

Genetic determination of the onset of heat stress on daily milk production in the US Holstein cattle

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ABSTRACT

Existence of individual variation in the onset of heat stress for daily milk yield of dairy cows was assessed. Data included 353,376 test-day records of 38,383 first-parity Holsteins from a random sample of US herds. Three hierarchical models were investigated. Model 1 inferred the value of a temperature-humidity index (THI) at which mean yield began to decline as well as the extent of that decline. Model 2 assumed individual variation in yield decline beyond a common THI threshold. Model 3 additionally assumed individual variation for the onset of heat stress. Deviance information criteria indicated the superiority of model 3 over model 2. For model 2, genetic correlation between milk yield in the absence of heat stress and the THI threshold for heat stress was -0.4 (0.11) [marginal posterior mean (marginal posterior standard deviation)]. For model 3, genetic correlations were -0.53 (0.05) between milk yield and THI threshold and -0.62 (0.08) between milk yield and yield decay beyond the THI threshold. Total standard deviation (sum of additive genetic and permanent environmental standard deviations) for the THI threshold was 3.95 (0.06), and more than half of that variation had an additive genetic origin [56% (5%)]. Because of the high genetic correlation [0.95 (0.03)] between yield decay and THI threshold with model 3, using only one of them as a selection criterion for heat tolerance would modify the other in the desired direction.

Key words: heat stress, milk yield, genetic variability, Holstein

INTRODUCTION

Resistance to heat stress is a trait of major economic importance, particularly in regions with hot climates. When ambient temperatures are high, animal perfor-

mance and reproductive rates decline (Fuquay, 1981). In spite of this trait's importance, direct phenotypic measurement can be difficult to obtain. Ravagnolo and Misztal (2000) estimated genetic parameters for resistance to heat stress indirectly by regressing phenotypic performance on temperature-humidity index (THI) values from a few days previous to milking. As THI values increase, animal performance declines, and these declines are subject to a threshold response, a point at which ambient temperatures exceed an animal's thermoneutral zone and performance begins to decline. A threshold around 72 THI, which corresponds to 22°C at 100% humidity, has been reported for US Holsteins (Ravagnolo et al., 2000; Freitas et al., 2006).

The most common approach for improving heat tolerance in beef cattle is crossbreeding of high-performance breeds with breeds that are locally adapted and more resistant to hot climates. In contrast, crossbreeding of high-performance dairy breeds such as Holstein to locally adapted breeds is unappealing because the crossbreds have substantially reduced yield capability compared with high-performance purebreds (McDowell et al., 1996). Thus, selective breeding of Holstein cows for heat tolerance has been proposed as an option for genetic improvement of heat tolerance.

For this purpose, reaction norm models implemented by using random regressions have been shown to be effective for genetic evaluation of heat tolerance. Several studies (Ravagnolo and Misztal, 2000, 2002; Freitas et al., 2006) estimated genetic parameters for both yield and reproduction traits under the influence of heat stress. Heritabilities for those traits increased as a function of THI.

Recently, Sánchez et al. (2009) proposed a hierarchical model that could be useful for identification of animals that are less sensitive to high temperatures. With this model, unlike in previous studies, two different criteria were used for defining an animal's level of heat tolerance. The first was the degree to which performance declined after some unknown THI threshold. The second was the THI value at which this perfor-

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mance drop begins. Thus, the higher the THI value at which yield begins to decline and the lower the rate of decline after heat stress starts, the more heat tolerant the animal is.

The objective of this study was to investigate the two aforementioned definitions of resistance to heat stress in a real dairy cattle data set. To achieve this goal, a model assuming variation on THI thresholds was compared with one assuming a single THI threshold for the entire population.

MATERIALS AND METHODS

Data

Test-day records for first-parity US Holsteins were provided by the Animal Improvement Programs Laboratory (ARS, USDA, Beltsville, MD). From this data set, only those records produced after 5 or before 305 DIM, on days with 2 or 3 milking sessions, and with associated THI values between 50 and 83 were retained. In addition, for records of a particular cow to be considered valid, it was necessary for her have at least 7 test-days, a known age on the test-day, and to be sired by a bull with more than 50 daughters, having a daughter THI range of at least 20 degrees. These edits reduced the data set to 2.8 million test-day records in 4,858 herds. Finally, for further reduction of the data set, 10% of the herds were randomly selected. The final data set used in the analysis included 353,376 milk yield test-day records of 38,383 cows in 15,508 herd-test-day (HTD) contemporary groups. Mean HTD class size was 22.8 records, and mean daily milk yield was 29.88 kg with a standard deviation of 6.84 kg. The pedigree file was constructed by tracing back 3 generations of ancestors and included 95,962 records.

Statistical Models

Three statistical models were used to investigate different aspects of the effect of heat stress on milk yield. Model 1 was used to infer the THI value at which mean yield began to decline and the extent of that decline:

$$y_{ijk\ell m} = \left[\text{DIM}(\text{MF}) \right]_i + \text{age}_j + \text{HY}_k + c_\ell + \beta \left\{ \max \left[0, \left(\text{THI}_{\ell m} - \tau_0 \right) \right] \right\} + e_{ijk\ell m}, \quad [1]$$

where $y_{ijk\ell m}$ is the m th observation on the animal ℓ produced in the i th class of the combination between DIM (31 levels) and milking frequency (MF, 2 levels), the j th class of age (8 levels), and the k th contemporary group (herd-year, HY); c_ℓ is a cow effect for which no

genetic structure was considered; β is a coefficient for linear regression on the number of test-day THI units above an overall threshold (τ_0) to be estimated; and $e_{ijk\ell m}$ is a residual term, which is assumed to be homoscedastic across test-day THI; $\text{THI}_{\ell m}$ refers to the test-day THI value index and was computed using the hourly average of this index of 3 d previous to milking. The hourly index was computed considering temperature (in °F) and humidity (in %) as described in Ravagnolo and Misztal (2000). Note that HY rather than HTD was used to define contemporary groups to avoid confounding the contemporary group definition with test-day THI.

To simplify notation of model 1, consider the vectors

$$\beta'_1 = \left[\text{DIM}(\text{MF})', \text{HY}', \text{age}' \right]$$

and $\mathbf{x}_{1,\ell m}$, which selects the appropriate elements in β'_1 for test-day yield m of cow ℓ . Using this alternative notation, model 1 is

$$y_{\ell m} = \mathbf{x}'_{1,\ell m} \beta_1 + c_\ell + \beta \left\{ \max \left[0, \left(\text{THI}_{\ell m} - \tau_0 \right) \right] \right\} + e_{\ell m}.$$

The inferential method implemented for estimating parameters for model 1 was a Bayesian Markov-chain Monte Carlo procedure, specifically a Gibbs sampler algorithm. The data-generating process can be described by the following multivariate normal (MVN) distribution:

$$\mathbf{y} \mid \beta_1, \mathbf{c}, \beta, \tau_0, \sigma_e^2 \sim \prod_{\ell=1}^N \prod_{m=1}^{M_\ell} N \left(\mathbf{x}'_{1,\ell m} \beta_1 + c_\ell + \beta \left\{ \max \left[0, \left(\text{THI}_{\ell m} - \tau_0 \right) \right] \right\}, \sigma_e^2 \right),$$

where N is the total number of cows with test-day records, M_ℓ is the number of test-day records for cow ℓ , and σ_e^2 is the residual variance. Assumed prior distributions for the parameters in model 1 were

$$p(\beta_1) \propto \prod_{I+J+K} U(-\infty, +\infty),$$

where I is the number of combined classes for DIM and MF; J is the number of age classes; K is the number of HY; and U indicates the density of a uniform distribution;

$$p(\mathbf{c} \mid \sigma_e^2) \propto \text{MVN}(\mathbf{0}, \mathbf{I}\sigma_e^2),$$

where σ_c^2 is cow variance and \mathbf{I} is an identity matrix;

$$p(\beta) \propto U(-\infty, +\infty);$$

$$p(\tau_0) \propto U(55.0, 90.0); \text{ and}$$

$$p(\sigma_e^2) \propto 1.$$

In a subsequent hierarchical stage, prior distribution for σ_c^2 was defined as $p(\sigma_c^2) \propto 1$.

Given these prior distributions and the assumed data-generating process, the joint posterior distribution can be constructed by multiplying the prior distribution by the conditional distribution of the data, given the parameters (conditional likelihood). Finally, for implementation of the Gibbs sampler, conditional posterior distributions must be obtained from the joint posterior distribution by retaining those parameters of interest. For this study, it is straightforward to show that the joint conditional posterior distribution for all position parameters $\theta' = (\beta_1', \mathbf{c}', \beta)$, given the variance component and threshold value, follows this normal process:

$$\theta \mid \sigma_c^2, \sigma_e^2, \tau_0, \mathbf{y} \sim MVN(\hat{\theta}, \mathbf{C}^{-1}\sigma_e^2),$$

where $\hat{\theta}$ are solutions to the traditional mixed model equations of Henderson et al. (1959), which can be represented by $\mathbf{C}\theta = \mathbf{r}$ (Sorensen and Gianola, 2002). Given prior and data-generating process assumptions, the conditional posterior distribution for both variance components is proportional to an inverse chi-squared distribution (Sorensen and Gianola, 2002).

Finally, the conditional posterior distribution for τ_0 (the THI value at which milk yield begins to decline) did not have a closed form:

$$p(\tau_0 \mid \theta, \sigma_e^2, \mathbf{y}) \propto \exp\left(-\sum_{\ell=1}^N \sum_{m=1}^{M_\ell} \frac{(y_{\ell m} - \mathbf{x}'_{1,\ell m} \beta_1 - c_\ell - \beta \{\max[0, (THI_{\ell m} - \tau_0)]\})^2}{2\sigma_e^2}\right).$$

Thus, a Metropolis step was implemented using a normal distribution centered on the current value of τ_0 as proposal density.

The Markov-chain Monte Carlo procedure can be summarized by the following steps:

1. Threshold τ_0 was sampled from its fully conditional posterior distribution using a Metropolis step;
2. Mixed-model equations were constructed using $\max[0, (THI_{\ell m} - \tau_0)]$ as a covariate;
3. Based on the constructed mixed-model equations, the position parameters were jointly sampled from the appropriate joint conditional posterior distribution by using a sparse Cholesky factor of \mathbf{C} ;
4. Variance associated with cow effect was sampled from the appropriate inverse-scaled chi-squared distribution; and
5. Residual variance was sampled from the appropriate inverse-scaled chi-squared distribution.

A second model was used to study the original definition of genetic tolerance to heat stress; that is, individual decline in phenotypic performance after a particular THI threshold:

$$y_{\ell m} = \mathbf{x}'_{1,\ell m} \beta_1 + \mu_\ell + \beta_\ell \left\{ \max[0, (THI_{\ell m} - \tau_0)] \right\} + e_{\ell m}, \tag{2}$$

where the new terms with respect to model 1 are μ_ℓ , a cow-specific intercept, and β_ℓ , a coefficient for linear regression, nested within cow ℓ , on the number of THI units above an overall threshold (τ_0). In this model, contrary to model 1, the k th contemporary group was defined by HTD instead of HY (see definition of $\mathbf{x}'_{1,\ell m}$ for model 1). The data-generating process again was described by an MVN distribution:

$$\mathbf{y} \mid \beta_1, \mathbf{c}, \boldsymbol{\mu}, \boldsymbol{\beta}, \tau_0, \sigma_e^2 \sim \prod_{\ell=1}^N \prod_{m=1}^{M_\ell} N(\mathbf{x}'_{1,\ell m} \beta_1 + \mu_\ell + \beta_\ell \{\max[0, (THI_{\ell m} - \tau_0)]\}, \sigma_e^2).$$

In addition to the prior assumptions for systematic parameters in model 1, the animal's specific random variables $\boldsymbol{\mu}$ and $\boldsymbol{\beta}$ (underlying variables) were assumed to have an MVN distribution:

$$p(\boldsymbol{\beta}, \boldsymbol{\mu} \mid \mathbf{P}_0) \propto MVN(\mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u}, \mathbf{P}_0 \otimes \mathbf{I}),$$

where \mathbf{X} is an incidence matrix for systematic effects, \mathbf{b} is a vector of systematic effects for the underlying variables such that $\mathbf{b}' = [\mathbf{b}'_\mu \quad \mathbf{b}'_\beta]$, \mathbf{Z} is an incidence ma-

trix for additive genetic effects, \mathbf{u} is a vector of additive genetic effects such that $\mathbf{u}' = [\mathbf{u}'_{\mu} \quad \mathbf{u}'_{\beta}]$, and \mathbf{P}_0 is the residual 2×2 (co)variance matrix between underlying variables, which is equivalent to the permanent environmental (co)variance matrix between observations (\mathbf{y}).

The \mathbf{b} vector should include systematic effects common to all records from the same cow. For this study, the only effect considered was an overall mean; however, for identification purposes, \mathbf{b}'_{β} was constrained to zero because it was confounded with HTD on the previous hierarchical level. Each HTD level corresponded exactly to a single THI value. The distribution for \mathbf{u} was MVN according to the infinitesimal model (Bulmer, 1980):

$$p(\mathbf{u} | \mathbf{G}_0) \propto MVN(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A}),$$

where \mathbf{G}_0 is the additive genetic 2×2 (co)variances matrix between underlying variables and \mathbf{A} is the known numerator relationship matrix between all animals in the population. In addition, the prior distributions for the remaining parameters (\mathbf{b}' and \mathbf{P}_0), which describe the distribution of the underlying variables, were improper uniform. In a final hierarchical stage, a uniform prior distribution was assumed for \mathbf{G}_0 .

This model and its hierarchical structure were similar to the model described by Sánchez et al. (2009), but a single threshold was assumed for all the animals. All the fully conditional posterior distributions for the position and dispersion parameters had standard forms and were described by Varona et al. (1997) in a study that involved a hierarchical model for fitting linear functions with intercept and slope. The only nonstandard conditional posterior distribution is that of the THI threshold:

$$p(\tau_0 | \beta_1, \mu, \beta, \sigma_e^2, \mathbf{y}) \propto \exp \left(- \sum_{\ell=1}^N \sum_{m=1}^{M_{\ell}} \frac{(y_{\ell m} - \mathbf{x}'_{1,\ell m} \beta_1 - \mu_{\ell} - \beta_{\ell} \{\max[0, (THI_{\ell m} - \tau_0)]\})^2}{2\sigma_e^2} \right).$$

Previous simulation studies under balanced conditions (J. P. Sánchez, unpublished data) showed the capability of the proposed method to estimate the overall threshold appropriately by using a Metropolis step for sampling this conditional posterior distribution. However, the procedure was not able to estimate the parameter appropriately with real observations. The overall threshold was shifted to the lower bound of its a priori defined parameter space. Because of that

problem, the threshold was constrained to the value estimated with model 1.

Model 3 can be described by

$$y_{\ell m} = \mathbf{x}'_{1,\ell m} \beta_1 + \mu_{\ell} + \beta_{\ell} \left\{ \max[0, (THI_{\ell m} - \tau_{0,\ell})] \right\} + e_{\ell m}. \quad [3]$$

Individual variation was assumed to exist for the threshold position, and contemporary groups were defined as HTD. Model 3 was the same as the model presented in the simulation study of Sánchez et al. (2009). The data-generating process for model 3 was a normal distribution:

$$\mathbf{y} | \beta_1, \mathbf{c}, \boldsymbol{\mu}, \boldsymbol{\beta}, \tau_0, \sigma_e^2 \sim \prod_{\ell=1}^N \prod_{m=1}^{M_{\ell}} N(\mathbf{x}'_{1,\ell m} \beta_1 + \mu_{\ell} + \beta_{\ell} \left\{ \max[0, (THI_{\ell m} - \tau_{0,\ell})] \right\}, \sigma_e^2).$$

Model 3 is similar to model 2, except that each animal with records had a unique threshold ($\tau_{0,\ell}$) rather than a population threshold (τ_0). The only difference regarding prior assumptions for model 2 was that the underlying variables were jointly described by different MVN distribution:

$$p(\boldsymbol{\beta}, \boldsymbol{\mu}, \boldsymbol{\tau}_0 | \mathbf{P}_0) \propto MVN(\mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u}, \mathbf{P}_0 \otimes \mathbf{I}).$$

Similar to model 2, $\mathbf{b}' = [\mathbf{b}'_{\mu} \quad \mathbf{b}'_{\beta} \quad \mathbf{b}'_{\tau_0}]$, \mathbf{b}'_{β} was constrained to zero, and in addition \mathbf{b}'_{τ_0} was fixed to the estimated value of the overall threshold obtained from model 1. In this case, \mathbf{P}_0 is the residual 3×3 (co)variance matrix between underlying variables. The distribution for $\mathbf{u}' = [\mathbf{u}'_{\mu} \quad \mathbf{u}'_{\beta} \quad \mathbf{u}'_{\tau_0}]$ was a priori MVN according to the genetic infinitesimal model (Bulmer, 1980):

$$p(\mathbf{u} | \mathbf{G}_0) \propto MVN(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A}),$$

where \mathbf{G}_0 has dimension 3×3 with the same meaning as for model 2.

The same prior assumptions for \mathbf{b}' and the dispersion matrix \mathbf{P}_0 in model 2 were adopted for model 3. All the position and dispersion parameters had known closed forms (Varona et al., 1997; Sorensen and Gianola, 2002; Sánchez et al., 2009). The only parameters with a nonstandard conditional posterior distribution were the thresholds associated with each animal, which could be expressed as:

$$p(\tau_{0,\ell} \mid \boldsymbol{\beta}_1, \boldsymbol{\mu}, \boldsymbol{\beta}, \boldsymbol{\tau}_0, \sigma_e^2, \mathbf{b}, \mathbf{P}_0, \mathbf{y}) \propto \exp \left\{ - \sum_{m=1}^{M_\ell} \frac{\left(y_{\ell m} - \mathbf{x}'_{1,\ell m} \boldsymbol{\beta}_1 - \mu_\ell - \beta_\ell \left\{ \max \left[0, \left(\text{THI}_{\ell m} - \tau_{0,\ell} \right) \right] \right\} \right)^2}{2\sigma_e^2} \right\} \times \exp \left\{ - \frac{2}{p_0^{\tau_0, \tau_0}} \left[\tau_{0,\ell} - \left\{ \mathbf{X}_{\tau_0} \mathbf{b}_{\tau_0} + \mathbf{Z}_{\tau_0} \mathbf{u}_{\tau_0} - \frac{\left[\left(\mu_\ell - \mathbf{X}_\mu \mathbf{b}_\mu - \mathbf{Z}_\mu \mathbf{u}_\mu \right) p_0^{\mu, \tau_0} + \left(\beta_\ell - \mathbf{X}_\beta \mathbf{b}_\beta - \mathbf{Z}_\beta \mathbf{u}_\beta \right) p_0^{\beta, \tau_0} \right]}{p_0^{\tau_0, \tau_0}} \right\} \right]^2 \right\}$$

where the scalars $p_0^{i,j}$ refer to the appropriate terms of the inverse of the residual (co)variance matrix in the second hierarchical stage (\mathbf{P}_0); that is, the (co)variance matrix for the permanent environmental effect on the observations (\mathbf{y}). The first factor in the previous equation came from the conditional likelihood and, as such, depended only on the assumed data-generating process. The second factor depended on the specific assumptions for the second hierarchical stage. For sampling this distribution, a Metropolis step was used along with a normal density centered in the current value of $\tau_{0,\ell}$ as proposal (i.e., random walk Metropolis).

Models 2 and 3 were compared by using the deviance information criterion (Spiegelhalter et al., 2002). For each model, a single Markov chain was run that had a length of 140,000 rounds for model 1 and 250,000 rounds for models 2 and 3; 20% (model 1) and 10% (models 2 and 3) of the chains samples were discarded

as the burn-in period. After burn-in, 1 in 30 samples for model 1 and 1 in 25 samples for models 2 and 3 were retained for analysis. Convergence of the chains was determined by visual inspection of the trace plots for the parameters of major interest.

The variance of the proposal distributions used for the Metropolis step were 0.08 (model 1) and 0.5 (model 3), which yielded acceptance rates after burn-in of 0.35 and 0.42, respectively. For model 3, the same proposal variance was used for all the animals, and the acceptance rate was the mean across all the animals with records. For model 2, the overall threshold position was constrained to 71 THI; thus, no Metropolis step was needed.

RESULTS

For an initial description of the relationship between milk yield and THI, the residuals from model 1 without

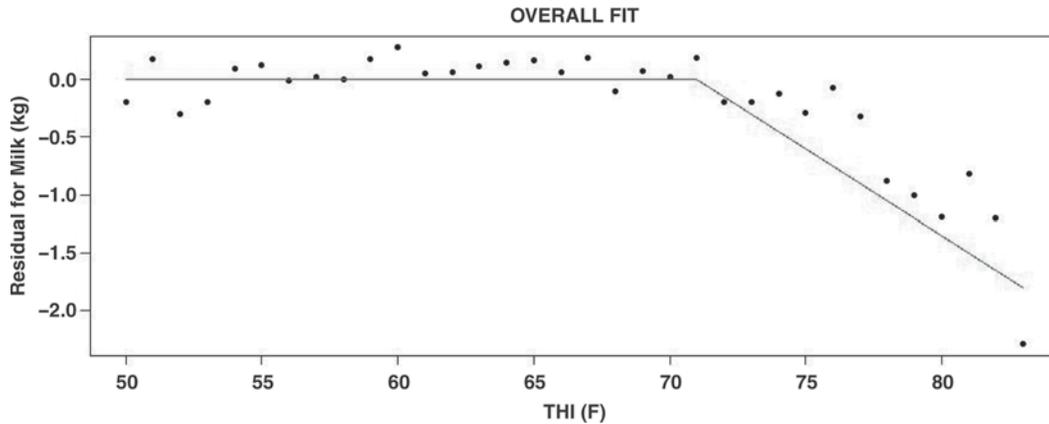


Figure 1. Residuals averaged by integer values for the temperature-humidity index (THI) of records from the model 1, with the load function of $\max \left[0, \left(\text{THI}_{\ell m} - \tau_0 \right) \right]$ excluded from it; the solid line represents the overall mean yield as a function of THI estimated from the complete model 1.

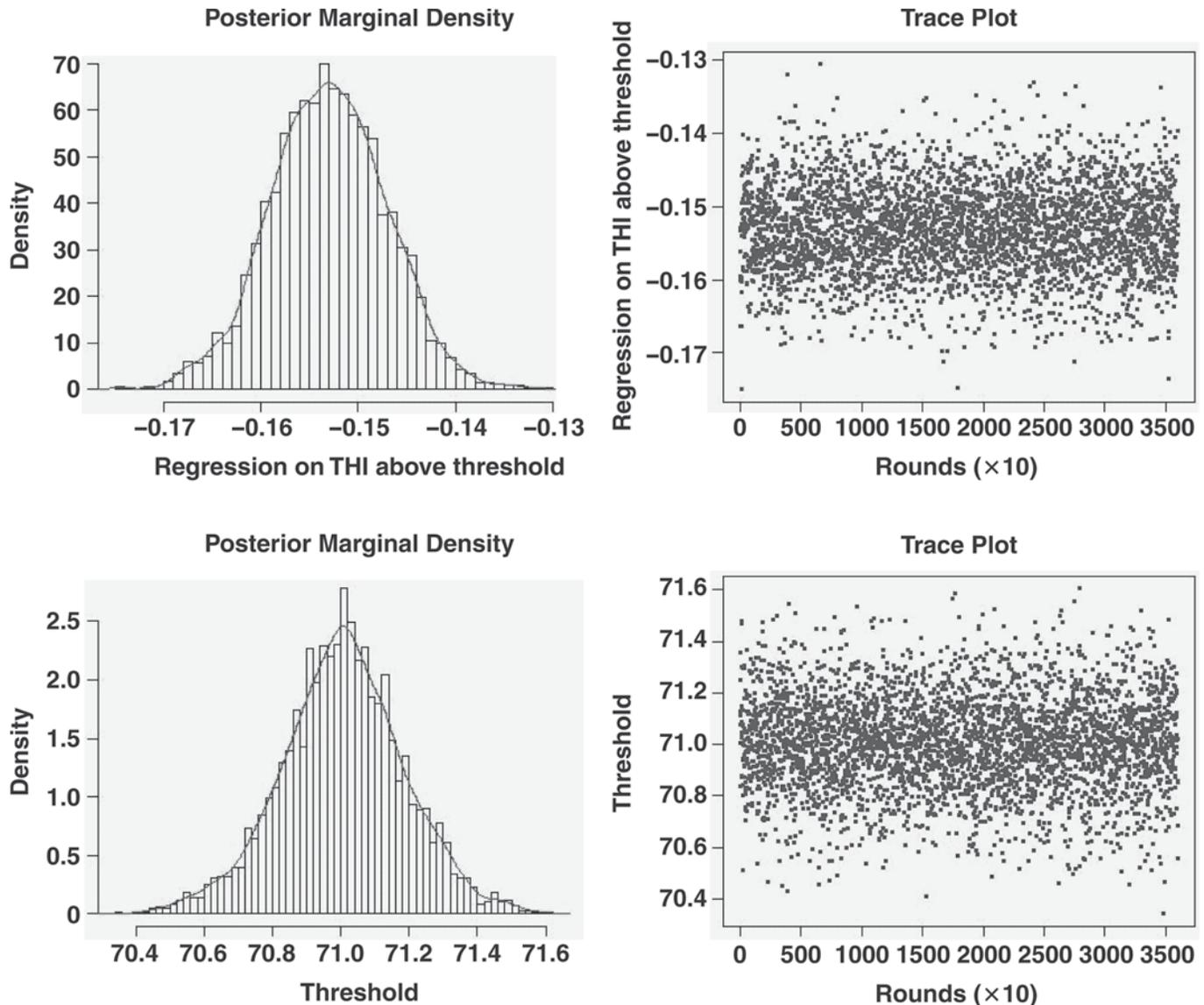


Figure 2. Marginal posterior distributions (left) and trace plots of the sampled values (right) for the overall threshold (below) and the regression coefficient beyond this threshold (above) estimated using model 1. THI = temperature-humidity index.

considering regression on the load function $\max[0, (THI_{\ell m} - \tau_0)]$ were calculated. Figure 1 shows means of those residuals by THI value. A decline in overall yield around 71 THI is evident. Using the complete model 1, the threshold for declining milk yield estimated as the marginal posterior mean was 71.00 (0.18) THI (marginal posterior standard deviation). Beyond that threshold, the estimated slope of the linear change in milk yield was -0.15 (0.01) kg/THI. Mean yield as a function of THI estimated from model 1 is also shown in Figure 1. Figure 2 shows the marginal posterior distributions for those 2 parameters as well as their trace plots. From this model, means of the mar-

ginal posterior distributions for the residual and cow variances were 14.00 (0.12) and 16.48 (0.04) kg^2 , respectively.

Table 1 shows the estimated genetic and environmental parameters on the underlying variable scale from model 2. The estimated heritability for milk yield in the absence of heat stress ($\text{THI} < 71.0$) was 0.14 (0.01). This parameter decreased to a minimum of 0.13 (0.01) at THI 76 and then started to increase until reaching a maximum of 0.18 (0.04) at a THI of 90. The entire heritability pattern (Figure 3a) was computed using the following linear function for obtaining the appropriate variance component patterns in each round of Gibbs sampler:

$$\hat{\sigma}_{v,t}^2 [r] = \begin{bmatrix} 1 & L_t \end{bmatrix} \hat{\mathbf{V}}_{0,v} [r] \begin{bmatrix} 1 \\ L_t \end{bmatrix},$$

where v = additive genetic (g) or permanent environmental (p) variance that yields $\hat{\mathbf{G}}_0^{[r]}$ or $\hat{\mathbf{P}}_0^{[r]}$ additive genetic or permanent environmental (co)variance matrix between intercept and slope sampled in round *r*, respectively; and L_t is the value of the function $\max[0, (THI_t - 71.0)]$, where THI_t is THI value *t* for which heritability will be computed. In a general setting including the estimation of the overall threshold, this function is $\hat{L}_t^{[r]} = \max[0, (THI_t - \tau_0^{[r]})]$. Finally, the marginal posterior sampled value for the heritability at THI *t* in round *r* was computed as

$$\hat{h}_t^{2[r]} = \frac{\hat{\sigma}_{g,t}^2 [r]}{\hat{\sigma}_{g,t}^2 [r] + \hat{\sigma}_{p,t}^2 [r] + \hat{\sigma}_e^2 [r]}.$$

Table 2 shows estimated genetic and environmental parameters on the underlying variable scale from model 3. Estimated heritability at a THI of 60 was 0.17 (0.01). The estimate of this parameter decreased to 0.13 (0.02) at THI 80 and then increased up to 0.16 (0.03) at a THI of 90. Computation of the heritability pattern (Figure 3b) used approximate equations for obtaining additive genetic and permanent environmental variances at different THI because variance compo-

nents at a given THI are nonlinear functions of $\hat{\mathbf{G}}_0$ and $\hat{\mathbf{P}}_0$. Sampling from the marginal posterior distribution of different variance components at THI *t* relied on generating total genetic and phenotypic values for all animals for a particular THI (following model equation); and then empirical variances for those values were computed and considered to be a sample from the appropriate marginal posterior distribution (Sánchez et al., 2009).

Variability of animal effects as a function of THI based on a sample of 200 animals is shown in Figure 4a for model 2 and in Figure 4b for model 3. For model 3, the total standard deviation (sum of additive genetic and permanent environmental standard deviations) for the THI threshold was 3.95 (0.06) (variances in Table 2), which yields an approximate range of variation for individual THI thresholds of 63 to 79.

Deviance information criterion values for models 2 and 3 were 1,338,527 and 1,325,871, and the equivalent numbers of parameters were 51,096 and 52,670, respectively. Those values agree with the actual number of parameters.

DISCUSSION

The deviance information criterion values support the assumption that individual variation exists for the onset of heat stress. Although this hypothesis was proposed in earlier studies on genetics of heat tolerance in dairy cattle (Ravagnolo and Misztal, 2000), it was not

Table 1. Marginal posterior statistics for genetic and environmental parameters of underlying variables in a model in which tolerance to heat stress was measured as individual decline in phenotypic performance after a particular temperature-humidity index threshold (model 2)

Parameter ¹	Mean	Median	SD	95% Highest posterior density region		Effective sample size, n
				Lower boundary	Upper boundary	
$\sigma_{(g+p)_I}^2$	15.44	15.44	0.15	15.13	15.74	808
$\sigma_{(g+p)_S}^2$	0.06	0.06	0.003	0.05	0.06	645
$\sigma_{g_I}^2$	4.17	4.17	0.32	3.55	4.81	311
$\sigma_{g_S}^2$	0.016	0.016	0.004	0.008	0.023	27
h_I^2	0.27	0.27	0.02	0.23	0.31	296
h_S^2	0.28	0.29	0.07	0.14	0.40	32
$\rho_{g_{I,S}}$	-0.40	-0.40	0.11	-0.62	-0.19	48
$\rho_{p_{I,S}}$	-0.47	-0.47	0.04	-0.55	-0.39	79

¹ $\sigma_{(g+p)}^2$ = total [additive genetic (g) + permanent environmental (p)] variance for intercept (I) or slope (S); σ_g^2 = additive genetic variance for I or S; h^2 = heritability ($\sigma_g^2 / \sigma_{(g+p)}^2$) for I or S; $\rho_{g_{I,S}}$ = genetic correlation between I and S; and $\rho_{p_{I,S}}$ = permanent environmental correlation between I and S.

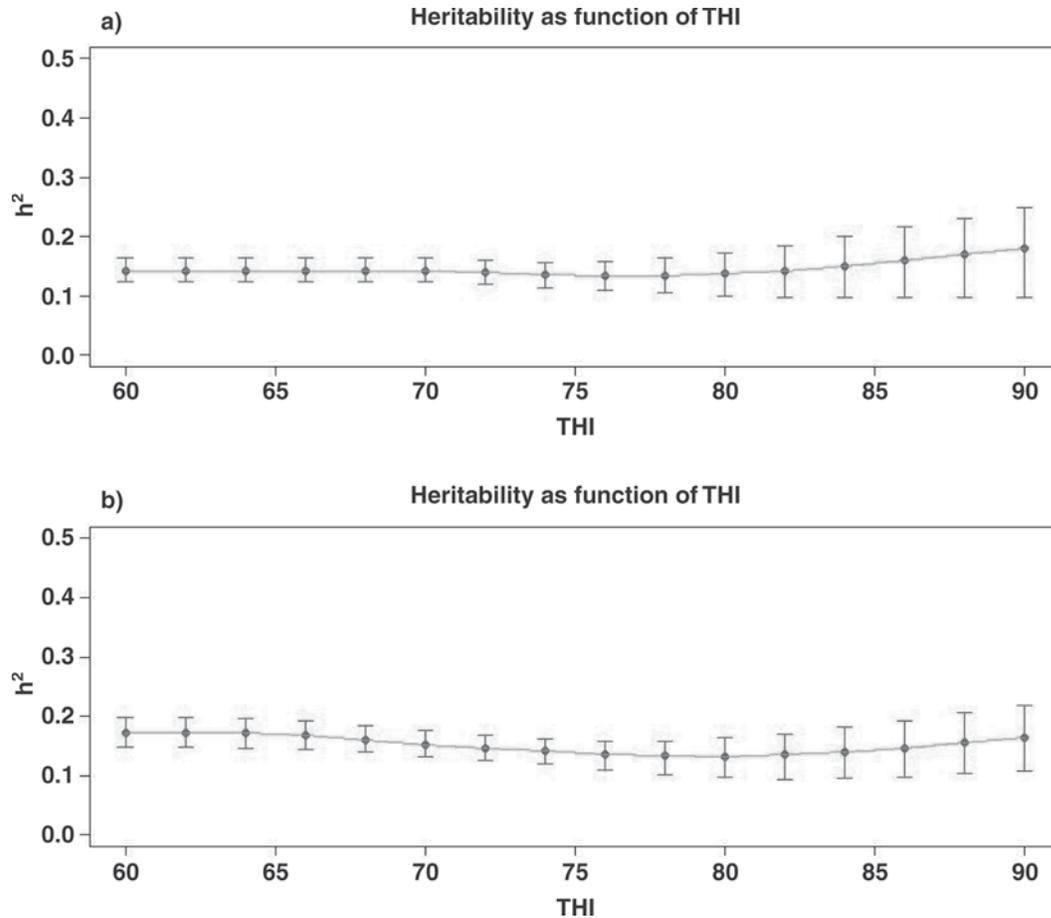


Figure 3. Heritability (h^2) of daily milk production as a function of temperature-humidity index (THI) estimated using model 2 (a) and model 3 (b).

modeled until now mainly because of statistical difficulties.

Model 1 estimates of the threshold for onset of heat stress for milk yield were within the range previously reported for different samples of the US Holstein population (Ravagnolo et al., 2000; Freitas et al., 2006; Bohmanova et al., 2007). Onset of heat stress in the southeastern United States generally occurs at lower THI than in other regions (Bohmanova et al., 2007), which could be a consequence of high humidity that negatively affects the efficiency of cooling systems. Estimated effect of heat stress for the present study based on Holstein data from the entire United States was less intense than in other studies that only included data from regions subject to heat stress (Ravagnolo and Misztal, 2000; Freitas et al., 2006; Bohmanova et al., 2007). That lessened intensity is reflected in the magnitude of the slope for mean performance decay (-0.15 kg/THI), which is similar to that for regions with less heat stress (Freitas et al., 2006). In contrast, the estimated threshold for the onset of heat stress in the present study was close to values previously esti-

ated for regions with extremely intense heat stress, such as the southeastern United States (Freitas et al., 2006).

Similar to previous studies (Ravagnolo and Misztal, 2000; Freitas et al., 2006), antagonistic correlations were found between yield in the absence of heat stress and heat tolerance as expressed through both environmental and genetic correlations between intercepts and slopes (models 2 and 3) and between intercepts and thresholds (model 3). In addition, correlations estimated with model 2 were similar in magnitude to those previously estimated from different samples of US Holsteins (Ravagnolo and Misztal, 2000; Freitas et al., 2006).

Previous studies on estimation of genetic parameters for heat tolerance (Ravagnolo and Misztal, 2000; Freitas et al., 2006) that used models similar to model 2 always reported lower heritability estimates in the absence of heat stress than for models that did not consider heat tolerance. Those studies showed that additive genetic variance and heritability tend to increase with THI (as also observed for model 2). Thus, reported heritabilities in the absence of heat stress were the lower bound for

Table 2. Marginal posterior statistics for genetic and environmental parameters of underlying variables in a model in which tolerance to heat stress was measured as individual decline in phenotypic performance after a temperature-humidity index threshold that varied by individual (model 3)

Parameter ¹	Mean	Median	SD	95% Highest posterior density region		Effective sample size, n
				Lower boundary	Upper boundary	
$\sigma_{(g+p)_I}^2$	15.93	15.93	0.15	15.63	16.24	614
$\sigma_{(g+p)_S}^2$	0.10	0.10	0.004	0.09	0.11	25
$\sigma_{(g+p)_T}^2$	11.02	11.03	0.29	10.40	11.55	41
$\sigma_{g_I}^2$	4.86	4.85	0.37	4.10	5.58	196
$\sigma_{g_S}^2$	0.016	0.016	0.002	0.012	0.020	41
$\sigma_{g_T}^2$	8.72	8.67	0.86	7.15	10.59	36
h_I^2	0.29	0.29	0.02	0.25	0.33	199
h_S^2	0.32	0.32	0.04	0.25	0.41	39
h_T^2	0.56	0.56	0.05	0.47	0.65	31
$\rho_{g_{I,S}}$	-0.62	-0.62	0.08	-0.77	-0.46	24
$\rho_{g_{I,T}}$	-0.53	-0.53	0.05	-0.63	-0.42	60
$\rho_{g_{S,T}}$	0.95	0.96	0.03	0.90	0.99	7
$\rho_{p_{I,S}}$	-0.45	-0.45	0.03	-0.52	-0.40	37
$\rho_{p_{I,T}}$	-0.26	-0.26	0.04	-0.35	-0.18	33
$\rho_{p_{S,T}}$	0.97	0.97	0.01	0.95	0.99	28

¹ $\sigma_{(g+p)}^2$ = total [additive genetic (g) + permanent environmental (p)] variance for intercept (I), slope (S), or threshold (T); σ_g^2 = additive genetic variance for I, S, or T; h^2 = heritability ($\sigma_g^2 / \sigma_{(g+p)}^2$) for I, S, or T; ρ_g = genetic correlation among I, S, and T; and ρ_p = permanent environmental correlation among I, S, and T.

the heritability pattern with THI. In models without an effect for heat tolerance, the reported heritabilities can be considered as weighted means across the heritability pattern with THI; therefore, heritability estimates from such models will be greater than those in the absence of heat stress. In fact, heritability estimates in the absence of heat stress from model 2 agree well with estimates reported by Freitas et al. (2006); their estimates of heritability of milk yield in the absence of heat stress ranged from 0.12 for southern California to 0.18 for Georgia, and their mean estimate across states was 0.14, which is the same as heritability estimated for the entire US Holstein population with model 2 when THI is lower than 71.

Slopes and individual thresholds from model 3 were strongly positively correlated (≥ 0.95) both genetically and environmentally. By considering either one as a selection criterion, the other will be modified. This relationship is favorable for selection because breeding for less negative slopes would increase the value of the thresholds for the onset of heat stress.

It must be noted that the meaning and values of the slopes from models 2 and 3 are similar but not

the same, which is reflected in the correlation (0.76) between predicted individual slopes (marginal posterior means) under the two models. The Pearson correlation coefficient between EBV (marginal posterior means) for slopes across models was 0.49. This small correlation across models could be explained by the high environmental and genetic correlations between slope and threshold for model 3 (Table 2); those relationships are not considered in model 2. The correlation coefficient between EBV for slopes from model 2 and EBV for threshold from model 3 has a similar magnitude (0.42). With model 3, heat tolerance effect could be considered to be split between slope and threshold, which are highly correlated to each other and equally correlated to the heat tolerance effect in model 2.

The methodology applied in this study was previously investigated in a simulation study by Sánchez et al. (2009). Their results were promising and showed the ability of the method to detect environmental and genetic sources of variation in heat tolerance properly, both for linear change in performance after an animal-specific threshold is reached and for the threshold itself. In agreement with that study, bad mixing was observed

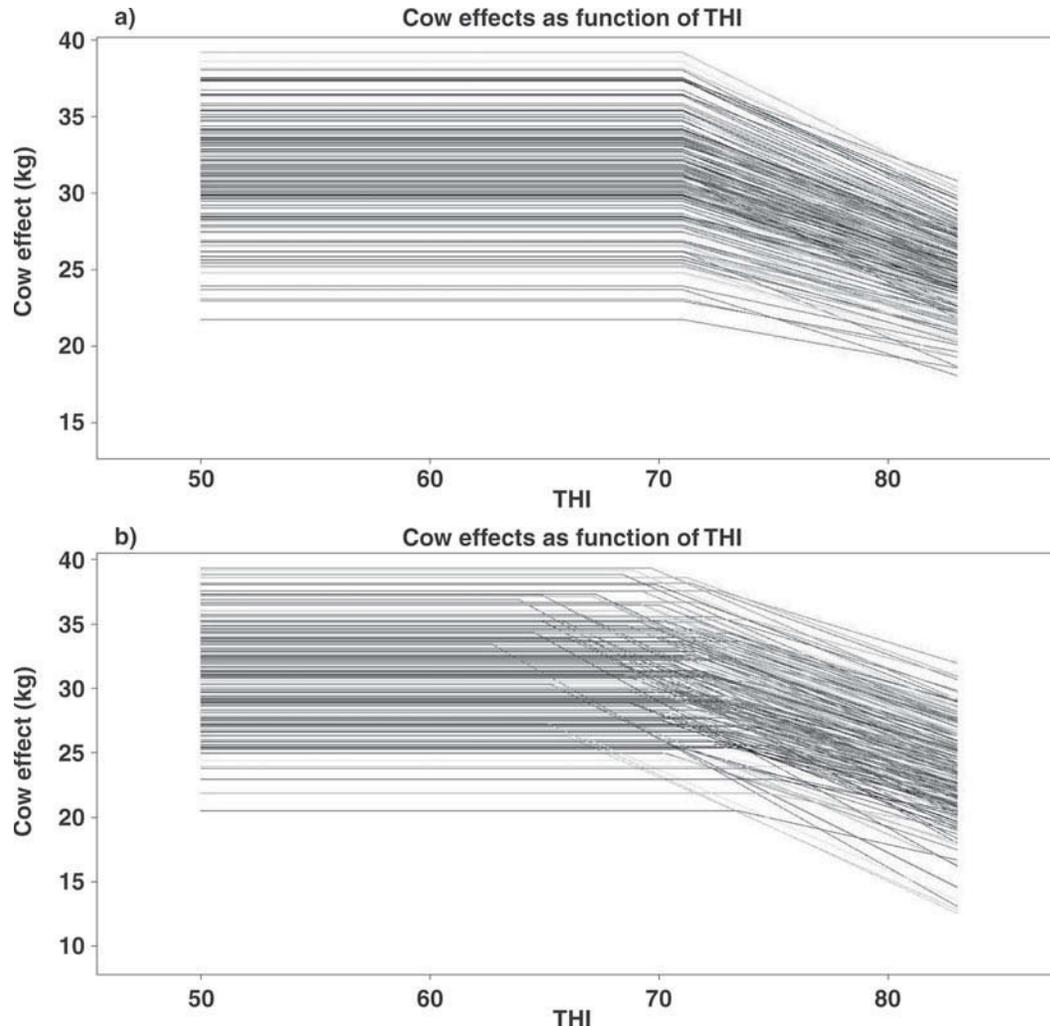


Figure 4. Prediction of cow effects as a function of temperature-humidity index (THI) using model 2 (a) and model 3 (b).

when correlations between underlying variables were extreme.

Unexpected results were obtained during the initial fitting of the animal models to the current data set. For example, the optimal change-point for model 2 converged to the lower bound of its a priori-defined parameter space. Also, the threshold mean for model 3 converged to a THI of 67.5, which was much lower than the THI threshold of 71 that was estimated with model 1. In addition, the mixing of the chain was extremely slow. To avoid those problems, the unique change-point (model 2) and the threshold mean (model 3) were constrained to a THI of 71, the value estimated from model 1. In spite of that constraint, sources of variation in the onset of heat stress for milk yield could still be determined.

Previous simulation studies (Sánchez et al., 2009) conducted under balanced data conditions demonstrated the ability of models 2 and 3 to recapture pa-

rameters used in the data simulation. To investigate why a threshold constraint was necessary, a simulation test was conducted under the current study's data and pedigree structure. New records were generated according to models 2 and 3 with parameters (variance components) estimated from the real data (Tables 1 and 2). All parameter values could be recaptured. The simulation test was repeated with several modifications in the generation of data, including fixing the value of the residuals (in both hierarchical levels) and the breeding values to those figures predicted using the real data set and the models with the threshold constraints at a THI of 71, instead of generating them from appropriate normal distributions. It was observed that only when the residuals in the first hierarchical stage were fixed, the procedure was not able to recover the real values used in the simulation, particularly the overall threshold in model 2 and the threshold variance in model 3. A close inspection of those residuals showed a departure

from normality, skewness and kurtosis coefficients were -0.33 and 3.78 , respectively, which could explain the need of constraint for getting reasonable results in our analyses. Based on this observation, a model that assumed a thick-tailed distribution (t-distribution) for the residuals in the first hierarchical stage would be preferable (Sorensen and Gianola, 2002).

Prior assumptions for estimating the overall threshold with model 2 were weaker than the corresponding assumptions for estimating individual thresholds with model 3. For model 2, no relationship between relatives was considered, and the overall threshold was not correlated a priori to other parameters in the model. However, model 3 still did not allow for proper estimation or identification of the mean threshold, although the misidentification problem of the overall threshold was less severe than with model 2. In previous studies with nonlinear hierarchical longitudinal models (Ferris et al., 1985; Varona et al., 1998; Rekaya et al., 2000), these prior assumptions have been shown to improve estimation greatly when compared with other techniques without such prior assumptions; for example, 2-step procedures and log-linear random regression models.

The major negative issue related to the proposed models is their highly parameterized structures that make the estimation procedures inefficient. Future research should address the observed slow mixing and convergence rates. Joint update algorithms, more parsimonious model parameterizations, or nonnormal residual distribution can be used to make the models more robust to departures in the data from model assumptions.

CONCLUSIONS

Variation in the onset of heat stress for daily milk yield exists in the US Holstein population. Part of that variability has a genetic origin that could be useful in genetic selection programs for heat tolerance. However, given the strong opposite correlation between the threshold for heat stress and the decline in milk yield after that threshold is reached, either heat tolerance trait could be modified in the desired direction by considering the other as a selection criterion. A model including effects for both heat tolerance traits is statistically preferable, and ranking of animals based on EBV for slopes from a model assuming variation only in yield decay would be different by 25% from that based on EBV for slopes from a model assuming variation both on slope and onset of heat stress.

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