Multibreed Genetic Parameters and Predicted Genetic Values for First Lactation 305-d Milk Yield, Fat Yield, and Fat Percentage in a *Bos taurus* ´ *Bos indicus* Multibreed Dairy Population in Thailand[1]

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Abstract

Estimates of multibreed covariance components, genetic parameters, and predicted genetic values for first lactation 305-d milk yield (MY), 305-d fat yield (FY), and 305-d fat percentage (FP) were obtained using production records from 481 purebred and crossbred cows in a Thai multibreed dairy population. Multibreed covariance components were estimated by restricted maximum likelihood procedures using a generalized expectation-maximization algorithm suitable for multibreed populations. Two multibreed sire-maternal grandsire models (BTBI and HO) that accounted for intrabreed additive genetic effects, and intralocus intra and interbreed nonadditive genetic effects were used for the analyses. The BTBI model considered *Bos taurus* (BT) and *Bos indicus* (BI) fractions, whereas the HO model accounted for Holstein (H) and Other breeds (O) fractions. Additive and nonadditive genetic covariance estimates for base population BI (or O) were larger than those for base population BT (or H) for all traits while base environmental covariance estimates for BI (or O) were smaller than BT (or H). Ranges of multibreed heritability estimates for MY (0.07 to 0.42), FY (0.08 to 0.45), and FP (0.04 to 0.39) across all breed group combinations represented in the data set were within the ranges of unibreed estimates found elsewhere. Estimates of interactibilities (ratios of multibreed nonadditive genetic variances to phenotypic variances) were smaller than those of heritabilities for all traits. Multibreed additive and nonadditive genetic correlations ranged from 0.37 to 0.79 for (MY,FY), and they were close to zero for (MY,FP) and (FY,FP). Ranges of sire additive, nonadditive, and total multibreed predicted genetic values (MPGV) were wider for MY and FY in the HO than in the BTBI model. The opposite occurred for FP. Sire rankings by additive, nonadditive, and total MPGV in the BTBI were highly correlated (0.98) to those in the HO model. High correlations (0.99) also existed between sire rankings by additive, nonadditive, and total MPGV within models. The analyses conducted here showed the feasibility of using multibreed procedures for prediction of genetic values and estimation of covariance components in highly unbalanced small multibreed field dairy datasets. However, the large standard errors of prediction obtained here pointed out the need for substantially larger and more balanced multibreed datasets to obtain more reliable genetic predictions useable for genetic improvement programs in Thailand.

Key words: covariance components, dairy cattle, milk production, multibreed population, sire evaluation

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Introduction

Milk production in Thailand is based on crossbred animals whose composition is usually 75% or more Holstein (H), the remainder coming from various *Bos indicus* (Native, Red Sindhi, Brahman) and, to a lesser extent, from *Bos taurus* (Jersey, Red Dane) breeds. The composition of this crossbred population has been largely determined by a government policy that suggested in 1971 the use of H semen and crossbreeding with local animals to improve milk production in Thailand. Subsequently, crossbred bulls (5/8 H and higher) were produced in Thailand by the Dairy Farming Promotion Organization (DPO) and the Department of Livestock Development. Currently, semen from H and crossbred H bulls is been used nationwide through artificial insemination (AI) services (Sukhato and Kengvikkum, 2000).

Dairy data collected by DPO were used to obtain sire additive genetic predictions starting in 1996, using intrabreed prediction models and procedures (D.P.O., 1999). Separate evaluations were conducted for purebred H and crossbred (H × Other (O) breeds). The intrabreed genetic evaluation procedure used by DPO deviated genetic predictions from a base expressed in *Bos taurus* (BT) and *Bos indicus* (BI) fractions. Improved versions of intrabreed animal models were used by Koonawootrittriron *et al.* (2002) to evaluate all animals in a 1991-2000 accumulated DPO data set. Koonawootrittriron *et al.* (2002) considered two genetic bases, the one used by DPO, based on BT and BI fractions (BTBI model) and another one that deviated genetic predictions from a Holstein (H) and Other Breed (O) base (HO model). The HO base was used to account for the fact that nearly all animals in the DPO population had some H fraction.

Because of the existence of purebred and crossbred animals in the DPO data set, multibreed genetic evaluation procedures (Elzo, 1983; Elzo and Famula, 1985) need to be explored. Multibreed procedures yield more detailed genetic predictions (additive, nonadditive, total) than the previously used intrabreed procedures (additive only). Multibreed additive genetic predictions refer to allelic deviations from a common multibreed genetic base. Multibreed nonadditive genetic effects consider intrabreed and interbreed intralocus interactions between sire and dam alleles. Multibreed total genetic predictions are simply the sum of additive and nonadditive genetic predictions. The same two genetic bases studied in unibreed models by Koonawootrittriron *et al.* (2002), however, because of the complexity of multibreed models and the small size of the available DPO data set, sire-maternal grandsire multibreed models will be used instead of animal models.

Thus, the objectives of this study were: 1) to estimate additive, nonadditive, and total genetic covariance components and genetic parameters for 305-d milk yield, 305-d fat yield, and 305-d fat percentage, using multibreed sire-maternal grandsire BTBI and HO models, and 2) to compare sire additive, nonadditive, and total multibreed predicted genetic values (MPGV) obtained from the multibreed BTBI and HO models.

Materials and Methods

Animals, Records, and Traits

The base DPO data set used here was the same one used by Koonawootrittriron *et al.* (2002). This unedited data set consisted of first lactation 12,505 monthly test-day milk yields, and 10,042 monthly test-day fat percentages from 921 cows located in 68 farms in Central Thailand, and collected between 1991 and 2000. Test-day fat yields (10,042) were computed by multiplication of test-day milk yields and test-day fat percentages. Subsequently, 1) 305-d fat percentage (FP) was computed as the average of all test-day fat percentages, and 2) 305-d milk

yield (MY) and 305-d fat yield (FY) were computed using formula [1] in Koonawootrittriron *et al.* (2002). For completeness, this formula is:

$$TPY = (P_1 \times D_1) + \sum_{i=2}^{k}[(\frac{P_i + P_{i-1}}{2}) \times D_i] + (P_{k+1} \times D_{k+1}) \qquad [1]$$

where TPY is the 305-d production yield (MY or FY) of a cow, P_1 is the test-day production yield sample in the first month after calving, D_1 is the interval between five days after calving and the last day of the fist sampling month, P_i is the test-day production yield sample in month i (i = 2, … , k), D_i is the interval between the last day of month i - 1 and i (i = 2, … , k), P_{k+1} is the test-day production yield sample in the last month of reaching 305-d in lactation, and D_{k+1} is the interval between the 305-d of lactation and the last day of the month before reaching 305-d in lactation. A program was written in SAS to perform these computations (SAS, 1990).

The resulting data set containing MY, FY, and FP was used as input file for program THAIPED (Elzo, 2000a) to create a pedigree and an edited data file. Only cows with measurements in all three traits (MY, FY, and FP) were included in the edited data file. The edited data file was tested for connectedness between sires and herd-year-season subclasses using program THAICSET (Elzo, 2000b). Cow records from single sire herd-year-seasons were eliminated. Only herd-year-season subclasses with two or more sires, one of them represented in two or more herd-year-season subclasses became part of the largest connected data set. The resulting multibreed connected data set contained MY, FY, and FP from 481 cows. The connected data set and the pedigree file were used as input files for the MREMLEM program (Elzo, 2001) to compute additive and nonadditive genetic, environmental, and phenotypic covariance components, as well as covariance ratios (heritabilities, interactibilities, and genetic, environmental, and phenotypic correlations).

Table 1. Numbers of sires, dams, and calves by breed-group-of-sire × breed-group-of-dam combination

| Breed-group-of-dam | Breed-group-of-sire | | |
	Holstein	(0.63-0.99)H (0.37-0.01)O [1]	Jersey
(0.8-1.0)H (0.2-0.0)O	78 [2]	4	1
	115 [3]	9	3
	127 [4]	9	3
(0.6-0.8)H (0.4-0.2)O	103	6	2
	168	12	2
	178	12	2
(0.4-0.6)H (0.6-0.4)O	76	5	1
	92	7	1
	106	7	1
(0.2-0.4)H (0.8-0.6)O	17	2	-
	15	2	-
	17	2	-
(0.0-0.2)H (1.0-0.8)O	14	1	-
	15	2	-
	15	2	-

[1] H = Holstein, O = Other breeds: Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane; [2] Number of sires; [3] Number of dams; [4] Number of fe males with records.

Table 1 contains numbers of sires, dams, and females with records in the multibreed connected data set by breed-group-of-sire × breed-group-of-dam combination. On the sire side, these numbers clearly reflect the government suggestion of utilizing H semen on the existing cow population. On the dam side, the number suggest that the preferred cows were 60% to 80% H, with smaller numbers above 80% H and below 60% H. Use of straightbred sires of breeds other than H was almost nonexistent. The crossbred H bulls used amounted to less than 6% of the H sires. This may have been due in part to lack of connectedness (e.g., single-sire herd-year-seasons) of crossbred sires. Numbers of sires, dams, and cows with records classified according to their BT and BI fractions were similar to numbers in the first two columns of Table 1.

Table 2 shows the phenotypic means and standard deviations for each trait by breed-group-of-sire × breed-group-of-dam combination as defined in Table 1. Table 2 also contains means and standard deviations by breed group of sire (last 3 rows), and by breed group of dam (last column), and for the complete multibreed data set (last 3 cells of the Overall column). Daughters of H sires produced more milk and fat than daughters of other breed groups. Sixty to eighty percent H crossbred cows had higher milk and fat production levels than any other breed group, although their means were close to 80% to 100% H and 40% to 60% H dams.

Table 2. Means and standard deviations for milk yield, fat yield, and fat percentage by breed-group-of-sire × breed-group-of-dam combination

	Breed-group-of-sire			
Breed-group-of-dam	Holstein	(0.63-0.99)H (0.37-0.01)O [1]	Jersey	Overall
(0.8-1.0)H (0.2-0.0)O	4,116.11±1,167.91[2]	3,541.22±1,134.84	3,670.33±389.69	4,069.27±1,160.11
	150.39±36.55 [3]	133.33±45.10	148.00±9.54	149.22±44.67
	3.66±0.38 [4]	3.79±0.40	3.93±0.25	3.67±0.38
(0.6-0.8)H (0.4-0.2)O	4,202.53±1,153.57	3,381.75±1461.46	3,073.50±983.59	4,139.47±1,188.67
	155.28±44.06	129.50±54.60	111.00±42.43	153.21±45.14
	3.73±0.43	3.86±0.33	3.55±0.21	3.73±0.42
(0.4-0.6)H (0.6-0.4)O	4,058.58±1,125.15	4,113.14±1,004.98	.	4,063.04±1,109.17
	150.18±37.23	157.86±35.14	.	150.94±41.59
	3.72±0.41	3.83±0.34	.	3.74±0.41
(0.2-0.4)H (0.8-0.6)O	3,774.29±1,619.58	2,531.50±617.30	.	3,643.47±1,583.13
	138.94±58.11	90.50±36.06	.	133.84±57.51
	3.71±0.35	3.50±0.57	.	3.69±0.37
(0.0-0.2)H (1.0-0.8)O	3,597.93±1,270.55	2,270.50±161.93	.	3,500.59±1,220.52
	133.40±49.91	114.00±8.49	.	131.12±47.18
	3.71±0.37	4.15±0.34	.	3.76±0.41
Overall	4,106.41±1,177.22	3,495.25±1,218.39	3,557.17±657.62	4,058.90±1,184.45
	151.29±44.77	133.38±46.37	141.50±33.74	149.97±44.92
	3.70±0.40	3.83±0.37	3.88±0.37	3.72±0.40

[1] H = Holstein, O = Other breeds: Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane; [2] milk yield (kg); [3] fat yield (kg); [4] fat percentage (%).

Estimation of Multibreed Covariance Components and Genetic Predictions

Covariance components were estimated using multibreed restricted maximum likelihood procedures (MREMLEM; Elzo, 1994, 1996). The MREMLEM procedure uses a generalized expectation-maximization (GEM) algorithm (Dempster *et al.*, 1977) to compute MREMLEM covariance components. The MREMLEM program (Elzo, 2001) computes additive and nonadditive genetic, and environmental covariance matrices simultaneously. To ensure that all variances and covariances were within their permissible ranges, the Cholesky matrices of

covariance matrices were computed first, and then the covariance matrices themselves by multiplying the Cholesky matrices by their transposes (Elzo, 1996).

A disadvantage of expectation-maximization algorithms is that they do not compute the information matrix. However, although the MREMLEM did not provide standard errors, large standard errors of estimation of covariance components should be expected because of the unbalancedness and the small size of the data set.

Multibreed Model. The model used was a multibreed sire-maternal grandsire model that accounted for intrabreed additive genetic effects, and intralocus intra and interbreed nonadditive genetic effects. Although desirable, the structure and size of the data set prevented the use of a multibreed animal model. Preliminary analyses showed that the extreme unbalancedness of the data caused confounding and multicollinearity among additive and nonadditive sire genetic group effects, thus unbiased estimates of them were impossible to obtain. Consequently, the final form of the multibreed sire-maternal grandsire model contained random additive and nonadditive sire genetic effects, and accounted for additive and nonadditive genetic as well as environmental heterogeneity of variances and covariances across breed group combinations (BT and BI in the BTBI model, and H and O, in the HO model). Because sire genetic group effects were not included in the model, sire additive, nonadditive, and total multibreed genetic predictions for the BTBI and HO models were deviated from common pooled additive-nonadditive genetic bases within each model (BTBI multibreed base, and HO multibreed base).

The data set permitted the analysis of at most two traits at a time. Thus, there were three computer runs for the BTBI and the HO models: 1) MY and FY, 2) MY and FP, and 3) FY and FP. These analyses yielded two estimates of variances for each trait and a single covariance. Each pair of variance estimates (for MY, FY, and FP) was averaged to produce a single variance estimate.

The multibreed sire-maternal grandsire model for a two-trait analysis was as follows.

$$y = Xb + Z_{mg}\,g_{mg} + Z_a\,u_a + Z_n\,u_n + e \qquad\qquad [2]$$

$$
\begin{aligned}
E[y] &= Xb + Z_{mg}\,g_{mg} \\
var(y) &= Z_a\,G_a\,Z_a{}' + Z_n\,G_n\,Z_n{}' + R
\end{aligned}
$$

where

y = vector of cow records, ordered by traits within cows,

b = vector of fixed environmental effects: herd-year-seasons, and a covariate for age of dam effects modeled as a function of the BT fraction of the dam (BTBI model), and the H fraction of the dam (HO model). Seasons were classified as winter (November to February), summer (March to June), and rainy (July to October).

g_{mg} = vector of fixed maternal granddam and unknown maternal grandsire regression genetic group effects. In the DPO data set, the g_{mg} vector contained dam regression genetic group effects because all dams of cows had unknown sires.

u_a = vector of random sire and maternal grandsire additive direct genetic effects,

u_n = $[u_{n1}\ u_{n2}\ u_{n3}\ ]'$ = vector of random sire nonadditive intralocus direct genetic effects: two intrabreed (BT×BT, BI×BI, BTBI model; H×H, O×O, HO model) and one interbreed (BT×BI, BTBI model; H×O, HO model). Sire nonadditive intralocus direct genetic effects are defined to be due to intralocus intrabreed and interbreed interactions between alleles from a sire and alleles from dams of all breed groups mated to a particular sire. These interactions measure the average interactive ability of a sire across all breed groups of dams, i.e., the interactive ability of a sire within a sire subclass. Intralocus interactions within a sire subclass yield an

incomplete assessment of dominance effects. To have a complete assessment of dominance effects a statistical model would also have to have terms for the interactive ability of a dam within a dam subclass, and for the interactive ability of a specific sire × dam combination. Thus, the sire maternal grandsire model used here predicts only an average dominance effect in the progeny of an individual sire and dams of all breed groups in a multibreed population. It is an *approximation* to a complete multibreed model capable of measuring all intrabreed and interbreed dominance effects. The complete nonadditive model was not computationally feasible with the DPO data set.

e = vector of residual effects,

X = incidence matrix relating cow records to elements of b. The elements of X are ones, zeroes, and BT fraction of dams (BTBI model) or H fraction of dams (HO model),

Z_{mg} = incidence matrix relating cow records to elements of g_{mg}. The elements of Z_{mg} for the BTBI model are the BT fractions of maternal granddams, BT fractions of unknown maternal grandsires, and zeroes. For the HO model, the elements of Z_{mg} are H fractions of maternal granddams, H fractions of unknown maternal grandsires, and zeroes. For example, a 7/8 BT 1/8 BI daughter of a BT sire and a 3/4 BT 1/4 BI dam would contribute with a .5 to her maternal granddam group, and a 1 to her unknown maternal grandsire group.

Z_a = incidence matrix relating cow records to elements of u_a. The elements of Z_a are ones if sires of cows are known, .5's if maternal grandsires of cows are known, and zeroes.

Z_n = incidence matrix relating cow records to elements of u_n through probabilities of intrabreed and interbreed intralocus combinations in females with records. The elements of Z_n are probabilities of alleles of base populations BT and(or) BI in a single locus. Matrix Z_n = block-diagonal $\{Z_{n1} Z_{n2} Z_{n3}\}$. For the BTBI model: 1) the elements of Z_{n1} are the intralocus probabilities of ($BT_{sire of cow}$, $BT_{dam of cow}$), 2) the elements of Z_{n2} are the intralocus probabilities of ($BI_{sire of cow}$, $BI_{dam of cow}$), and 3) the elements of Z_{n3} are the intralocus probabilities of $[(BT_{sire of cow}, BI_{dam of cow}) + (BI_{sire of cow}, BT_{dam of cow})]$. Substitute H for BT and O for BI in the previous probabilities. For example, a 3/4 BT 1/4 BI daughter of a BT sire and a 1/2 BT 1/2 BI dam would contribute with .5 to Z_{n1}, 0 to Z_{n2}, and .5 to Z_{n3}.

G_a = $var(u_a)$ = multibreed sire and maternal grandsire additive genetic covariance matrix. (Elzo, 1990a, 1994). Matrix $G_a = T^T B_a T$, where 1) T is a lower triangular matrix that has ones on the diagonal, .5's in the off-diagonals between an animal in u_a and his sire if known, .25's in the off-diagonals between an animal in u_a and his maternal grandsire if known, and zeroes elsewhere, 2) T^T is the transpose of T, and 3) B_a is a block-diagonal matrix (block size = nt × nt, nt = number of traits) of sire and maternal grandsire multibreed residual genetic variances and covariances. The nt × nt covariance matrix for the ith sire or maternal grandsire in vector u_a is equal to $var(u_{ai})$ – {$var(1/2\ u_{asi})$, if si is known} – {$var(1/4\ u_{ami})$, if mi is known}, where the subscripts i = individual (sire or maternal grandsire) in u_a, si = sire of individual in u_a, and mi = maternal grandsire of individual in u_a. If there is no inbreeding, the $var(u_{ai}) = p_{BTi}\ var(a_{BT}) + p_{BIi}\ var(a_{BI}) + (p_{BTsi}\ p_{BIsi} + 1/4\ p_{BTmi}\ p_{BImi})\ var(a_{BTBI})$ in a sire-maternal grandsire model, where: 1) p_{Xy} = fraction of base population X (X = BT, BI) alleles in animal y, y = i (sire or maternal grandsire in u_a), si (sire of i), and mi (maternal grandsire of i), 2) $var(a_X)$ = additive genetic variance in base

population X, X = BT, BI, and 3) var(a_{BTBI}) = additive genetic variance due the presence of alleles of base populations BT and BI in the same individual. The var(a_{BTBI}) is an additional additive variance present in crossbred animals because the mean effects of alleles differs across base populations. This variance was called segregation variance by Wright (1968), and it is proportional to the fraction of heterozygous loci in the *parents* of an individual. The var($1/2\ u_{asi}$) and var($1/4\ u_{ami}$) are computed in similar fashion. For the HO model substitute H for BT and O for BI in the preceding formulas. For example, the multibreed additive genetic variance of a 3/4 BT 1/4 BI sire, whose sire was BT, his dam was 1/2 BT 1/2 BI, his maternal grandsire was BT, and his maternal granddam was BI, is equal to 3/4 var(a_{BT}) + 1/4 var(a_{BI}) + [$1 \times 0 + 1/4\ (1 \times 0)$] var($a_{BTBI}$). Because matrix T relates animals to its ancestors, recurrent formulas can be used to construct G_a and its inverse G_a^{-1} (for specific details on these computational procedures with and without inbreeding, see Elzo, 1990a). These recurrent procedures require knowledge of only base population covariances. Multibreed covariances are computed as linear combinations of base covariances as described above for the BTBI and HO cases.

G_n = var(u_n) = var([$u_{n1}\ u_{n2}\ u_{n3}$]') = block-diagonal multibreed sire regression nonadditive genetic covariance matrix (Elzo, 1990b, 1994). The term regression refers to the fact sire $\times$ breed-group-of-dam intralocus interaction effects were modeled as a function of intra and interbreed intralocus interactions. Matrix G_n = block-diagonal{$G_{n1}\ G_{n2}\ G_{n3}$}. Each submatrix G_{nj}, j = 1,2,3, can be written in the same form as the matrix of additive genetic effects. Thus, matrix $G_{nj} = T^T B_{ni} T$, where 1) T and T^T are the same matrices described above for G_a, and 2) B_{nj} is a block-diagonal matrix (nt $\times$ nt blocks) with elements equal to var(u_{nji}) – {var($1/2\ u_{njsi}$), if si is known} – {var($1/4\ u_{njmi}$), if mi is known}, where the subscripts i = individual in u_{nj}, si = sire of individual in u_{nj}, and mi = maternal grandsire of individual in u_{nj}. If there is no inbreeding, the var(u_{nji}) = var(u_{njsi}) = var(u_{njmi}) = var(u_{nj}). Thus, var(u_{nji}) = (1 – {1/2 , if si is known} – {1/4 , if mi is known}). Recurrent computational procedures that can be used to compute each submatrix G_{nj}, j = 1,2,3, and their inverses are described in detail in Elzo (1990b).

and,

R = block-diagonal (nt $\times$ nt blocks) multibreed residual covariance matrix. The nt $\times$ nt matrix for the ith cow with nt records is equal to the sum of the nt $\times$ nt multibreed residual genetic covariance matrix for cow i + the nt $\times$ nt multibreed residual environmental covariance matrix for cow i. Residual environmental effects here are assumed to contain environmental effects and nonadditive genetic effects not explained by $Z_n u_n$ in the model. Thus, residual environmental covariance matrices are a function of environmental covariances, and nonadditive genetic covariances due to nonadditive genetic effects not accounted for in the sire-maternal grandsire model. The nt $\times$ nt multibreed residual genetic covariance matrix for cow i is computed using the same formulas described to compute the diagonal submatrices of G_a above, except that here subscripts i = cow i, si = sire of cow i, and mi = maternal grandsire of cow i. The nt $\times$ nt multibreed residual environmental covariance matrix for cow i is also computed using the formulas used to compute the diagonal submatrices of G_a above, except that: 1) subscripts i = cow i, si = sire of cow i, and mi = maternal grandsire of cow i, and 2) multibreed residual environmental covariances replace multibreed additive genetic covariances. For

additional details on the construction of R see Elzo (1994) and Elzo and Wakeman (1998).

MREMLEM Algorithm. The starting values used for the two-trait MREMLEM analyses were variance estimates (additive and nonadditive genetic, and environmental) from preliminary single-trait MREMLEM analyses, and zeroes for all covariances between traits. In the estimation step, the multibreed mixed model equations were set up by storing only nonzero elements of the left and right hand sides. Multibreed computational algorithms were used to obtain the inverse of the multibreed additive covariance matrix (Elzo, 1990a), and the inverse of the regression nonadditive genetic covariance matrix (Elzo, 1990b). In the maximization step, covariances were estimated using the Cholesky maximization strategy (Elzo, 1996). The convergence criterion was that the square root of the ratio of the sum of squares of the differences between covariance estimates in two successive GEM iterations, divided by the sum of squares of the covariances in the first of them, was less than 10^{-4}.

Base Genetic, Environmental, and Phenotypic Covariances. Separate sets of three pairwise runs (MY-FY, MY-FP, and FY-FP) were conducted to estimate base covariance components for the BTBI and HO models. Seven 3×3 matrices were computed for each model. For the BTBI model, these matrices were: 1) two additive genetic intrabreed (BT and BI), 2) three nonadditive genetic intralocus (intrabreed BT/BT and BI/BI, and interbreed BT/BI), and 3) two environmental (BT and BI). The corresponding matrices for the HO model were: 1) two additive genetic intrabreed (H and O), 2) three nonadditive genetic intralocus (intrabreed H/H and O/O, and interbreed H/O), and 3) two environmental (H and O). The elements of each covariance matrix were: var(MY), cov(MY,FY), cov(MY,FP), var(FY), cov(FY,FP), and var(FP).

Multibreed Genetic Covariances and Genetic Parameters. Base covariance estimates were used to compute multibreed covariances and genetic parameters (heritabilities, interactibilities, genetic, environmental, and phenotypic correlations) for specific breed group combinations. Here, interactibility refers to *intrabreed and interbreed* nonadditive interactions between alleles from *individual sires* and alleles from *all dams* mated to them.

Multibreed additive and nonadditive genetic, environmental, and phenotypic covariances were obtained as weighted averages of appropriate base covariances (Elzo, 1994; Elzo and Wakeman, 1998). As an example, consider MY and FY, and breed group combination BT × 3/4BT 1/4BI:

1) the (MY,FY) multibreed additive genetic covariance is equal to (probability of BT alleles in breed group combination BT × 3/4BT 1/4BI) × additive cov(BT_{MY}, BT_{FY}) + (probability of BI alleles in breed group combination BT × 3/4BT 1/4BI) × additive cov(BI_{MY}, BI_{FY}) + (probability of BT *and* BI alleles in 3/4BT 1/4BI and in BT, *assumed* to be zero in this research) × additive cov($BTBI_{MY}$, $BTBI_{FY}$),

2) the (MY,FY) multibreed nonadditive genetic covariance is equal to (probability of BI/BT intralocus interactions in breed group combination BT × 3/4BT 1/4BI) × nonadditive cov(BT/BI_{MY}, BT/BI_{FY}) + (probability of BT/BT intralocus interactions in breed group combination BT × 3/4BT 1/4BI) × nonadditive cov(BT/BT_{MY}, BT/BT_{FY}),

3) the (MY,FY) multibreed environmental covariance is equal to (probability of BT alleles in breed group combination BT × 3/4BT 1/4BI) × environmental cov(BT_{MY}, BT_{FY}) + (probability of BI alleles in breed group combination BT × 3/4BT 1/4BI) × environmental cov(BI_{MY}, BI_{FY}) + (probability of BT *and* BI alleles in 3/4BT 1/4BI and in BT, *assumed* to be zero in this research) × environmental cov($BTBI_{MY}$, $BTBI_{FY}$), and

4) the (MY,FY) multibreed phenotypic covariance is equal to the sum of the multibreed additive + nonaddditive + environmental covariances.

Additive and nonadditive genetic, environmental, and phenotypic ratios were computed using the multibreed covariances computed for each considered breed group combination. As an example, consider again breed group combination BT × 3/4BT 1/4BI:

1) its heritability for MY is the ratio of its multibreed additive genetic variance for MY and its phenotypic variance for MY,
2) its interactibility for MY is the ratio of its multibreed nonaddditive genetic variance to its phenotypic variance for MY,
3) its (MY,FY) multibreed additive correlation is the ratio of its (MY, FY) multibreed additive covariance to the product of its multibreed additive standard deviations for MY and FY,
4) its (MY,FY) multibreed nonaddditive correlation is the ratio of its (MY, FY) multibreed nonaddditive covariance to the product of its multibreed nonaddditive standard deviations for MY and FY,
5) its (MY,FY) multibreed environmental correlation is the ratio of its (MY, FY) multibreed environmental covariance to the product of its multibreed environmental standard deviations for MY and FY, and
6) its (MY,FY) multibreed phenotypic correlation is the ratio of its (MY, FY) multibreed phenotypic covariance to the product of its multibreed phenotypic standard deviations for MY and FY.

Multibreed Genetic Predictions. Two additional two-trait runs were carried out to compute sire additive, nonaddditive, and total multibreed predicted genetic values (MPGV) using the average variances and of covariances estimated from the two-trait analyses. The first run (MY-FY) computed sire predictions for MY and FY, and the second run (MY-FP) sire predictions for FP. For nonaddditive and total MPGV, it was assumed that all sires were to be mated to 1/2BT 1/2BI females (BTBI model) and 1/2H 1/2O females (HO model).

Three predictions per sire were obtained for the BTBI and the HO models. For the BTBI model, these sire predictions were:

1) sire additive MPGV = sire additive predictions from the mixed model equations,
2) sire nonaddditive MPGV = fraction (BT/BT) × sire MPGV for BT/BT + fraction (BI/BI) × sire MPGV for BI/BI + fraction (BT/BI) × sire MPGV for BT/BI, and
3) sire total MPGV = sire additive MPGV + sire nonaddditive MPGV.

For the HO model, H must be substituted for BT and O for BI. Standard errors of prediction were computed as: 1) the square root of the diagonal elements of the inverse of the left hand side of the multibreed mixed model equations for sire additive MPGV, and 2) the square root of linear combinations of variance of prediction errors from the inverse of the left-hand side of the multibreed mixed model equations for sire nonaddditive and total MPGV.

Results and Discussion

Multibreed Covariance Component and Genetic Parameter Estimates

Base covariances. Table 3 contains multibreed REML estimates of base additive genetic, nonaddditive genetic and environmental covariances for MY, FY, and FP obtained using the BTBI and the HO models. Substantially larger values of base additive genetic covariance estimates were obtained for BI than for BT for all traits, suggesting possible differences in the amount of additive genetic variability present in these two populations. Similar differences were

obtained when H and O were defined as the base populations, which is not surprising given all but three of the sires present in the data set were either H or H crossbreds. The opposite situation occurred for base environmental covariance estimates, which were larger for BT (and H) than for BI (and O), indicating perhaps a wider range of adaptive abilities in BT (and H) animals. Base nonadditive genetic covariances had the smallest estimates for BT/BT (and H/H) interactions, nonadditive covariances due to BT/BI had intermediate values, and the largest values were those due to BI/BI interactions, reaffirming the suggestion of larger genetic variability in BI animals. These estimates, however, must be viewed with caution because of the small size and the skewed distribution of the data towards BT and H.

Table 3. Estimates of base additive genetic, nonadditive genetic, and environmental covariances for 305-d milk yield (MY), fat yield (FY), and fat percentage (FP) by the BTBI and HO models

Covariance components [1]	MY, MY (kg^2)	MY, FY (kg^2)	MY, FP $(kg \times \%)$	FY, FY (kg^2)	FY, FP $(kg \times \%)$	FP, FP $(\%^2)$
BTBI Model:						
Additive intrabreed BT	69,601	1,068.6	-0.89	84.3	-0.04	0.02
Additive intrabreed BI	781,418	25,504.0	1.22	1242.7	0.86	0.13
Nonadditive intrabreed BT/BT	60,020	1,281.3	-0.86	61.9	0.01	0.01
Nonadditive intrabreed BI/BI	465,600	34.9	0.00	670.1	0.00	0.05
Nonadditive interbreed BT/BI	236,174	3,615.3	-0.36	359.4	0.08	0.04
Environmental intrabreed BT	616,096	22,286.3	-62.9	884.9	1.92	0.09
Environmental intrabreed BI	85,815	0.0	-4.88	2.1	0.33	0.06
HO Model:						
Additive intrabreed H	58,870	1397.9	1.72	99.1	-0.02	0.01
Additive intrabreed O	548,541	11987.1	-27.78	635.7	0.50	0.21
Nonadditive intrabreed H/H	70,134	1660.6	-0.84	91.9	0.02	0.01
Nonadditive intrabreed O/O	443,451	380.9	0.08	688.2	0.01	0.05
Nonadditive interbreed H/O	138,869	2713.5	-0.72	211.0	0.04	0.04
Environmental intrabreed H	703,975	25,255.0	-47.31	989.6	1.86	0.08
Environmental intrabreed O	3,335	0.0	-109.58	2.3	2.78	3.85

[1] BT = *Bos Taurus*, BI = *Bos indicus*, H = Holstein, O = Other breeds: Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane.

Multibreed covariances. Multibreed additive and nonadditive genetic covariances for BT×BI (and H×O) crossbred groups reflect the combined variation due to BT and BI (or H and O) alleles. Table 4 shows estimates of multibreed additive genetic, nonadditive genetic, and environmental covariances for six breed group combinations: BT × BT, BT × 3/4BT 1/4BI, BT × 1/2BT 1/2BI, BT × 1/4BT 3/4BI, BT × BI, and 3/4BT 1/4BI × 3/4BT 1/4BI. These breed group combinations were chosen because they represented the mating types most represented in the DPO data set. Additive genetic, nonadditive genetic, and environmental multibreed covariances were computed as linear combinations of appropriate base additive, nonadditive, and environmental covariances. Except for breed group combinations representing the base populations (BT, BI, H, and O), information from all base covariances was used to compute multibreed covariances. Thus, their accuracy should be higher than that of base covariances.

Estimates of multibreed covariances in Table 4 were reasonable given that sires in this multibreed population were primarily H, and dams were from various *Bos indicus* and, to a lesser extent, from various *Bos taurus* breeds. Assuming that the sample of H sires brought into the DPO cattle population were genetically more similar to one another than a random sample from the H population, it is reasonable to expect estimates of genetic covariances for MY, FY, and FP,

from these bulls to be smaller than that of the H population. The small values of the H genetic covariance estimates for MY, FY, and FP in BT (or H) support this assumption. On the other hand, genetic covariance estimates for MY, FY, and FP were much larger for BI, perhaps due to lack of selection for milk traits in *Bos indicus* animals. Similarly high genetic covariance estimates were obtained for O, due to the presence not only of *Bos indicus* genetic material but also to genetic effects from three Jersey sires.

Table 4. Estimates of multibreed additive genetic, nonadditive genetic, and environmental covariances for 305-d milk yield (MY), fat yield (FY), and fat percentage (FP) for six breed group combinations by model

Covariance components [1]		MY, MY (kg^2)	MY, FY (kg^2)	MY, FP $(kg \times \%)$	FY, FY (kg^2)	FY, FP $(kg \times \%)$	FP, FP $(\%^2)$
BTBI Model							
BT × BT:	Additive	69,601	1,068.6	-0.89	84.3	-0.04	0.02
	Nonadditive	60,020	1,281.3	-0.86	61.9	0.01	0.01
	Environmental	616,096	22,286.3	-62.90	884.9	1.92	0.09
BT × 3/4BT 1/4BI:	Additive	158,579	4,123.1	-0.63	229.1	0.08	0.03
	Nonadditive	104,059	1,864.8	-0.74	136.3	0.03	0.02
	Environmental	549,811	19,500.5	-55.64	774.5	1.72	0.08
BT × 1/2BT 1/2BI:	Additive	247,556	7,177.5	-0.37	373.9	0.18	0.04
	Nonadditive	148,097	2,448.3	-0.61	210.7	0.04	0.03
	Environmental	483,526	16,714.8	-48.40	664.2	1.52	0.08
BT × 1/4BT 3/4BI:	Additive	336,533	10,231.9	-0.10	518.7	0.30	0.06
	Nonadditive	192,136	3,031.8	-0.48	285.0	0.06	0.04
	Environmental	417,241	13,929.0	-41.14	553.8	1.32	0.08
BT × BI:	Additive	425,510	13,286.3	0.16	663.5	0.04	0.07
	Nonadditive	236,174	3,615.3	-0.36	359.4	0.08	0.04
	Environmental	350,956	11,143.2	-33.90	443.5	1.12	0.07
3/4BT 1/4BI × 3/4BT 1/4BI: Additive		247,556	7,177.5	-0.37	373.9	0.19	0.04
	Nonadditive	151,427	2,078.6	-0.62	211.5	0.04	0.03
	Environmental	483,526	16,714.8	-48.40	664.2	0.15	0.08
HO model							
H × H:	Additive	58,870	1397.9	1.72	99.1	-0.02	0.01
	Nonadditive	70,134	1660.6	-0.84	91.9	0.02	0.01
	Environmental	703,975	25,255	-47.31	989.6	1.86	0.08
H × 3/4H 1/4O:	Additive	120,079	2,721.5	-1.97	166.2	0.04	0.03
	Nonadditive	87,318	1,923.8	-0.81	121.7	0.02	0.02
	Environmental	616,395	22,098.1	-55.10	866.2	1.98	0.54
H × 1/2H 1/2O:	Additive	181,288	4,045.2	-5.65	233.3	0.11	0.05
	Nonadditive	104,501	2,187.1	-0.78	151.5	0.03	0.02
	Environmental	528,815	18,941.2	-62.87	742.8	2.09	1.02
H × 1/4H 3/4O:	Additive	242,497	5,368.8	-9.34	300.3	0.17	0.08
	Nonadditive	121,685	2,450.3	-0.75	181.2	0.03	0.03
	Environmental	441,235	15,784.4	-70.66	619.4	2.21	1.49
H × O:	Additive	303,706	6,692.5	-13.03	367.4	0.24	0.10
	Nonadditive	138,869	2,713.5	-0.72	211.0	0.04	0.04
	Environmental	353,655	12,627.5	-78.45	496.0	0.23	1.96
3/4H 1/4O × 3/4H 1/4O: Additive		181,288	4,045.2	-5.65	233.3	0.11	0.05
	Nonadditive	119,242	1,975.5	-0.74	173.8	0.02	0.02
	Environmental	528,815	18,941.2	-62.88	742.8	2.09	1.02

[1] BT = *Bos Taurus*, BI = *Bos indicus*, H = Holstein, O = Other breeds: Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane.

Estimates of environmental covariances were about 10 times the value of genetic covariances for BT (and H), but only up to 5 times the value of genetic covariances for crossbred groups (Table 4). These values may be an indication of a larger effect of tropical environmental conditions (e.g., heat, humidity, parasitic load) on BT (or H) animals than on BI (or O) animals, and that crossbred animals show more environmental resilience than purebred BT (or H) animals.

Estimates of genetic and environmental covariances (Table 4) and of covariance ratios (Tables 5, 6, and 7) provide a more detailed representation of the kinds and amounts of variability present in the DPO multibreed population compared to the sets of covariances and covariance ratios estimated in the unibreed analyses of Koonawootrittriron *et al.* (2002). When unibreed REML procedures are used with multibreed data sets they estimate *across-breed-group* covariances and genetic parameters. Thus, covariance and genetic parameters estimated by Koonawootrittriron *et al.* (2002) represent the variability among animals from all breed group combinations present in the DPO multibreed population. On the other hand, multibreed REML procedures estimate *within-breed-group* covariances and genetic parameters. Consequently, a different set of covariances and genetic parameters is estimated for animals from each breed group combination.

Multibreed heritabilities and additive genetic correlations. Estimates of heritabilities (Table 5) were low for all traits in the BT (0.09 for MY, 0.08 for FY, and 0.13 for FP), and the H (0.07 for MY, 0.08 for FY, and 0.04 for FP) base populations. These heritability estimates suggest that the H semen imported to Thailand came from H sires of similar genetic background for MY, FY, and FP, and(or) that purebred H progenies from these H sires would have rather similar performances under the climatological, management, nutritional, and health care conditions of the herds included in the DPO data set. This conjecture needs to be validated using a multibreed animal model when additional multibreed data becomes available.

Table 5. Estimates of heritabilities and additive genetic correlations for 305-d milk yield (MY), fat yield (FY), and fat percentage (FP) for six breed group combinations by model

Breed group combination [1]	Genetic Parameter [2]					
	h^2 (MY)	r_A (MY, FY)	r_A (MY, FP)	h^2 (FY)	r_A (FY, FP)	h^2 (FP)
BTBI Model:						
BT × BT	0.09	0.44	-0.03	0.08	-0.03	0.13
BT × 3/4BT 1/4BI	0.20	0.68	-0.01	0.20	0.03	0.23
BT × 1/2BT 1/2BI	0.28	0.75	0.00	0.30	0.05	0.29
BT × 1/4BT 3/4BI	0.36	0.77	0.00	0.38	0.05	0.35
BT × BI	0.42	0.79	0.00	0.45	0.06	0.39
3/4BT 1/4BI × 3/4BT 1/4BI	0.28	0.75	0.00	0.30	0.05	0.30
HO Model:						
H × H	0.07	0.58	0.11	0.08	-0.04	0.04
H × 3/4H 1/4O	0.15	0.61	-0.03	0.14	0.02	0.05
H × 1/2H 1/2O	0.22	0.62	-0.06	0.21	0.03	0.05
H × 1/4H 3/4O	0.30	0.63	-0.07	0.27	0.03	0.05
H × O	0.38	0.63	-0.07	0.34	0.04	0.05
3/4H 1/4O × 3/4H 1/4O	0.22	0.62	-0.06	0.20	0.03	0.05

[1] BT = *Bos Taurus*, BI = *Bos indicus*, H = Holstein, O = Other breeds: Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane; [2] h^2 = heritability, r_A = additive genetic correlation.

Because of the influence of the BI (and O) base covariances, heritability estimates for crossbred groups were substantially higher than for BT or H. For example, estimates of heritability for the largest breed group combination under the BTBI model, BT × 3/4BT 1/4BI, were 0.20 for MY, 0.20 for FY, and 0.23 for FP. The corresponding values for the largest breed

group combination under the HO model, H × 3/4H 1/4O, were 0.15 for MY, 0.14 for FY, and 0.05 for FP. These heritability estimates seem appropriate because low levels of variation should be expected in this data set due to its small size and because H was the predominant breed fraction in most animals. The range of heritability estimates across crossbred groups (Table 5) was 0.20 to 0.42 for MY, 0.20 to 0.45 for FY, and 0.23 to 0.39 for FP in the BTBI model, and 0.15 to 0.38 for MY, 0.14 to 0.34 for FY, and 0.05 to 0.05 for FP in the HO model. The upper limit of these ranges is close to, but still below, the heritability values estimated using unibreed REML procedures by Kuha (1999) and Koonawootrittriron *et al.* (2002), but similar to the heritability values obtained for these traits by Kanloung *et al.* (1999). This agrees with the expectation of higher estimates of covariances when computed across breed group combinations using unibreed REML.

Multibreed additive genetic correlations between MY and FY were all positive (Table 5) for all breed group combinations under the BTBI and the HO models, as expected given the part-whole relationship that exists between these two traits. Correlation values between MY and FY ranged from 0.44 to 0.79, thus they were substantially lower than the 0.99 values obtained by Koonawootrittriron *et al.* (2002), and more in agreement with correlation values obtained for H in Thailand (Pootong, 1987; Kanloung *et al.*, 1999; Kuha, 1999) and in other tropical countries (Australia: Visscher and Goddard, 1995; Brazil: Costa *et al.*, 2000). Additive genetic correlation estimates between MY and FP were close to zero for the BTBI and HO models in all breed group combinations. This near-zero correlation values between MY and FP were similar to the -0.08 estimate found in an earlier DPO study by Kuha (1999).

Multibreed interactibilities. Estimates of multibreed nonadditive ratios (Table 6) were somewhat smaller than multibreed additive ratios in Table 4. The numerators of the interactibilities in Table 6 are linear combinations of expected intrabreed (BT/BT, BI/BI in the BTBI model; H/H, O/O in the HO model) and interbreed (BT/BI, in the BTBI model and H/O in the HO model) nonadditive covariances present in a specific breed group combination. Interactibilities here differ from those estimated in beef cattle multibreed herds previously (Elzo and Wakeman, 1998; Elzo et al., 1998a,b) in that the numerator of past interactibility ratios included only interbreed nonadditive variation. Interbreed nonadditive genetic effects have traditionally been used to estimate mean nonadditive effects and nonadditive genetic variances in multibreed data sets. However, here the largest nonadditive variances were those for BI/BI and O/O, followed by those for BT/BI and H/O, the smallest being those for BT/BT and H/H. Thus, breed group combinations with the largest expected fractions of BI/BI and BT/BI will have the largest interactibility values.

The most important observation here is that estimates of multibreed nonadditive intrabreed and interbreed genetic variances were nonzero for all traits. This means that animals in this multibreed population can be differentiated not only in terms of their additive genetic ability but also in terms of their nonadditive genetic ability, and that this additional information should help make more accurate mating and selection decisions in the DPO multibreed population.

Multibreed nonadditive genetic correlations (Table 6) had the same pattern as multibreed additive genetic correlations. Positive multibreed nonadditive genetic correlations existed between MY and FY (0.37 to 0.66) and near zero between MY and FP for all breed group combinations. The agreement in sign between additive and nonadditive genetic correlations found here suggests that selection of animals for MY in this population will increase MY and FY, but it will not affect FP either additively or nonadditively.

Table 6. Estimates of interactibilities and nonadditive genetic correlations for 305-d milk yield (MY), fat yield (FY), and fat percentage (FP) for six breed group combinations by model

Breed group combination [1]	Genetic Parameter [2]					
	i^2 (MY)	r_N (MY, FY)	r_N (MY, FP)	i^2 (FY)	r_N (FY, FP)	i^2 (FP)
BTBI Model:						
BT × BT	0.08	0.66	-0.03	0.06	0.01	0.10
BT × 3/4BT 1/4BI	0.13	0.50	-0.02	0.12	0.02	0.15
BT × 1/2BT 1/2BI	0.17	0.44	-0.01	0.17	0.02	0.18
BT × 1/4BT 3/4BI	0.20	0.41	-0.01	0.21	0.02	0.21
BT × BI	0.23	0.39	0.00	0.25	0.02	0.23
3/4BT 1/4BI × 3/4BT 1/4BI	0.17	0.37	-0.01	0.17	0.02	0.18
HO Model:						
H × H	0.08	0.65	-0.03	0.08	0.01	0.15
H × 3/4H 1/4O	0.11	0.59	-0.02	0.11	0.01	0.03
H × 1/2H 1/2O	0.13	0.55	-0.02	0.13	0.01	0.02
H × 1/4H 3/4O	0.15	0.52	-0.01	0.16	0.01	0.02
H × O	0.17	0.50	-0.01	0.20	0.01	0.02
3/4H 1/4O × 3/4H 1/4O	0.14	0.43	-0.01	0.15	0.01	0.02

[1] BT = *Bos Taurus*, BI = *Bos indicus*, H = Holstein, O = Other breeds: Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane;   [2] i^2 = interactibility, r_N = nonadditive genetic correlation.

Multibreed environmental and phenotypic correlations. Multibreed environmental correlation estimates (Table 7) between MY and FY (0.89 to 0.96) were higher than multibreed phenotypic (0.73 to 0.90), and multibreed additive (0.44 to 0.79) and nonadditive (0.37 to 0.66) genetic correlations. Multibreed environmental correlations between MY and FP were low and negative (-0.09 to –0.27), and somewhat larger than the phenotypic ones (-0.07 to -0.22), and the near-zero values of the additive and nonadditive genetic correlations.

Table 7. Estimates of environmental and phenotypic correlations for 305-d milk yield (MY), fat yield (FY), and fat percentage (FP) for six breed group combinations by model

Breed group combination [1]	Environmental correlation [2]			Phenotypic correlation [3]		
	$r_{E (MY, FY)}$	$r_{E (MY, FP)}$	$r_{E (FY, FP)}$	$r_{P (MY, FY)}$	$r_{P (MY, FP)}$	$r_{P (FY, FP)}$
BTBI Model:						
BT × BT	0.95	-0.27	0.22	0.89	-0.22	0.18
BT × 3/4BT 1/4BI	0.94	-0.26	0.22	0.84	-0.17	0.15
BT × 1/2BT 1/2BI	0.93	-0.25	0.21	0.79	-0.14	0.13
BT × 1/4BT 3/4BI	0.92	-0.23	0.20	0.76	-0.10	0.11
BT × BI	0.89	-0.21	0.20	0.73	-0.08	0.10
3/4BT 1/4BI × 3/4BT 1/4BI	0.93	-0.25	0.21	0.78	-0.14	0.13
HO Model:						
H × H	0.96	-0.21	0.22	0.90	-0.17	0.18
H × 3/4H 1/4O	0.96	-0.09	0.09	0.87	-0.08	0.08
H × 1/2H 1/2O	0.96	-0.09	0.08	0.83	-0.07	0.06
H × 1/4H 3/4O	0.95	-0.09	0.07	0.79	-0.07	0.06
H × O	0.95	-0.09	0.07	0.75	-0.07	0.05
3/4H 1/4O × 3/4H 1/4O	0.96	-0.09	0.08	0.81	-0.07	0.06

[1] BT = *Bos Taurus*, BI = *Bos indicus*, H = Holstein, O = Other breeds: Native, Brahman, Red Sindhi, Sahiwal, Jersey, Red Dane;   [2] r_E = environmental correlation;   [3] r_P = phenotypic correlation.

Lastly, multibreed environmental correlations between FY and FP were all low and positive (0.07 to 0.22) and, again, slightly larger than the corresponding phenotypic correlations (0.05 to 0.18). The degree of accuracy of these correlations is expected to be low (recall GEM provides no standard errors). The agreement in sign among genetic, environmental, and phenotypic correlations suggests that genetic improvement, and improvement in environmental conditions will probably work in the same direction. Phenotypic correlations between MY, FY, and FP found here for H crossbred groups were similar to unibreed estimates from other Thai multibreed data sets (Chaiwatanasin, 1983; Katkasame, 1996).

Additive, Nonadditive, and Total Multibreed Genetic Predictions

Multibreed additive, nonadditive, and total genetic predictions for the BTBI and HO models were computed as deviations from a common multibreed genetic base for each model (BTBI multibreed base, and HO multibreed base). These common multibreed genetic bases are pooled additive-nonadditive genetic bases. They were affected by additive genetic effects of all breed origins, and by nonadditive intrabreed and interbreed genetic effects from all breed group combinations presented in the DPO multibreed data set. To compare sire MPGV from the BTBI and HO models: 1) sire additive MPGV were deviated from the mean additive MPGV of all H sires (new multibreed additive base), 2) sire nonadditive MPGV were deviated from the mean nonadditive MPGV of all H sires (new multibreed nonadditive base), and 3) sire total MPGV were recomputed as the sum of 1 and 2. These bases are different from the additive genetic bases used in the unibreed BTBI (genetic base = BI) and HO (genetic base = O) analyses (Koonawootrittriron *et al.,* 2002) of this DPO data set. Direct comparisons between additive genetic predictions across models (unibreed animal *vs.* multibreed sire-maternal grandsire) within the DPO data set cannot be done. This is also the case for previous DPO additive sire genetic evaluations (Katkasame, 1996; Kuha, 1999; DPO, 1997, 1998, 1999).

Table 8 contain ranges of sire additive, nonadditive, and total MPGV and their standard errors of prediction for MY, FY, and FP under the BTBI and the HO models, as deviations from H additive and nonadditive multibreed genetic bases. Because of the low number of progeny per sire, standard errors of prediction were large for additive, nonadditive, and total sire MPGV. Differences in sire MPGV between the BTBI and HO models will be mostly due to differences in the additive and nonadditive covariance matrices used for each sire in each model. Sire MPGV ranges for MY additive and total were wider in the HO than in the BTBI model because of the negative MPGV of one of the three Jersey sires present in this DPO data set (-189.51 ± 342.37 kg and –238.12 ± 451.70 kg). All maximum MPGV values for MY were from a H sire. The negative MPGV of this Jersey sire were magnified in the HO model because of the larger additive genetic variance estimated for MY for the O base population. A similar situation occurred for FY, additive, nonadditive, and total MPGV minimum values in the HO model were from the same Jersey bull that had the lowest additive and total MPGV for MY, whereas the corresponding maximum values were from another Jersey sire. Contrarily, in the BTBI model, the minimum and maximum additive, nonadditive, and total MPGV values were from H and H crossbred sires. Lastly, all minimum and maximum values for FP were from different H and H crossbred sires in the BTBI and HO models. Different estimates of additive, nonadditive, and environmental genetic covariances across models produced different sire MPGV in the BTBI and HO models, thus the change in MPGV ranges. These different sire MPGV in the BTBI and HO models in turn affected somewhat the ranking of sires across models, although sire ranking by additive, nonadditive, and total MPGV in the BTBI and HO models remained highly correlated (0.98).

The ranking of sires by additive, nonadditive, and total MPGV within models was also highly correlated (0.99). This indicates that H and crossbred H sires of high additive genetic

ability also had high nonadditive genetic ability, and vice versa. However, there were exceptions, especially in the middle and bottom thirds of the sires in the DPO data set, where some H and H crossbred sires ranked differently for additive and nonadditive MPGV. Identification of sires that have good additive *and* nonadditive genetic abilities will be important to select appropriate sires for particular herds and selection goals.

Table 8. Ranges of sire additive, nonadditive, and total MPGV for 305-d milk yield (MY), fat yield (FY), and fat percentage (FP) by model

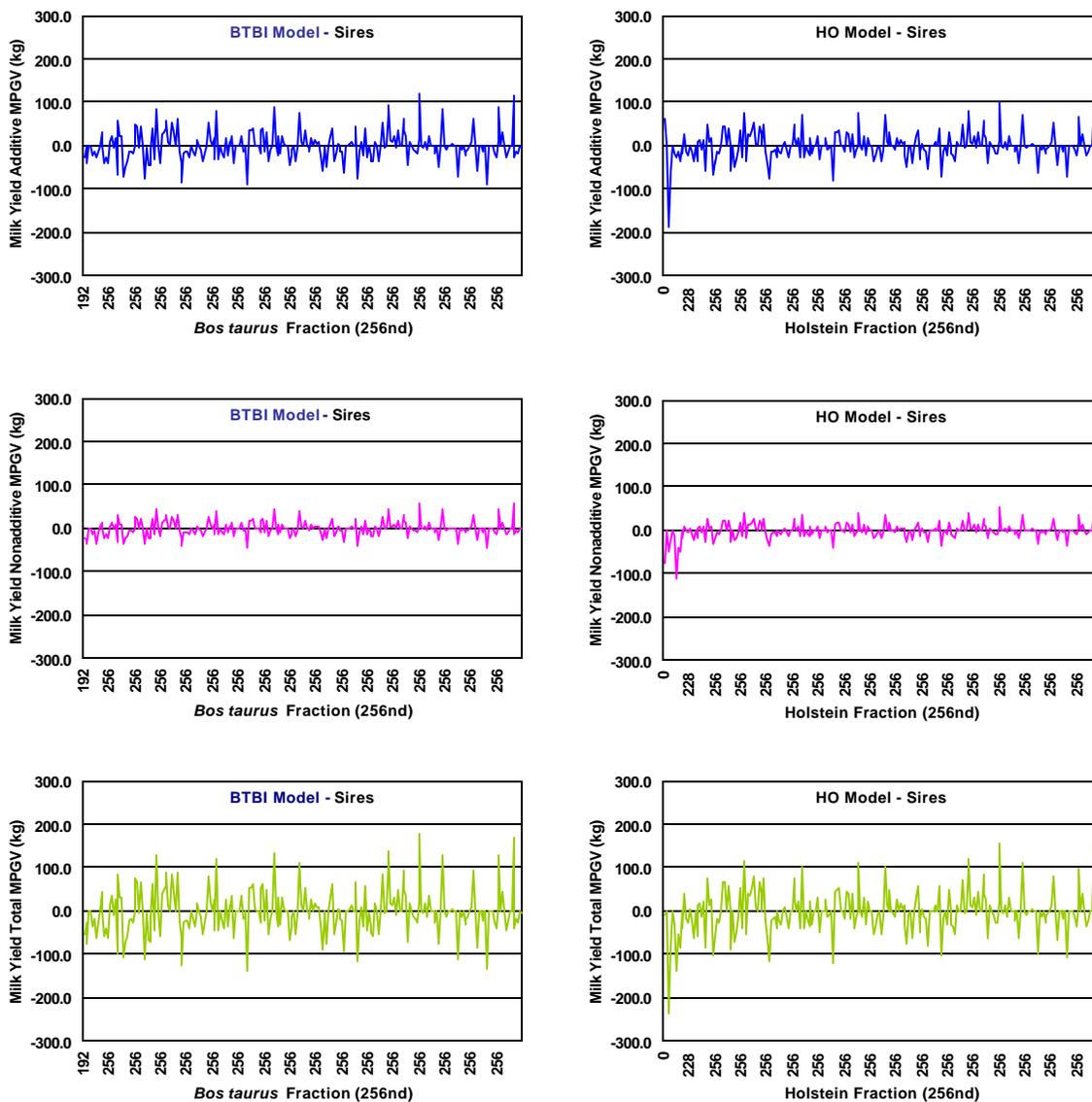| MPGV	BTBI model	HO model
MY: Additive (kg)	-91.90 ± 156.60[1] to 117.57 ± 154.77	-189.51 ± 342.37 to 103.46 ± 148.41
Nonadditive (kg)	-45.95 ± 350.00 to 58.79 ± 349.84	-110.79 ± 322.56 to 51.73 ± 341.13
Total (kg)	-137.86 ± 413.85 to 176.35 ± 412.67	-238.12 ± 451.70 to 155.19 ± 400.52
FY: Additive (kg)	-3.29 ± 6.14 to 3.66 ± 6.07	-7.67 ± 11.80 to 6.44 ± 11.72
Nonadditive (kg)	-1.64 ± 13.30 to 1.98 ± 13.26	-4.94 ± 13.00 to 9.23 ± 12.34
Total (kg)	-4.93 ± 15.89 to 5.49 ± 15.83	-12.61 ± 16.58 to 15.68 ± 15.64
FP: Additive (%)	-0.053 ± 0.072 to 0.051 ± 0.070	-0.031 ± 0.072 to 0.035 ± 0.071
Nonadditive (%)	-0.026 ± 0.122 to 0.027 ± 0.120	-0.016 ± 0.122 to 0.018 ± 0.122
Total (%)	-0.079 ± 0.158 to 0.076 ± 0.156	-0.047 ± 0.159 to 0.053 ± 0.158

[1] Standard error

To help visualize the variability that existed among sires in the DPO data set, Figure 1 shows the MY additive, nonadditive, and total MPGV of all evaluated sires under the BTBI and HO models. Sires were separated by breed composition and ordered by sequential number within breed composition. This ordering of sires shows both the degree of variability that existed among sires for additive, nonadditive, and total MPGV, and whether it existed some trend in the MPGV of bulls chosen as sires over time in the DPO population. Recall that the three Jersey sires were assigned to the BT group in the BTBI model, and to the O group in the HO model. Thus, these Jersey bulls appear as the first three points in the HO graphs because they are 100% O, and among the other 100% BT sires in the BTBI graphs.

Graphs in Figure 1 illustrate the degree of additive and nonadditive variation that existed among sires in the DPO data set. They also show that additive sire MPGV were larger than nonadditive sire MPGV. Sires that had positive additive MPGV also had positive nonadditive MPGV, which was reconfirmed by the larger deviations for total MPGV shown in the third pair of graphs of Figure 1. Similar sets of graphs were obtained for FY and FP.

Furthermore, graphs like those in Figure 1 would help visualize potential sires to be chosen for straight breeding and(or) crossbreeding purposes, and how they would compare to other sires in the population based on their MPGV. Sires could be chosen primarily based on their additive or total MPGV. Sires should not be chosen based on nonadditive MPGV alone because these genetic effects are recreated anew during fertilization (Elzo *et al.*, 1998a). If sires are chosen based on their additive MPGV, then selection emphasis will be placed only on additive genetic effects. If sires are chosen based on their total MPGV, then selection will emphasize a combination of additive and nonadditive genetic effects. Perhaps the safest alternative would be to chose sires using the two-step procedure suggested by Elzo *et al.* (1998a). In step 1, the best sires are chosen according to their additive MPGV. In step 2, the best sires *among those selected in step 1* are chosen according to their total MPGV. This strategy will maximize additive genetic progress, and it will also increase the average combining ability of sires in the DPO population. In an extreme case, the choice of a sire could even be tailored to the breed composition of each dam in a herd. This could be feasible if artificial insemination is available. Under natural service conditions, however, sires will probably be chosen based on

their additive or total MPGV for a group of females of some breed composition or range of breed compositions.

Figure 1. Additive, nonadditive, and total milk yield sire MPGV ordered by sire sequential number within BT fraction in 256nds (BTBI model) and H fraction in 256nds (HO model)

Figure 2 shows sire additive, nonadditive, and total MPGV genetic trends for MY, FY, and FP obtained in the DPO data set from females born from 1998 to 1997 that had their first lactation from 1991 to 2000. Yearly means were computed by multiplying each sire additive, nonadditive, and total MPGV by its number of progeny per year, and dividing the total by the number of progeny of all sires in each year.
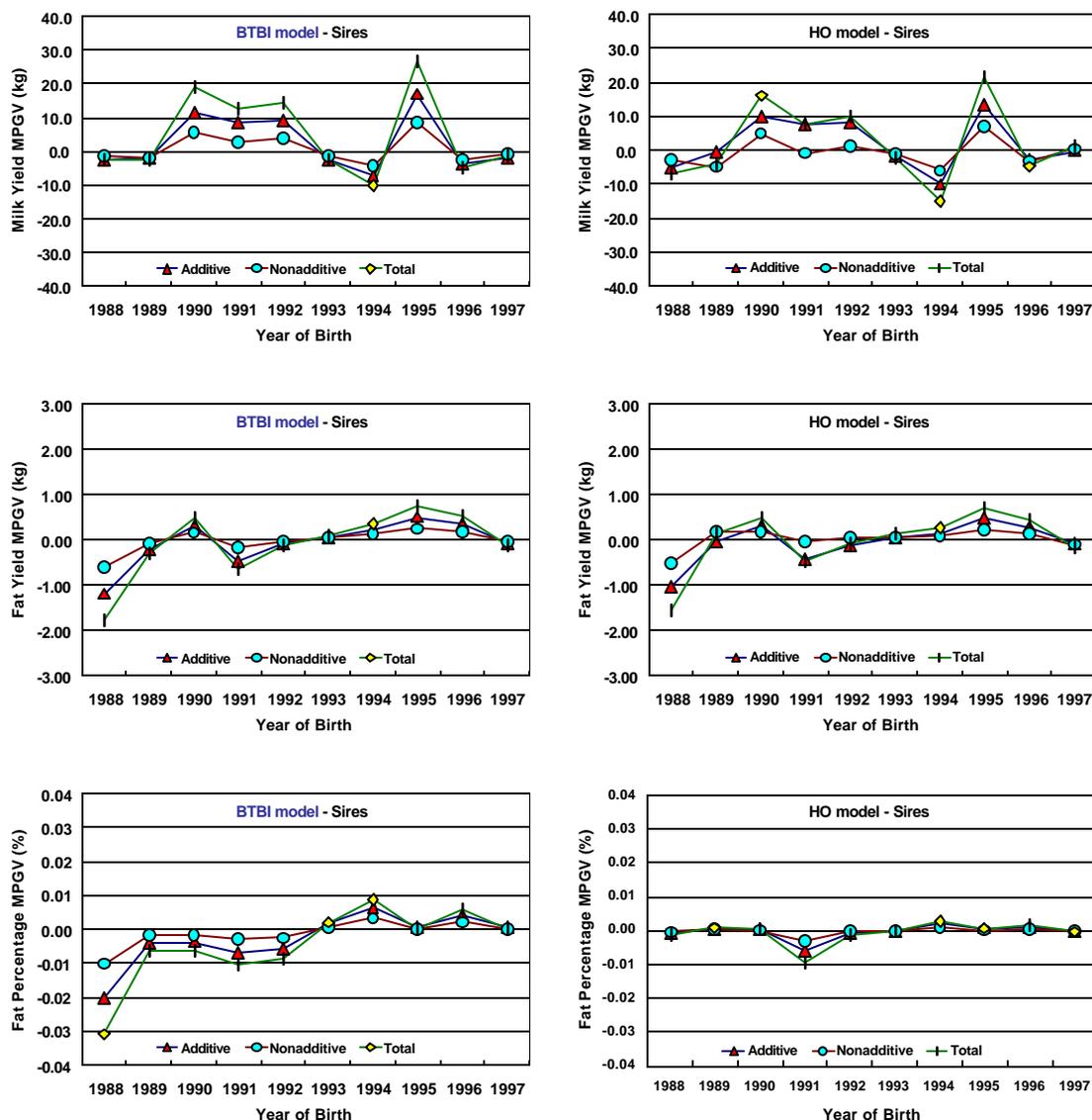
Figure 2. Genetic trends for additive, nonadditive, and total MPGV yearly means for milk yield, fat yield, and fat percentage, under the BTBI and the HO models

Graphs in Figure 2 show: 1) variation for additive, nonadditive, and total yearly means, but no real trend for MY (BTBI and HO models), 2) slight upward trends for additive, nonadditive, and total yearly means for FY (BTBI and HO models), and 3) a small upward trend for additive, nonadditive, and total yearly means for FP in the BTBI model, but not in the HO model. Yearly means were computed using sire additive, nonadditive, and total MPGV that had large standard errors of prediction. Thus, these yearly means and the genetic trends they depict should be viewed with caution, and interpreted only as first approximations. The editing process here eliminated all animals without test-day monthly records. If this information became available and(or) data from other sources in Thailand could be included in a combined multibreed

dataset, a more realistic set of additive, nonadditive, and total genetic trends could be estimated. This type of graphs would need to be recomputed after each genetic evaluation to monitor the impact of sires from foreign and national origin on the Thai dairy multibreed population.

Conclusions

The successful completion of the covariance estimation and genetic prediction of additive, nonadditive, and total multibreed genetic effects suggests that multibreed covariance estimation and genetic prediction procedures can be used in extremely unbalanced small multibreed field dairy data sets. However, results obtained with small datasets should be interpreted with caution because the accuracy of prediction of genetic values, and the accuracy of estimation of covariance components and genetic parameters will be low. The multibreed procedures used here provided more variability information (additive, nonadditive, total on all base populations, and any multibreed combination thereof) than that provided by unibreed procedures. Estimates of multibreed covariances and genetic values in the DPO data set were more conservative than those obtained using unibreed procedures. The large standard errors of the multibreed genetic predictions computed in this small data set are an indication of the likely low accuracy of the covariances and genetic parameters estimated here. Thus, this study needs to be repeated with a substantially larger and better-distributed multibreed data set. Information from crossbred Holstein × *Bos indicus* and straightbred *Bos indicus* sires would need to be added to the DPO data set to have more accurate and fair genetic comparisons of sires of various genetic backgrounds under Thai environmental conditions.

Acknowledgements

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