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Genetic components of heat stress for dairy cattle with multiple lactations

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ABSTRACT

Data included 585,119 test-day records for milk, fat, and protein yields from the first, second, and third parities of 38,608 Holsteins in Georgia. Daily temperature-humidity indexes (THI) were available from public weather stations. Models included a repeatability test-day model with a random regression on a function of THI and a test-day random regression model using linear splines with knots at 5, 50, 200, and 305 d in milk and a function of THI. Random effects were additive genetic and permanent environmental in the repeatability model and additive genetic, permanent environmental, and herd year in the random regression model. Additionally, models included fixed effects for herd test day, calving age, milking frequency, and lactation stage. Phenotypic variance increased by 50 to 60% from the first to second parity for all yield traits with the repeatability model and by 12 to 15% from the second to third parity. General additive genetic variance increased by 25 to 35% from the first to second parity for all yield traits but decreased slightly from the second to third parity for milk and protein yields. Genetic variance for heat tolerance doubled from the first to second parity and increased by 20 to 100% from the second to third parity. Genetic correlations among general additive effects were lowest between the first and second parities (0.84 to 0.88) and were highest between the second and third parities (0.96 to 0.98). Genetic correlations among parities for the effect of heat tolerance ranged from 0.56 to 0.79. Genetic correlations between general and heat-tolerance effects across parities and yield traits ranged from −0.30 to −0.50. With the random regression model, genetic variance for heat tolerance for milk yield was approximately one-half that of the repeatability model. For milk yield, the most negative genetic correlation (approximately −0.45) between general and heat-tolerance effects was between 50 and 200 d in milk for the first parity and between 200 and 305 d in milk for the second and third parities. The genetic variance of heat tolerance increased substantially from the first to third parity. Genetic estimates of heat tolerance may be inflated with the repeatability model because of timing of lactations to avoid peak yield during hot seasons.
Key words: heat stress, variance component, random regression model

INTRODUCTION

Heat stress in dairy cattle affects production (Maust et al., 1972; Fuquay, 1981; Bryant et al., 2007) and reproduction (Ravagnolo and Misztal, 2002; Jordan, 2003; Garcia-Ispierto et al., 2007). Economic losses attributable to heat stress are estimated to be between \$897 million and \$1,500 million per year for the US dairy industry (St-Pierre et al., 2003). Different approaches are used to manage heat stress in dairy cattle, including cooling, shading, and nutrition (West, 1999, 2003; Kadzere et al., 2002).

Misztal (1999) proposed a model to study the genetic component of heat stress in dairy cattle by using performance data and public weather information. Additive genetic variability for heat tolerance was shown to be important for milk, fat, and protein production of first-parity cows; additive genetic variance at a high temperature-humidity index (**THI**) was similar to additive variance under nonstress conditions (Ravagnolo and Misztal, 2000). Comparison of on-farm weather data with public information has shown that the latter are accurate sources of information (Freitas et al., 2006b). Bohmanova et al. (2005) developed a genetic evaluation for heat tolerance for first-parity US Holstein cows based on public weather data. Estimated breeding values were calculated for approximately 10 million animals by using a repeatability test-day model with a random regression on THI. Daughters of bulls with high genetic merit for heat tolerance had lower milk yields, higher contents of milk solids, more robust bodies, better udders, longer productive lives, and higher pregnancy rates than did daughters of bulls with low genetic merit for heat tolerance.

Longitudinal data are commonly analyzed with random regression models (Schaeffer, 2004). Different functions can be applied to model (co)variances across DIM. Splines have been used to model (co)variances

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Table 1. Numbers of Holstein cows and test-day records and lactation means and SD of milk, fat, and protein yields by parity

Parity	Cows, n	Test days, n	Milk, kg	Fat, kg × 100	Protein, kg × 100
1	38,608	350,623	27.5 ± 7.0	94.8 ± 27.7	85.7 ± 20.4
2	17,549	160,262	31.6 ± 9.4	109.3 ± 36.3	97.5 ± 26.3
3	8,210	74,834	33.0 ± 10.1	114.8 ± 39.5	100.7 ± 28.1

in test-day models (White et al., 1999; Torres, 2001; Druet et al., 2003; Silvestre et al., 2005; Bohmanova et al., 2007) or to model growth traits (Meyer, 2005; Robbins et al., 2005; Sanchez et al., 2008). Linear splines have good numerical properties and local effects and are easily interpretable (Misztal, 2006). The objective of this study was to estimate variance components for milk, fat, and protein yields from the first 3 parities by using test-day models that included a random regression on a function of THI.

MATERIALS AND METHODS

Data

Holstein test-day records for milk, fat, and protein yields from the first 3 parities were obtained from the Animal Improvement Programs Laboratory, ARS, USDA (Beltsville, MD). Records were from cows registered between 1993 and 2004 in Georgia. Lactation records were required to have only 2 or 3 milkings per day and at least 4 test days, with the first test day at <75 DIM and test days between 5 and 305 DIM. Calving ages were restricted to 18 to 35 mo for parity 1, from 28 to 49 mo for parity 2, and from 40 to 63 mo for parity 3. Cows also were required to have the first lactation recorded. A 3-generation pedigree file of 68,103 animals was extracted for 38,608 cows with 585,119 test-day records. The data are summarized in Table 1.

Hourly THI (National Oceanic and Atmospheric Administration, 1976) was calculated from data from public weather stations as proposed by Ravagnolo et al. (2000):

$$\mathrm{THI(t,rh)} = (1.8\mathrm{t} + 32) - (0.55 - 0.0055\mathrm{rh})(1.8\mathrm{t} - 26),$$

where t is temperature in degrees Celsius and rh is relative humidity, expressed as a percentage. Herds were matched with the closest weather station, based on minimum distances from latitude and longitude information obtained from the zip code. Mean herd distance from a weather station was 61 km, with a maximum of 137 km and a minimum of 3 km. Mean daily THI for the third day before each test day from the weather station closest to the farm was assigned as the THI for that test day, as suggested by Bohmanova et al. (2008). A function (f) of THI was created:

$$\mathrm{f(THI)} = \begin{cases} 0 & \text{if THI } \leq \mathrm{THI_{threshold}} \\ \mathrm{THI} - \mathrm{THI_{threshold}} & \text{if THI } > \mathrm{THI_{threshold}} \end{cases},$$

where $\mathrm{THI_{threshold}}$ was set to 72, as in Ravagnolo et al. (2000).

Model

Two models were used to estimate variance components for multiple lactations. The first model was a multiple-trait extension of the repeatability test-day model (**REP**) proposed by Ravagnolo and Misztal (2000) to estimate variance components for heat tolerance, considering multiple lactations as different traits:

$$y_{ijklmno} = \mathrm{HTD}_{ij} + \mathrm{DIM}_{kl} + \mathrm{age}_{jm} + \mathrm{freq}_{n} + a_{\mathrm{general}_{jo}} + a_{\mathrm{ht}_{jo}}[\mathrm{f(THI)}_i] + p_{\mathrm{general}_{jo}} + p_{\mathrm{ht}_{jo}}[\mathrm{f(THI)}_i] + e_{ijklmno},$$

where $y_{ijklmno}$ is test-day milk, fat, or protein yield for cow o in age class m within parity j (1, 2, or 3) and DIM class k within season l for herd test-day i within parity j and milking frequency n (2 or 3 daily milkings); HTD is a fixed effect of herd test day within parity; DIM is a fixed effect of DIM class within season; age is a fixed effect of calving age class within parity; freq is a fixed effect of milking frequency; a is a general random additive genetic effect for the cow within parity; a_{ht} is a random additive genetic effect of heat tolerance of the cow within parity; p is a general random permanent environmental effect for the cow within parity; p_{ht} is a random permanent environmental effect of heat tolerance of the cow within parity; and $e_{ijklmno}$ is the random residual effect. Classes of DIM were grouped by 10 d beginning at 5 DIM through 305 DIM (31 classes). Seasons were defined as December through February, March through May, June through August, and September through November. Calving ages were grouped into every 2 mo within parity (22 classes).

Let $\mathbf{a}' = \left[\mathbf{a}'_{\mathrm{general}_j} \quad \mathbf{a}'_{\mathrm{ht}_j}\right]$ be the vector of random additive genetic effects and $\mathbf{p}' = \left[\mathbf{p}'_{\mathrm{general}_j} \quad \mathbf{p}'_{\mathrm{ht}_j}\right]$ be the vector of random permanent environmental effects for parities j = 1 to 3. The (co)variance structure was

$$\mathrm{Var}\begin{bmatrix}\mathbf{a}\\\mathbf{p}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\otimes\mathbf{G}_0 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\otimes\mathbf{P}_0 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\otimes\mathbf{R}_0\end{bmatrix},$$

where $\mathbf{A}$ is the numerator relationship matrix; $\mathbf{G}_0$ and $\mathbf{P}_0$ are 6 × 6 matrices of (co)variances for additive and permanent environmental effects, respectively; and $\mathbf{R}_0$ is a diagonal matrix of residual variances corresponding to each trait.

The second model was a multiple-trait random regression test-day model on DIM and f(THI) (**RRM**) with the same effects as for the REP model, except for a random effect for herd year (**h**). Random covariates included f(THI), which were modeled for DIM with linear splines using 4 knots at 5, 50, 200, and 305 DIM. The (co)variance structure was

$$\mathrm{Var}\begin{bmatrix}\mathbf{a}\\\mathbf{p}\\\mathbf{h}\\\mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{A}\otimes\mathbf{G}_0 & \mathbf{0} & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{I}\otimes\mathbf{P}_0 & \mathbf{0} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}\otimes\mathbf{H}_0 & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{I}\otimes\mathbf{R}_0\end{bmatrix},$$

where $\mathbf{G}_0 = \mathrm{Var(a)}$, $\mathbf{P}_0 = \mathrm{Var(p)}$, and $\mathbf{H}_0 = \mathrm{Var(h)}$. All square matrices with dimension j × (number of knots + 1) corresponded to (co)variances for additive, permanent environmental, and herd-year effects. Matrices for the RRM model were of the order 15 × 15. The RRM model was applied only to milk yield.

Analysis

Univariate analyses for traits and lactations were performed for all models by using the software AIREMLF90 (Misztal et al., 2002) to obtain initial estimates for multiple-trait analyses. Multiple-trait analyses were performed by using the software GIBBS2F90, a program that implements Gibbs sampling with a joint sampling of random correlated effects and traits (Misztal et al., 2002). A single chain of 300,000 samples was run, with the first 50,000 samples discarded as burn-in. Additive genetic, permanent environmental, herd year, and phenotypic variances and heritability were calculated for each combination of DIM and THI by using the remaining 250,000 samples. Posterior mean, high posterior density, and effective sample size were calculated for each parameter. Convergence was determined by graphical inspection of the posterior chain and by the effective sample size of the parameter of interest.

Table 2. Variance components estimated with a repeatability test-day model for first-parity yield traits

Parameter[1]	Milk, kg^2	Fat, (kg × 100)^2	Protein, (kg × 100)^2
$\sigma^2_{a_{general}}$	5.5	74.0	42.2
$100\sigma^2_{a_{ht}}$	2.8	21.9	17.4
$10\sigma_{a_{general},\,a_{ht}}$	−1.8	−18.3	−13.0
$\sigma^2_{p_{general}}$	12.0	133.0	101.0
$100\sigma^2_{p_{ht}}$	11.1	69.9	94.2
$10\sigma_{p_{general},\,p_{ht}}$	−5.2	−63.5	−53.0
σ^2_e	13.1	310.0	127.8

[1] $\sigma^2_{a_{general}}$ = general additive genetic variance for cow; $100\sigma^2_{a_{ht}}$ = additive genetic variance for heat tolerance at a temperature-humidity index (THI) of 82 (10 degrees over a THI threshold of 72); $10\sigma_{a_{general},\,a_{ht}}$ = additive genetic covariance between the general effect and the effect for heat tolerance at a THI of 82; $\sigma^2_{p_{general}}$ = general permanent environmental variance; $100\sigma^2_{p_{ht}}$ = permanent environmental variance for heat tolerance at a THI of 82; $10\sigma_{p_{general},\,p_{ht}}$ = permanent environmental covariance between the general effect and the effect for heat tolerance at a THI of 82; σ^2_e = residual variance.

RESULTS AND DISCUSSION

Estimates of variance components from REP univariate analyses of first-parity milk, fat, and protein yields (Table 2) were within the range of those estimated by Freitas et al. (2006a) for different regions of the United States. However, they were higher than those for Georgia reported previously by Ravagnolo and Misztal (2000). Values of the additive genetic variances for heat tolerances were presented for THI of 82 (10 degrees over the THI threshold of 72). The additive genetic variance for the heat tolerance effect is associated with 1 THI degree over the threshold (THI = 72). For t degrees over the threshold, the heat tolerance variance for the model in this study is t^2 higher.

Parameter values for the first 3 parities from the REP model are given in Table 3. Phenotypic variances (not shown) for milk, fat, and protein yields increased with parity: 50 to 60% from the first to second parity and 12 to 15% from the second to third parity. General additive genetic variances increased by 25 to 35% for all yield traits from the first to second parity but decreased slightly from the second to third parity for milk and protein yields; general additive genetic variance for fat yield continued to increase from the second to third parity. Additive genetic variance for heat tolerance increased by approximately 100% from the first to second parity for all yield traits. Increases from the second to third parity were 20% for milk yield and approximately 100% for fat and protein yields. The increase in addi-

Table 3. Variance components estimated with a repeatability test-day model for yield traits by parity and genetic correlations (r_g) between parities and genetic components

Parameter[1]	Milk, kg^2			Fat, $(kg \times 100)^2$			Protein, $(kg \times 100)^2$		
	Parity 1	Parity 2	Parity 3	Parity 1	Parity 2	Parity 3	Parity 1	Parity 2	Parity 3
$\sigma^2_{a_{general}}$	5.6	7.5	6.5	74.0	93.9	109.0	42.5	56.8	52.2
$100\sigma^2_{a_{ht}}$	3.7	7.2	8.9	37.0	74.9	141.7	21.7	47.8	107.8
$10\sigma_{a_{general}, a_{ht}}$	−2.1	−2.8	−3.6	−20.3	−24.0	−37.9	−13.2	−18.8	−37.4
σ^2_e	12.8	19.4	22.7	308.7	522.2	603.4	125.7	190.5	215.3
$r_{g_{general_{parity\,1,\,parity\,j}}}$		0.86	0.91		0.88	0.96		0.84	0.89
$r_{g_{general_{parity\,2,\,parity\,j}}}$			0.96			0.97			0.98
$r_{g_{ht_{parity\,1,\,parity\,j}}}$		0.72	0.79		0.71	0.61		0.56	0.75
$r_{g_{ht_{parity\,2,\,parity\,j}}}$			0.75			0.68			0.75
$r_{g_{general,\,ht}}$	−0.46	−0.38	−0.47	−0.39	−0.39	−0.30	−0.43	−0.36	−0.50

[1] $\sigma^2_{a_{general}}$ = general additive genetic variance for cow; $100\sigma^2_{a_{ht}}$ = additive genetic variance for heat tolerance at a temperature-humidity index (THI) of 82 (10 degrees over a THI threshold of 72); $10\sigma_{a_{general}, a_{ht}}$ = additive genetic covariance between the general effect and the effect for heat tolerance at a THI of 82; σ^2_e = residual variance.

tive genetic variance for heat tolerance for later parities was not unexpected; Armstrong (1994) reported that multiple-parity cows were more affected by heat stress than were first-parity cows. Genetic correlations between general and heat-tolerance effects were all negative and ranged from −0.30 to −0.50.

Total additive genetic variance as a function of THI (not shown) had a typical quadratic shape, as in Ravagnolo and Misztal (2000). Additive genetic variances for milk, fat, and protein yields as well as corresponding SE increased as a function of THI and parity. Heritability estimates (not shown) ranged from 0.10 to 0.24.

Genetic correlations between parities (Table 3) for the general additive effect (intercept) for milk, fat, and protein yields were positive and high (≥0.84); correlations between the second and third parity were ≥0.96. Genetic correlations between parities for additive heat tolerance were also positive but were slightly lower (0.56 to 0.79), which indicated either parity differences for heat tolerance or a wider high posterior density.

Posterior means of additive genetic (co)variances and genetic correlations for the RRM model (DIM knots and THI) are given in Table 4 for milk yield; curves for posterior means and 95% intervals for high posterior density at different THI and DIM are in Figure 1. General additive genetic variance for the first parity increased with DIM, whereas variances for the second and third parities had a typical U-shape, with higher variances at extreme DIM. On average, general additive genetic variances from the RRM model were higher for later parities (as was found for the REP model) despite higher estimates at high DIM.

Table 4. Posterior means for additive genetic variances (on diagonal) and covariances (below diagonal) estimated from a multiple-trait random regression test-day model on DIM (4 knots) and a function of temperature-humidity index (THI)[1] and genetic correlations (above diagonal) among DIM knots and THI for milk yield by parity

Item	Parity 1					Parity 2					Parity 3				
	5 DIM	50 DIM	200 DIM	305 DIM	THI	5 DIM	50 DIM	200 DIM	305 DIM	THI	5 DIM	50 DIM	200 DIM	305 DIM	THI
5 DIM	3.96	0.64	0.41	0.32	−0.25	8.73	0.74	0.47	0.37	−0.17	5.98	0.55	0.44	0.23	0.10
50 DIM	2.98	5.46	0.85	0.62	−0.45	6.39	8.50	0.70	0.51	−0.31	4.07	9.27	0.63	0.18	−0.21
200 DIM	2.03	4.99	6.28	0.84	−0.40	3.87	5.70	7.89	0.84	−0.43	3.24	5.83	9.24	0.76	−0.41
305 DIM	1.81	4.19	6.02	8.27	−0.27	4.47	5.96	9.56	16.35	−0.39	2.27	2.21	9.19	15.64	−0.37
THI	−0.07	−0.14	−0.13	−0.10	2.0	−0.10	−0.18	−0.23	−0.30	4.0	0.06	−0.17	−0.34	−0.40	7.0

[1]Heat tolerance at a THI of 10 degrees above a threshold THI of 72.

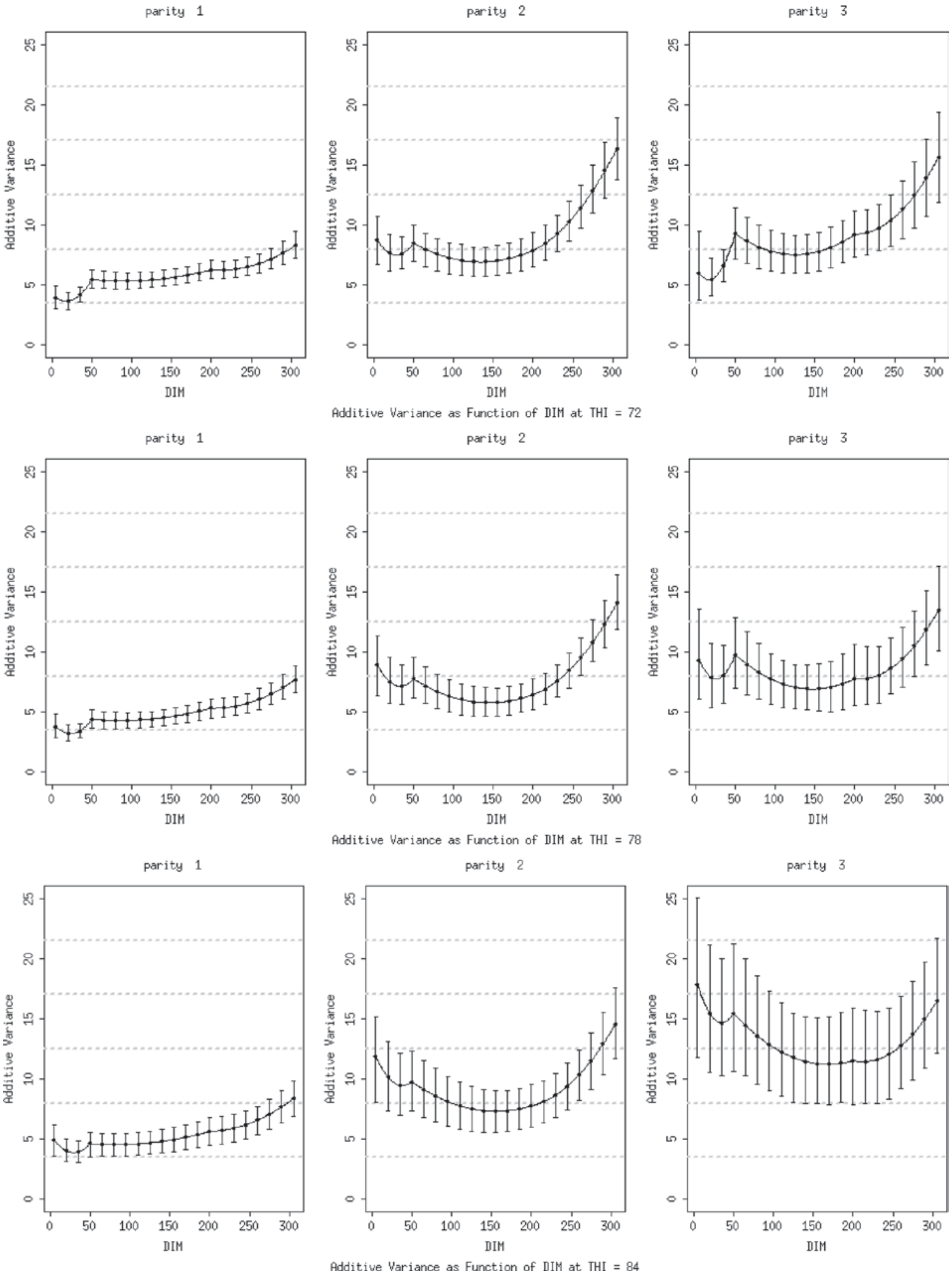

Figure 1. Posterior means and 95% high posterior density intervals for general additive genetic variance estimated using a multiple-trait random regression test-day model for milk yield in parity 1, 2, or 3 by DIM and temperature-humidity index (THI).

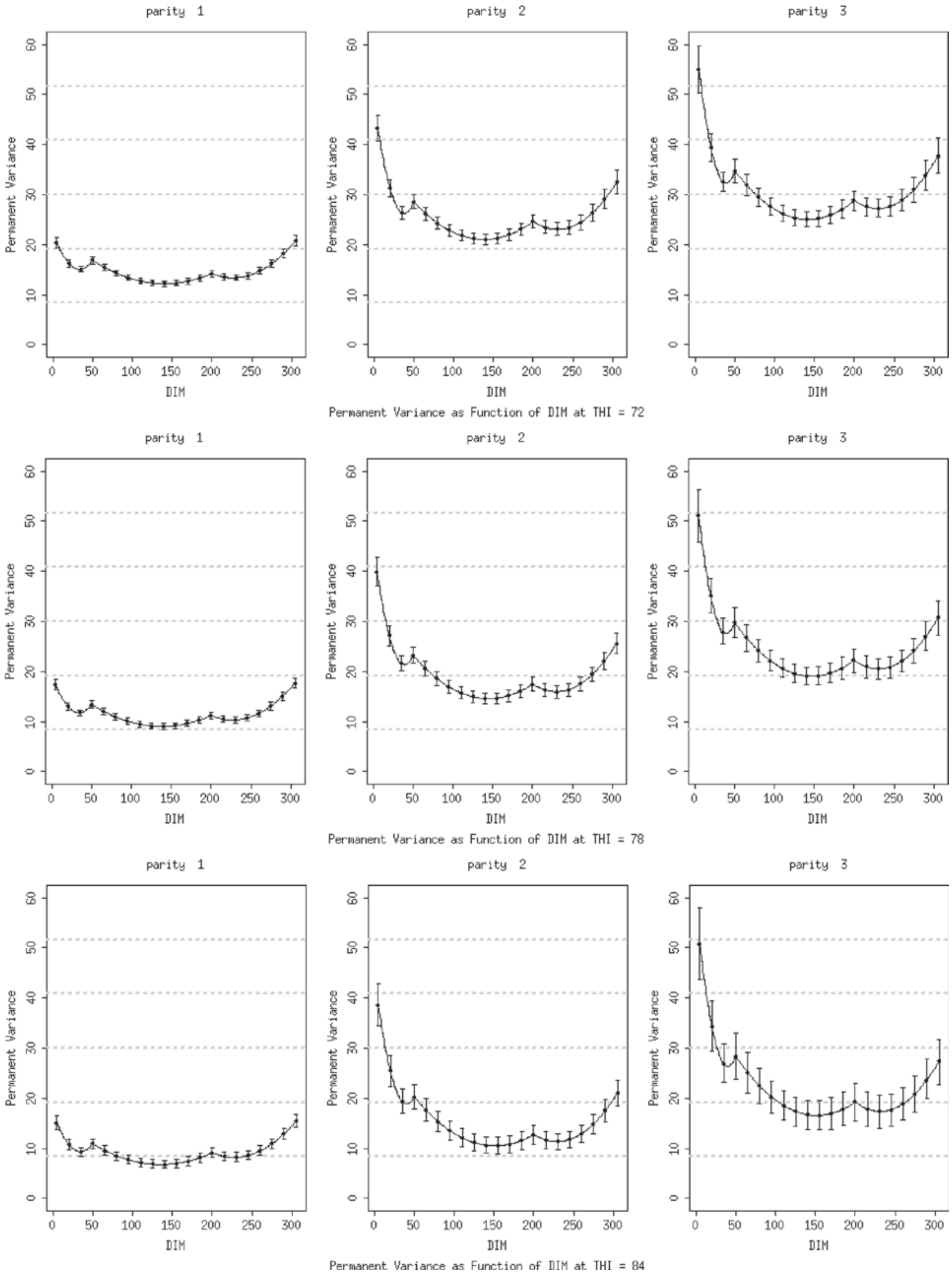

Figure 2. Posterior means and 95% high posterior density intervals for permanent environmental variance estimated using a multiple-trait random regression test-day model for milk yield in parity 1, 2, or 3 by DIM and temperature-humidity index (THI).

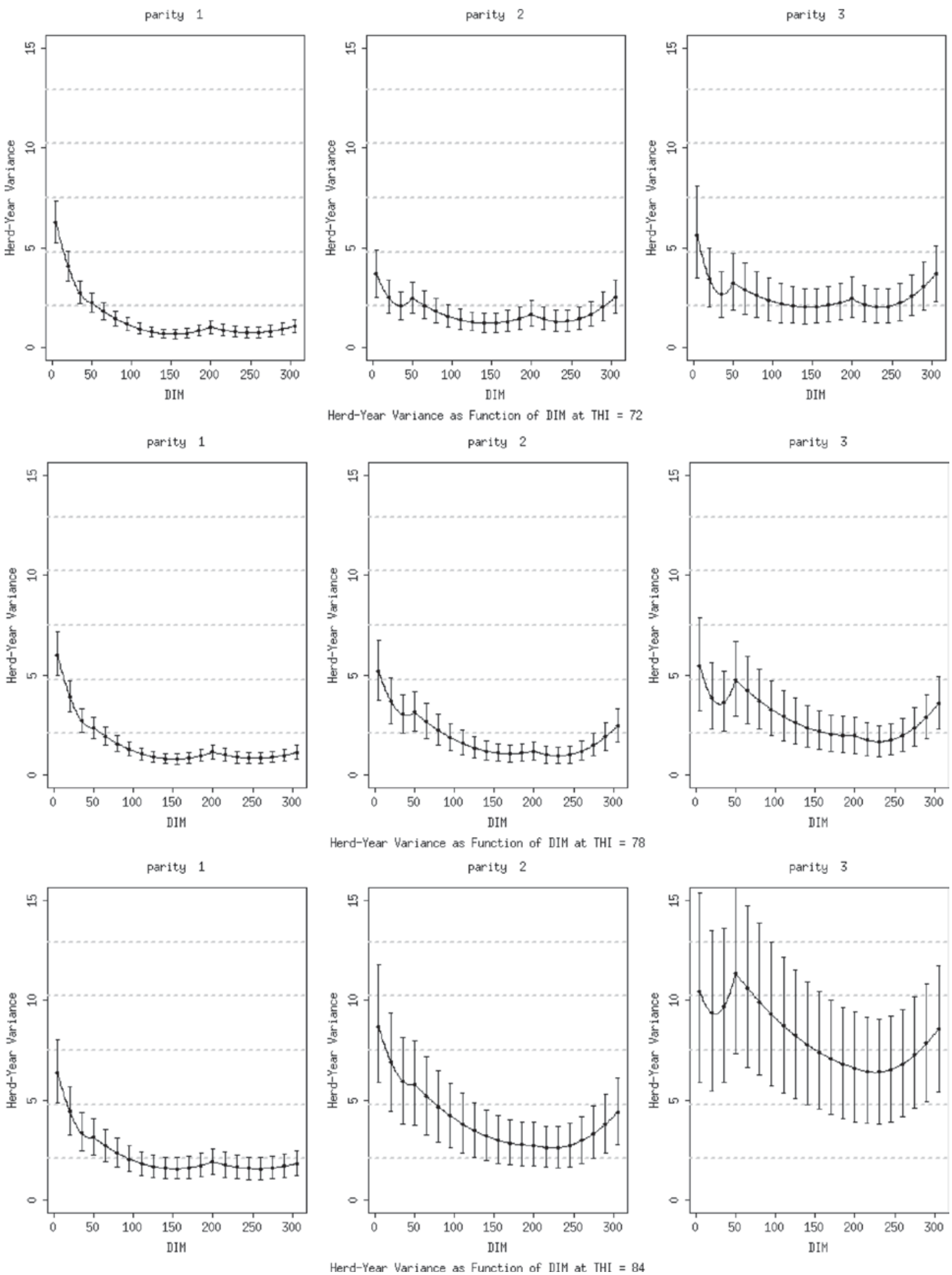

Figure 3. Posterior means and 95% high posterior density intervals for herd-year variance estimated using a multiple-trait random regression test-day model for milk yield in parity 1, 2, or 3 by DIM and temperature-humidity index (THI).

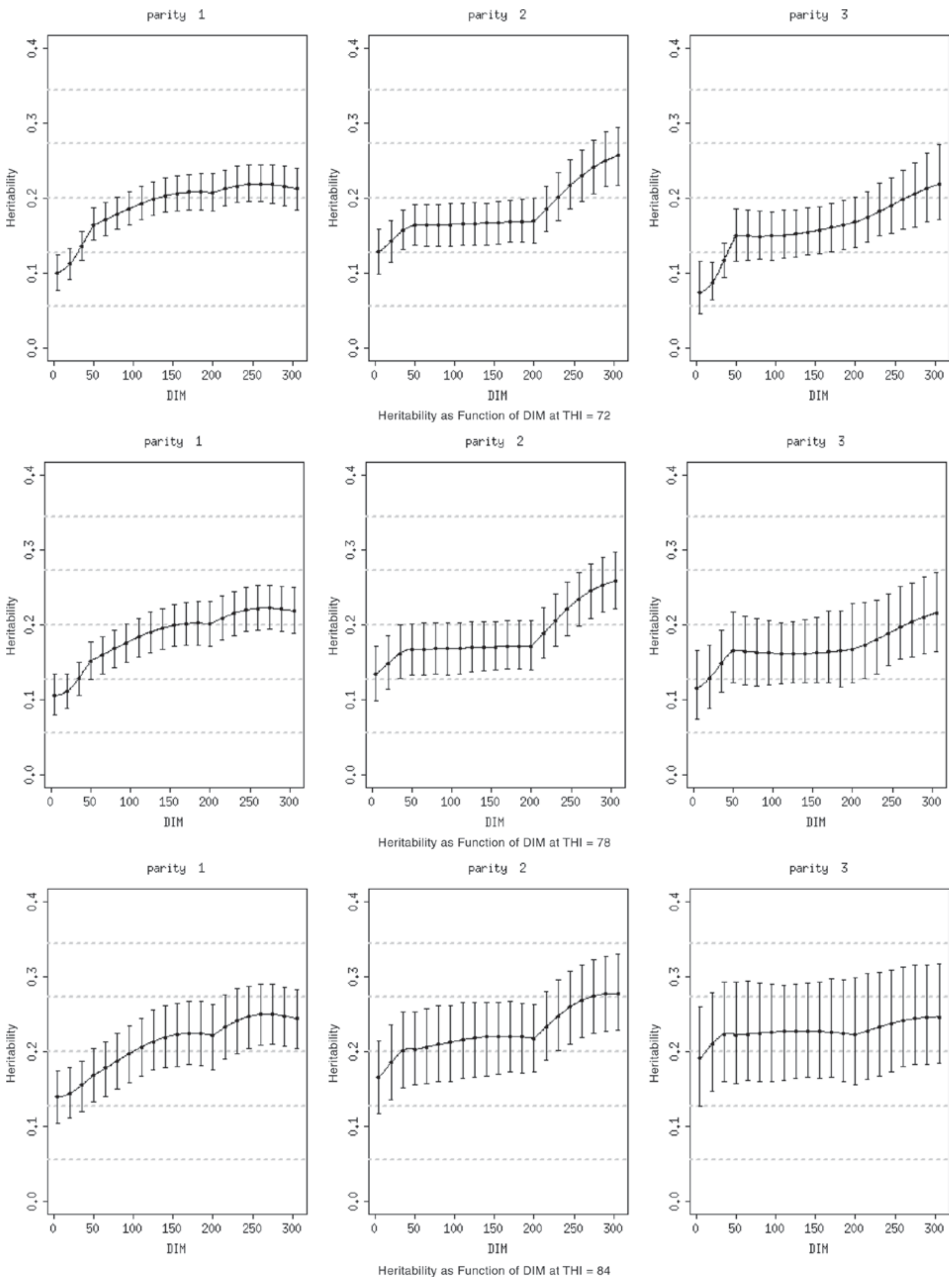

Figure 4. Posterior means and 95% high posterior density intervals for heritability estimated using a multiple-trait random regression test-day model for milk yield in parity 1, 2, or 3 by DIM and temperature-humidity index (THI).

Negative correlations between the general additive genetic effect and heat stress were found for all parities, except at the beginning of the third parity (0.10). Correlations differed between lactation stages within and between parities. For the first parity, the most negative correlation was at 50 DIM (−0.45); for later parities, the most negative correlation was at DIM 200 (−0.43 for the second parity and −0.41 for the third parity).

Although only 4 knots were fitted across DIM, genetic correlations appeared to be most negative during midlactation. Maust et al. (1972) and Perera et al. (1986) also reported that milk yield of cows under summer heat stress was most adversely affected during midlactation. Moreover, Abeni et al. (2007) showed that changes in blood parameters related to energy balance and enzyme activity under heat stress were greatest for midlactation cows.

Additive genetic variances for heat tolerance for milk yield from the RRM model (2.0 to 4.0; Table 4) were approximately one-half those from the REP model (3.7 to 8.9; Table 3), which indicates that lactations are managed to avoid maximum production during the hottest season and that the REP model does not account for that management timing. Genetic correlations for heat tolerance between different parities (not shown) were also lower for the RRM model compared with the REP model. Whether corresponding decreases would occur for fat and protein yields is unknown.

Curves for posterior means and 95% intervals for high posterior density at different DIM, THI, and parity are given in Figure 2 for permanent environmental variance and in Figure 3 for herd-year variance. For all parities, permanent environmental variances were greater than general additive genetic variances (Figure 1) and were U-shaped across DIM. Herd-year variances accounted for less variation during lactation, except at the beginning of lactation and somewhat at the end of second- and third-parity lactations. Those findings agree with studies that include random herd-year curves to account for environmental variation attributable to herds (de Roos et al., 2004; Hammami et al., 2008).

Heritability estimates at different DIM, THI, and parity are given in Figure 4. They ranged from 0.10 to 0.25 for the first parity, 0.13 to 0.28 for the second parity, and 0.08 to 0.25 for the third parity. Heritability estimates were lower at the beginning of lactation but increased with DIM and THI.

In general, genetic parameters vary from farm to farm and from region to region (Freitas et al. 2006a). Accounting for such differences is difficult and may result in almost no reranking of animal evaluations (Wiggans and VanRaden, 1991). Therefore, the parameters estimated in this study are likely to be useful as a preliminary step in developing national genetic evaluations for heat tolerance.

The model in this study assumes a linear sensitivity to THI as well as fixed thresholds. Relaxing these assumptions would require more complicated models as well as larger numbers of high-quality records. Sánchez et al. (2009) used a model that assumed variable thresholds and slopes of heat tolerance per cow. The model was very complex and the correlations between the threshold and the slopes were greater than 0.95. This indicated that animals with a high threshold for heat stress also have fewer declines in milk production at high temperatures. Thus, the effect of improving the model for ranking purposes is likely to be limited.

Additive genetic effects for heat stress and yield traits increased greatly from the first to third parity. Consequently, later parity cows are expected to be much more susceptible to heat stress than are first-parity cows. Variances for heat tolerance from an RRM may be lower than those from an REP, which assumes the same variance across parities and does not account for management practices that avoid maximum production during the hottest seasons.

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