.0	.16	.02
Foot angle	30.1	.3	4.5	.8	.13	.02
Fore udder attachment	34.9	.4	10.8	1.1	.24	.02
Udder height	39.4	.4	7.3	1.1	.16	.02
Udder width	36.7	.4	8.6	1.1	.19	.02
Udder cleft	25.1	.3	2.8	.7	.10	.02
Udder depth	12.2	.1	4.1	.4	.25	.02
Front teat placement	25.8	.3	7.4	.8	.22	.02

<sup>1</sup>Divided by  $10^5$ .

<sup>2</sup>Divided by 100.

of  $\beta$ , which should reflect approximately the proportion of error variance in the expectation of  $a'A^{-1}a$ . For  $\beta = 0$ , the algorithm is the same as that given by Harville (5). For  $\beta < 0$ , it is slower, and it diverges for  $\beta \approx 1$ . In SM, choices of  $\beta \leq .95$  were found to give good convergence (19). In AM, the optimal value of  $\beta$  was between .5 and .8; an average value of .6 was best in this study.

#### RESULTS AND DISCUSSION

The computation of the 33 trace points took 8 h of CPU time on a Cray-2 (Cray Research Inc., Minneapolis, MN) supercomputer. After 100 iterations of applying canonical transformation, computing solutions, and calculating new values for variances and covariances, which took another 10 h of CPU time, the estimates of G and R were changing less than .014% on average in one round, and computations were terminated.

Estimates of heritability, genetic and residual variances, and standard errors are in Table 2. Heritabilities for milk, fat, and protein yields were .44, .42, and .40, respectively.

These estimates were higher than most other estimates of heritability using the SM (10), possibly indicating a large difference in selection intensities between males and females (22). Higher values for heritabilities in this study could also result from the use of registered animals only and from accounting for genetic levels of unknown parents. For comparison, in a study using an intraherd AM in which herds were stratified by yield level, heritabilities for milk and fat were .37 and .42 in the highest producing herds, respectively (21). Heritabilities for the type traits were generally slightly higher than those obtained in independent studies (17, 20), indicating smaller differences in selection intensities for these traits between cows and sires (22). Largest differences between estimates obtained in this study and those currently used in Holstein Association genetic evaluations (20) were .06 for fore udder attachment and .05 for udder cleft.

Genetic and residual correlations between the yield and type traits are in Table 3. Genetic correlations among linear type traits were similar to those reported by VanRaden et al. (20); the largest difference in absolute magnitude

TABLE 3. Genetic (above diagonal) and residual (below diagonal) correlations ( $\times 100$ ) for the 18 traits.<sup>1</sup>

	MY	FY	PY	FS	ST	SR	BD	DF	RA	TW	RL	FA	FU	UH	UW	UC	UD	TP
MY	...	69	90	16	06	02	15	59	18	11	09	10	-31	19	31	01	-44	-03
FY	79	...	78	33	13	13	26	68	01	12	-01	13	-12	28	33	17	-29	01
PY	95	83	...	27	13	10	23	67	11	11	05	17	-21	32	40	15	-38	-01
FS	23	15	20	...	75	62	70	29	-15	65	-11	28	54	59	60	52	33	56
ST	11	08	10	30	...	71	81	27	03	68	-09	28	18	16	19	23	26	21
SR	06	05	08	30	49	...	90	-06	-01	76	-20	46	16	23	41	34	-01	24
BD	12	10	12	33	54	69	...	31	00	78	-06	32	10	25	40	25	-10	23
DF	23	14	17	30	12	-11	07	...	14	13	26	-18	-19	16	14	-12	-30	-05
RA	-02	02	00	-12	07	00	01	-06	...	-20	-26	-05	-09	-15	-11	-08	-05	-10
TW	07	06	09	25	28	36	33	00	-03	...	-09	32	22	30	41	18	05	15
RL	-01	03	-01	-05	-03	-08	-06	12	04	-02	...	-40	02	00	-09	-20	04	-15
FA	01	00	01	29	12	15	14	02	-06	14	-12	...	06	05	13	-09	-11	-01
FU	04	01	02	49	12	13	13	11	-11	11	-05	16	...	47	39	51	78	67
UH	17	11	14	52	15	15	16	17	-10	15	-08	17	43	...	91	48	13	47
UW	22	16	21	52	18	20	20	17	-06	23	-06	18	39	69	...	41	-03	43
UC	06	03	04	41	03	00	04	21	-07	06	05	12	30	30	29	...	42	66
UD	-14	-14	-15	27	11	-02	-04	04	-05	01	-03	11	33	19	13	27	...	43
TP	06	05	05	37	04	01	03	15	-05	05	05	11	35	24	25	41	25	...

<sup>1</sup>MY = Milk yield, FY = fat yield, PY = protein yield, FS = final score, ST = stature, SR = strength, BD = body depth, DF = dairy form, RA = rump angle, TW = thurl width, RL = rear leg set, FA = foot angle, FU = fore udder attachment, UH = udder height, UW = udder width, UC = udder cleft, UD = udder depth, TP = front teat placement.

was .33 for the correlation between udder depth and rear udder width. Seven traits had genetic correlations with yield traits greater than .20 (absolute value) and only 4 traits had genetic correlations with yield greater than .30. Genetic correlations between milk yield and type traits ranged from  $-.44$  (udder depth) to  $.59$  for dairy form. Genetic correlations between udder depth and other udder traits were similar to those reported in other studies (8, 9, 20). Final score was most highly correlated with fat yield (.33). Correlations of type traits with fat and protein yields were similar to those with milk yield, except that they tended to be slightly larger in magnitude. Single-trait selection for milk yield would result in deeper udders with more loosely attached fore udders. Traits associated with body size would be least affected by selection for milk yield.

#### Response to Selection for Milk Yield

Using parameter estimates obtained for yield and type traits, correlated responses in type traits were calculated assuming a specified response to selection for milk yield. Obtaining a 4525-kg response (increase) in milk yield, which could occur over a 25-yr period, would increase dairy form 10.8 points, body depth 3.1 points, rear udder width 4.6 points, and decrease udder depth and fore udder attachment 4.4 and 4.9 points, respectively. Correlated change for udder depth and fore udder attachment is in an undesirable direction.

A restricted index was also used to calculate maximum response in milk yield while maintaining udder depth at its current value. Using the restricted index would result in a 15% decrease in genetic gain for milk yield. Standardized weights for milk yield and udder depth are 70:30, or approximately a 2:1 ratio, which is equivalent to current weights in the Type-Production Index (15).

#### CONCLUSION

Estimates of heritability for yield and type traits using an AM are moderately high. Genetic correlations between yield and some linear type traits were antagonistic. Continued

selection for milk yield would cause deterioration in some conformational traits. The udder traits would be those most affected. Selection to maintain udder depth would decrease progress for milk yield by about 15%.

Estimation of variance components by REML procedures for a multitrait AM is computationally feasible for data containing up to 30,000 animals. The computer cost experienced in this study could have been further reduced with several programming changes. For example, the solutions to the mixed model equations could be obtained using robust iterative methods. Use of the JCG method in ITPACK (7) resulted in a fivefold reduction of the iteration time, provided that the coefficient matrix was not restricted to full rank as is required by SMPAK (7). The inversion time could decrease 50 times if only selected elements of the inverse were computed from the sparse factors of the coefficient matrix (3). Use of such techniques might allow the results presented here to be computed on a workstation or fast personal computer or allow much larger populations to be analyzed on a super-computer.

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#### REFERENCES

- Bertrand, J. A., P. J. Berger, A. E. Freeman, and D. H. Kelley. 1985. Profitability in daughters of high versus average Holstein sires selected for milk yield of daughters. *J. Dairy Sci.* 68:2287.
- Dempster, A. P., N. M. Laird, and D. B. Rubin. 1977. Maximum likelihood from incomplete data via the EM algorithm. *J. R. Stat. Soc. B* 39:1.
- Duff, I. S., A. M. Erisman, and J. K. Reid. 1989. Page 273 in *Direct methods for sparse matrices*. Clarendon Press, Oxford, Engl.
- Foster, W. W., A. E. Freeman, and P. J. Berger. 1988. Linear type trait analysis with genetic parameter estimation. *J. Dairy Sci.* 71:223.

5 Harville, D. A. 1977. Maximum likelihood approaches to variance component estimation and to related problems. *J. Am. Stat. Assoc.* 82:97.

6 Jensen, J., and I. Mao. 1988. Transformation algorithms in analysis of single trait and of multitrait models with equal design matrices and one random factor per trait: a review. *J. Anim. Sci.* 66:2750.

7 Kincaid, D. R., J. R. Respes, D. M. Young, and R. G. Grimes. 1982. Algorithm 586 ITPACK 2C: a FORTRAN package for solving sparse linear systems by adaptive accelerated iterative methods. *ACM Trans. Math. Software* 8:302.

8 Klei, L., E. J. Pollak, and R. L. Quaas. 1988. Genetic and environmental parameters associated with linearized type appraisal scores. *J. Dairy Sci.* 71:2744.

9 Lawstuen, D. A., L. B. Hansen, and L. P. Johnson. 1987. Inheritance and relationships of linear type traits for age classes of Holsteins. *J. Dairy Sci.* 70:1027.

10 Maijala, K., and M. Hanna. 1974. Reliable phenotypic and genetic parameters in dairy cattle. *Proc. 1st World Congr. Genet. Appl. Livest. Prod., Madrid, Spain I:* 541.

11 Meyer, K., S. Brotherstone, W. G. Hill, and M. R. Edwards. 1987. Inheritance of linear type traits in dairy cattle and correlations with milk production. *Anim. Prod.* 44:1.

12 Misztal, I. 1990. Restricted maximum likelihood estimation of variance components in animal model using sparse matrix inversion and a supercomputer. *J. Dairy Sci.* 73:163.

13 Misztal, I., and Y. Da. 1990. On a property of the trace function in restricted maximum likelihood estimation of variance components. *J. Dairy Sci.* 73:3583.

14 Norman, H. D., R. L. Powell, J. R. Wright, and B. G. Cassell. 1988. Phenotypic and genetic relationship between linear functional type traits and milk yield for five breeds. *J. Dairy Sci.* 71:1880.

15 Registered Holstein Type-Production Sire Summaries. 1991. Vol. I, p. 20. Holstein Assoc., Brattleboro, VT.

16 Rogers, G. W., and B. T. McDaniel. 1989. The usefulness of selection for yield and functional type traits. *J. Dairy Sci.* 72:187.

17 Short, T. H., T. J. Lawlor, and K. L. Lee. 1991. Genetic parameters for three experimental linear type traits. *J. Dairy Sci.* 74:2020.

18 Thompson, J. R., K. L. Lee, A. E. Freeman, and L. P. Johnson. 1983. Evaluation of a linearized type appraisal system for Holstein cattle. *J. Dairy Sci.* 66:325.

19 VanRaden, P. M. 1986. Computational strategies for estimation of variance components. Ph.D. Diss., Iowa State Univ., Ames.

20 VanRaden, P. M., E. L. Jensen, T. J. Lawlor, and D. A. Funk. 1990. Prediction of transmitting abilities for Holstein type traits. *J. Dairy Sci.* 73:191.

21 Van Vleck, L. D., M. C. Dong, and G. R. Wiggans. 1987. Genetic (co)variances for milk and fat yield in California, New York, and Wisconsin for an animal model by restricted maximum likelihood. *J. Dairy Sci.* 71:3053.

22 Visscher, P. M., and R. Thompson. 1990. REML estimates of parameters for fat yield in pedigree herds in the U.K. using an individual animal model; male and female heritability estimates. *Proc. 4th World Congr. Genet. Appl. Livest. Prod. Edinburgh, Scotland XIV:*233.

APPENDIX

Extrapolation and Interpolation of the Trace Function

Assume that the trace function has been tabulated for p points:  $t_i = t(\alpha_i)$ ,  $i = 1, p$ . The parameters  $\delta$  are obtained by equating t to the approximating function in m points. For  $m = 1$  and arbitrary point k,

$$t(\alpha_k) = n/(\delta + \alpha_k) \implies \delta = n/t(\alpha_k) - \alpha_k \tag{6}$$

For  $m = 2$  and points  $t_k$  and  $t_{k+1}$

$$t(\alpha_k) = n[w_1/(\delta_1 + \alpha_k) + w_2/(\delta_2 + \alpha_k)] \tag{7}$$

$$t(\alpha_{k+1}) = n[w_1/(\delta_1 + \alpha_{k+1}) + w_2/(\delta_2 + \alpha_{k+1})]$$

where  $w_1 + w_2 = 1$ .

This system of nonlinear equations leads to the quadratic equation for  $\delta_2$  and, for example, can be solved using these formulas:

$$\begin{aligned} \tau_1 &= t_1/n \\ \tau_2 &= t_2/n \\ p_1 &= w_1 - \tau_1 \alpha_1 \\ p_2 &= w_1 - \tau_2 \alpha_2 \\ q_1 &= 1 - \tau_1 \alpha_1 \\ q_2 &= 1 - \tau_2 \alpha_2 \\ a &= p_1 \tau_2 - p_2 \tau_1 \\ b &= p_1 (w_1 - q_2) + \tau_2 \alpha_1 q_1 - p_2 (w_1 - q_1) - \tau_1 \alpha_2 q_2 \\ c &= \alpha_1 q_1 (w_1 - q_2) - \alpha_2 q_2 (w_1 - q_1) \\ \delta_2 &= [-b - (b^2 - 4 a c)^{.5}]/2a \\ \delta_1 &= (\delta_2 p_1 + \alpha_1 q_1)/(\tau_1 \delta_2 + \tau_1 \alpha_1 - w_2). \end{aligned}$$

Example

Three trace points from a test data set with four random effects ( $n = 4$ ) are given.

i	$\alpha_i$	$t_i$
1	2.0	1.8333
2	3.0	1.2500
3	4.0	.9500

Let us compute the approximation to  $t_3$  without using this point. Using [6] and point  $t_2$ ,  $\delta = 4/1.8333 - 2 = .1818$  and  $t_2 \approx 4/(3 + .1818) \approx 1.2571$  for a relative error of .57%. Using [7], points  $t_1$  and  $t_2$ , and assuming  $w_1 = .2$  and  $w_2 = .8$ ,  $\tau_1 = .4583$ ,  $\tau_2 = .2375$ ,  $p_1 = -.7166$ ,  $p_2 = -.75$ ,  $q_1 = .0833$ ,  $q_2 = .05$ ,  $a = .1735$ ,  $b = -.0721$ ,  $c = .0017$ ,  $\delta_2 = .0246$ ,  $\delta_1 = 1.1651$ , and  $t_3 \approx 1.25007$  for a relative error of .006%. In comparison, a linear interpolation would result in  $t_3 \approx [t_2 + t_4]/2 = 1.3915$  for a relative error of 11.2%.