

GENETICS OF HEAT TOLERANCE FOR PRODUCTION TRAITS IN DAIRY CATTLE

by

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(Under the Direction of Ignacy Misztal)

ABSTRACT

The first study estimates variance components for heat stress (**HS**) for the first three lactations using test day models. Repeatability (**MREP**) and random regression (**MRRM**) models included a random regression on a function of temperature-humidity index. Regular genetic variance increased from the first to second parity but slightly declined in the third parity. Genetic variance of HS strongly increased with parity. With the MRRM, the variance of the HS effect was about half of that of the MREP.

The second study compares different computing options of preconditioned conjugate gradient algorithms for a large scale genetic evaluation using multiple-traits test-day random-regression models accounting for HS. Preconditioners were: diagonal, block diagonals due to traits (**BT**), block diagonal due to traits and correlated effects (**BTCORR**), and BT with the random effects reparameterized for diagonal (co)variance matrices within traits (**BTDIAG**). When sufficient memory is available, BTCORR was the fastest and the simplest to implement.

INDEX WORDS: Heat stress, Genetic evaluation, Variance components, Dairy cattle

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CHAPTER 1

INTRODUCTION

Heat stress is a major issue in the dairy industry because of the large losses it generates. It not only impacts milk production but also affects the reproductive performance of the animals.

Different approaches have been proposed to manage heat stress in dairy cattle e.g. cooling, shading, and nutrition. Assuming substantial additive genetic variation for heat tolerance, genetic improvement of animals is another alternative to handle the heat stress. Temperature and humidity indexes obtained from public weather data can be used to assess the impact of temperature and humidity on an animal's performance. Genetic evaluations that combine these indices with performance records can provide breeding values for heat tolerance that could be used for selection purposes.

A methodology for a large scale genetic evaluation was developed using repeatability test day models in first parity cows. First parity cows have lower production compared to cows of later parities, thus multiple-parity cows are expected to be more sensible to heat stress. Random regression models can be used to model the genetic and environmental variation during lactation, allowing more adjustments due to heat tolerance at different stages of lactation.

The first objective of this study was to estimate the variance components of milk, fat and protein yield with a multiple-parity test day model accounting for heat stress. Models considered were repeatability and random regression.

The second objective was to evaluate different computing options for the national genetic evaluation for heat tolerance using a multiple-parity random regression test-day model.

CHAPTER 2

REVIEW OF LITERATURE

Heat stress

The production of farm animals is influenced by several environmental factors, including the thermal environment. Environmental temperature is affected by air temperature, relative humidity, air movement, solar radiation, wind and the thermal environment of animals (Yousef, 1985), which leads to the concept of “effective ambient temperature” (EAT) that describes the combinations of all of them (National Research Council, 1981).

As homeothermic animals, dairy cattle try to maintain a relatively constant body temperature by balancing the heat gained from their metabolism and the environment. Animals try to maintain that balance by losing heat from the body surface by conduction, convection and radiation. There is also a continuous loss of heat from the respiratory tract and skin surface. The net rate of heat loss depends on the characteristics of the surrounding environment and on the resistance to the heat flow of the tissue, skin and its covering (National Research Council, 1981).

The relationship between animals and their thermal environment leads to the concept of a thermo neutral zone (TNZ). It could be defined as “the range of EAT within which the heat from maintenance and productive functions of the animal in non stressful situations offsets the heat loss to the environment without requiring an increase in rate of metabolic heat production” (National Research Council, 1981). Animals experience heat stress when the environmental temperature is higher than the animal’s TNZ. At 20°C animals do not experience changes in basic metabolic rate, and this is considered the thermo neutral temperature (National Research

Council, 1981). Any combination of environmental variables that are higher than the temperature range for the animal's TNZ (5-20°C) may result in heat stress.

Animal response to heat stress

The general homeostatic responses to thermal stress in mammals include a decrease in fecal and urinary water losses, a reduction in feed intake and production, and an increase in sweating, respiratory and heart rates. Most of the adjustments made by the cow involve dissipating heat to the environment and reducing the production of metabolic heat (Kadzere et al., 2002).

As milk production increases in dairy cattle, the metabolic heat production rises with the metabolizing of large amounts of nutrients, which makes the high producing cow more vulnerable to high environmental temperatures and humidity than animals that are metabolically less active (Kadzere et al., 2002). High producing dairy cows must dissipate large amounts of heat produced during the metabolism of high dietary energy used for body maintenance and milk synthesis. If the heat production exceeds the capacity of the heat dissipating mechanisms, the body temperature will rise. Maintenance of homeothermy is critical to the cow, thus slight increases in body temperature will depress feed intake, heat production and subsequently milk production (Coppock et al., 1982).

Heat stress impact on production

Several studies reported that heat stress in dairy cattle affects production (Maust et al., 1972, Fuquay, 1981, Bryant et al., 2007b) and reproduction (Ravagnolo and Misztal, 2002, Jordan, 2003, Garcia-Ispierto et al., 2007, Morton et al., 2007). Economic losses due to heat stress for the U.S. dairy industry are estimated to be between \$897 and \$1500 million dollars per year (St-Pierre et al., 2003).

Based on several reviews, Fuquay (1981) concluded that there is an association between high environmental temperatures and reductions in both livestock production and reproduction. He concluded that for a range of species and different production traits the upper critical temperature is around 24 to 27 °C.

Heat stress is commonly assessed by the temperature-humidity index (**THI**) (National Research Council, 1981). Different combinations of temperature and humidity were proposed. National Oceanic and Atmospheric Administration defined the THI index as follows:

$$THI = T - (0.55 - 0.0055 * RH) * (T - 58) \text{ (NOAA, 1976)}$$

where T is the dry bulb temperature in ° F and RH is the relative humidity in percentage. Different indexes of temperature and humidity were compared to measure losses in milk production due to heat stress for two regions of the U.S. with different climatic profiles (Bohmanova et al., 2007). Optimal THI was different in humid and semiarid regions.

Igono et al. (1992) showed that milk production is lower during heat stress compared to non-heat stress periods, and the upper critical values of THI where milk production decreased were 64, 72 and 76 for the minimum, mean, and maximum THI, respectively.

Bryant et al. (2007a) found that hot weather conditions under a grazing system reduced milk yield, milk solids yield, and fat and protein concentrations in Holstein-Friesians, New Zealand Jerseys and their crossbreds. This study also provides evidence that, within each breed, cows with high genetic merit were more susceptible to the effects of the environmental heat than their counterparts with lower genetic merit.

There is a lag effect between the onset of high temperature and humidity on milk production. While there is a high correlation of rectal temperature and energy intake with THI on the current day, milk yield and milk composition have a higher correlation with the weather

conditions in the previous two or three days (Maust et al., 1972). In a review of several studies, West (2003) arrived to a similar conclusion and suggests that this delay could be related to the reduction of feed intake, a delay between intake and utilization of nutrients, or to hormonal changes.

Collier et al. (2006) indicated that the acclimation to heat stress is under endocrine control and involves changes in the receptor populations in the target tissues as well as in the hormonal secretion rate. Spiers et al. (2004) studied the chain of predictors that range from the ambient stress to the animal performance through the thermal strain. They concluded that high environmental temperature produced changes in rectal temperature and respiration rate that were related to changes in feed intake, which is associated with the changes in milk production.

Changes in the milk yield are different according to the lactation stage. Cows in mid lactation were the most adversely affected, cows in early lactation were the least affected, and those in late lactation were intermediately affected (Maust et al., 1972). The authors suggest that although cows in early lactation produce the highest milk yield, they have the lowest feed intake and are in a negative energy balance, so milk production is supported with the catabolism of body fat to replace deficits in energy intake.

Perera et al. (1986) found that cows in mid lactation were the most adversely affected by the summer climate. Under mild conditions of heat stress, Abeni et al. (2007) found that cows in the early, mid and late stages of lactation decrease milk yield by 13 %, 24 % and 16.5 % respectively. The authors found that despite the moderate effects on milk production due to THI, some blood parameters related to energy balance and enzyme activities had significant alterations and cows in the middle of lactation had the highest changes in those parameters.

High-milk-producing cows are more affected by heat stress compared to lower-milk-producing cows (Kadzere et al., 2002), and multiple-parity cows are known to be more affected by heat stress than first-parity cows (Armstrong, 1994). The heat stress during the dry period also affects the milk production in the next lactation, as it was reported in several works (Wolfenson et al., 1988, West, 2003, Avendaño-Reyes et al., 2006).

Different strategies have been proposed to reduce the heat stress in cattle: physical modification of the environment, genetic development of breeds less affected by heat stress, and nutritional management (Beede and Collier, 1986). Systems of cooling in housing and milk facilities were proposed to alleviate the impact of heat stress on milk production (Armstrong, 1994, Collier et al., 2006, Smith et al., 2006); while West (1999) reviewed aspects of nutrition strategies for the management of heat-stressed cows.

Genetic studies on heat stress

Misztal (1999) proposed a model to study the genetic component of heat stress in dairy cattle using performance data augmented with public weather information. This model assumes that production is unaffected until a certain level of THI, and above that level the production declines linearly with increasing THI. If the variation in the slopes contains sizeable genetic additive components, selection for heat tolerant animals is possible.

Ravagnolo et al. (2000) compared different models to study the relationship of milk, fat and protein production with climate variables using combinations of temperature and humidity from public weather information. They show that public weather data combined in a THI index contain useful information to account for the effect of heat stress in milk production traits. In addition, on-farm weather data was compared with public information, showing that the public weather stations are an accurate source of information (Freitas et al., 2006).

Applying such methodology, Ravagnolo and Misztal (2000) showed that the additive genetic variability for heat tolerance was important for milk, fat and protein production in first-parity cows. Moreover, the additive genetic variance at high THI was similar to the additive variance in a non-stress situation. The authors concluded that genetic selection for heat stress is possible. Given the magnitude of the genetic correlation, combined selection for heat tolerance and production can be used. Finocchiario et al. (2005), working with a Mediterranean dairy sheep breed, found results that were in agreement with those of Ravagnolo and Misztal (2000).

Hayes et al. (2003) studied genotype \times environment interactions ($G \times E$) on milk production traits with environmental descriptors. They found a $G \times E$ for THI, where the genetic correlation between protein yields at the extreme percentiles of THI was 0.90. The authors argue that the little variation found for the genetic additive variance for heat stress can be explained by the lack of extreme heat stress conditions.

A genetic evaluation for heat tolerance using the methodology proposed by Ravagnolo and Misztal (2000) was carried out for first-parity U.S. Holstein cows (Bohmanova et al., 2005b). Estimated breeding values were calculated for approximately 10 million animals using a repeatability test-day model with a random regression on THI. Bulls with higher heat tolerances had daughters with lower milk yield, higher contents of milk solids, more robust bodies, better udders, longer productive lives and higher daughter pregnancy rates.

Test-day models

Currently, test-day models have mostly replaced 305 d lactation models in dairy cattle genetic evaluations, although this has not occurred in the U.S. thus far. Compared with the lactation model in which test day (**TD**) records are combined to obtain total yield, test-day models use each particular record separately. The advantages of TD models are flexibility to

accommodate different recording schemes, reduction of the generation interval, and accounting for time-dependent effects for each test day (Swalve, 2000). The use of test-day models allows the utilization of incomplete lactation records in situations in which a cow has records in progress or has been culled, avoiding the use of procedures to extend records (Jensen, 2001).

Ptak and Schaeffer (1993) introduced the repeatability test-day model, in which the shape of the lactation curves are modeled using fixed regression within specific fixed effects (e.g. age-season groups). In their study, the function of days in milk (DIM) to account for the shape of the lactation curve was as in Ali and Schaeffer (1987), although other functions could be used (Wilmink, 1987). The repeatability model assumes that TDs are repeated measures of the same trait, resulting in a unique genetic additive variance across DIM. This model has been used widely due to simplicity and low computational cost (Van Der Werf and Schaeffer, 1997).

Longitudinal data are usually analyzed with random regression models (Schaeffer, 2004). These models are extensions of the repeatability models in which a (co)variance function is used to model the variance of traits that change over time. Variations in lactation curves are modeled by fixed curves and deviations for these curves by random effects. Generally the random curves include the additive genetic and the permanent environment effects.

Random regression models were initially presented by Henderson, Jr. (1982) and then proposed for use in the dairy cattle genetic evaluation by Schaeffer and Dekkers (1994). Different functions can be applied to model (co)variances across DIM. Kirkpatrick et al. (1990) proposed the use of Legendre Polynomial from the family of orthogonal functions. Another type of functions are the splines (White et al., 1999, Druet et al., 2003, Silvestre et al., 2005), which were also applied to model growth traits (Bohmanova et al., 2005a, Meyer, 2005, Robbins et al., 2005, Sanchez et al., 2008).

Splines are piecewise polynomial functions of different orders that are fit through control points called knots (Wold, 1974). Misztal (2006) studied the properties of random regression models using linear splines. Compared with polynomials, linear splines have better numerical properties, result in a sparser system of equations, have local effects, and are easy to implement and interpret.

White et al. (1999) compared cubic splines to model lactation curves with a random regression model with a simple function of DIM. They concluded that splines provided more flexibility to model lactation curves but at a higher computational cost. Druet et al. (2003) compared several functions to model the fixed regression of lactations curves. They found that the regression splines were flexible, fit the data well, were relatively insensitive to outliers, and yielded smooth curves with a small number of parameters.

Estimates from random regression models usually show higher variances at the extremes of the lactation compared to multiple trait models (Rekaya et al., 1999). The use of random regression for the permanent environment while considering heterogeneous residual variance reduced these extreme values, but still some discrepancies were present (Rekaya et al., 1999). Pool and Meuwissen (2000) reported that using TD records for complete lactations improved the goodness of fit. They suggested that complete lactations should be used to estimate variance components.

Other authors proposed the use of herd-specific lactations curves to account for higher genetic variances at the extremes of lactations. Using data of first parity cows, Gengler and Wiggans (2001) found that the variance of herd-year was not negligible at the beginning of the lactation. de Roos et al. (2004) worked with data from the first three parities. They found that the genetic additive variance was lower in the first 100 d, especially in the second and third lactation

and they suggested the usage of herd curves in a random regression model. In agreement with previous results, Hammani et al. (2008) reported that herd-year random effect accounted for some variation at both the beginning and end of the lactation.

Recently, J. Bohmanova (personal communication) compared random regression models using either Legendre polynomials or linear splines for milk production traits. She found that the model with linear splines gave lower estimates of variances at the extremes of the lactation. Based on several criteria for model comparison, the models with linear splines with six knots performed the best.

Large scale genetic evaluations are routinely performed by iterative methods using the preconditioned conjugate gradient algorithm (**PCG**). A critical point of the PCG algorithm is the preconditioner (Lidauer et al., 1999, Strandén and Lidauer, 1999, Tsuruta et al., 2001). Strandén et al. (2002) compared different preconditioners for fixed and random effects under single trait random regression models. Convergence was improved when the preconditioner included blocks due to all of the fixed effects and blocks due to all correlated effects for each animal. However, the memory requirements were increased. The diagonalization of a (co)variance matrix for random effects reduced the number of iterations without increasing memory requirements (Strandén et al., 2002).

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CHAPTER 3

HEAT TOLERANCE IN PRODUCTION TRAITS FOR MULTIPLE LACTATION:
VARIANCE COMPONENTS¹

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ABSTRACT

Data included 585,119 test-days (**TD**) in the first to third parities for milk, fat and protein from 38,608 Holsteins in GA. Daily temperature humidity indices (**THI**) were available from public weather stations. Models included a repeatability test-day model (**MREP**) with a random regression on heat stress index and a test-day random regression model (**MRRM**) using linear splines with four knots and the heat stress index, which was defined as THI over 22°C from the 3rd day before the TD from the closest weather station to the farm. Knots for splines in the MRRM were placed at 5, 50, 200 and 305 days-in-milk (**DIM**). Random effects were additive and permanent environment in the MREP and additive, permanent environment and herd-year in the MRRM. Additionally, models included herd test day, age, milking frequency and DIM classes as fixed effects. In the MREP and for milk, fat and protein, the phenotypic variance increased by 50-60% from the first to second parity and additionally by 12-15% in the third parity. The regular genetic variance increased by 30-40% from the first to second parity but slightly declined in the third parity for milk and protein. The heat stress variance doubled from the first to second parity and additionally increased by 20-100% in the third parity. The genetic correlations between parities for the regular animal effect were ≥ 0.84 , but they were ≥ 0.96 between second and third. The genetic correlations among parities for the heat-stress effect were between 0.56-0.79. The genetic correlations between regular and heat stress effects across parities and traits were between -0.30 and -0.47. With the MRRM, the variance of the heat stress effect was about half of that of the MREP. The most negative (~ -0.42) genetic correlation for milk between regular and heat stress effects was at 50-200 DIM for first and between 200-305 DIM for the second and third parities. Genetic variance of heat stress strongly increases with

each parity. It is inflated with the MREP due to timing of lactations to avoid the peak production during heat stress.

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-Ispuerto et al., 2007). Economic losses due to heat stress for the U.S. dairy industry are estimated to be between \$897 and \$1500 million dollars per year (St-Pierre et al., 2003). Different approaches are used to manage heat stress in dairy cattle, including cooling, shading and nutrition (West, 1999, Kadzere et al., 2002, West, 2003).

Misztal (1999) proposed a model to study the genetic component of heat stress in dairy cattle using performance data with public weather information. Existence of additive genetic variability for heat tolerance was shown to be important for milk, fat and protein production in first-parity cows; additive genetic variance at high THI was similar to the additive variance in a non stress situation (Ravagnolo and Misztal, 2000). Comparison of on-farm weather data with public information has shown that they are accurate sources of information (Freitas et al., 2006b). A genetic evaluation for heat tolerance using this methodology was carried out for first-parity U.S. Holstein cows and public weather data (Bohmanova et al., 2005). Estimated breeding values were calculated for approximately 10 million animals using a repeatability test-day model with a random regression on THI. Bulls with higher heat tolerances have daughters with lower milk yield, higher contents of milk solids, more robust bodies, better udders, longer productive lives and higher daughter pregnancy rates.

Longitudinal data is usually analyzed with random regression models (Schaeffer, 2004). Different functions can be applied to model (co)variances across DIM. Splines have been used to model such (co)variances either 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 are not only simple, but they have good numerical properties, local effects and easy interpretations (Misztal, 2006).

The objective of this study was to estimate variance components for the first three lactations for milk, fat and protein yield using test day models that include a random regression on a function of THI.

MATERIAL AND METHODS

Data

Data were obtained from AIPL USDA and included TD records for milk, fat and protein from the first three lactations. Records were from cows registered between 1993 and 2004 in Georgia. Edits required lactations with 2 or 3 milkings per day and at least 4 TD; the first TD < 75 and TD between 5 and 305 DIM. Additional editing required the age at calving to be between 18 to 35, 28 to 49 and 40 to 63 months for the first, second and third parities respectively. Cows were also required to have a valid first lactation. A three generation pedigree file of 68103 animals was extracted for 38610 cows with records. The data are summarized in Table 3-1 and Table 3-2.

Weather data were obtained from the public weather stations and hourly THI was calculated as proposed by Ravagnolo et al. (2000):

$$THI(t, h) = (1.8 \times T + 32) - (0.55 - 0.0055 \times RH) \times (1.8 \times T - 26) \quad (\text{NOAA, 1976})$$

where T is the temperature in degrees Celsius, and RH is the relative humidity in percentage.

Herds were matched with the closest weather station and TD records were assigned the average daily THI of the third day before the TD. This 3 d lag was suggested in previous studies by Bohmanova et al. (2008).

A function of THI ($f(thi)$) was created:

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

where the value of the $THI_{Threshold}$ was set to 72 as in Ravagnolo et al. (2000).

Model

Two models were applied to estimate variance components for multiple lactations. The first model was an extension of the repeatability test-day model (**MREP**) proposed by Ravagnolo and Misztal (2000) to estimate variance components for heat tolerance but considered multiple lactations as different traits:

$$y_{ijklmno} = htd_{in} + \text{dim}_j + age_k + freq_l + a_{1:mn} + f(thi) \times a_{2:mn} + p_{1:mn} + f(thi) \times p_{2:mn} + e_{ijklmno}$$

where $y_{ijklmno}$ is the test-day milk/fat/protein yield; htd_{in} is the fixed herd test-day i within parity n ; dim_j is the fixed DIM class within season ($j=1$ to 124, 4 seasons and 31 classes for DIM); age_k is the fixed calving age class within parity k ($k=1$ to 22); $freq_l$ is the fixed milking frequency class l ($l=1$ to 2); $a_{1:mn}$ is the general random additive genetic effect of animal m in parity n ; $f(thi)$ is the heat stress function for the herd-test day i ; $a_{2:mn}$ is the random additive genetic effect of heat tolerance for the animal m in parity n ; $p_{1:mn}$ is the random permanent environmental effect of the cow m ; $p_{2:mn}$ is the random permanent environmental effect of heat tolerance of the cow m ; and $e_{ijklmno}$ is the random residual effect.

Let $a' = [a'_{1:n} \ a'_{2:n}]$ be vector of genetic additive effects and $p' = [p'_{1:n} \ p'_{2:n}]$ the vector of random permanent effects for parities $n=1$ to 3.

The (co)variance structure was:

$$V \begin{bmatrix} \mathbf{a} \\ \mathbf{p} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_o & & \\ & \mathbf{I} \otimes \mathbf{P}_o & \\ & & \mathbf{I} \otimes \mathbf{R}_o \end{bmatrix}$$

where \mathbf{A} is the numerator relationship matrix, and \mathbf{G}_o and \mathbf{P}_o are 6x6 matrices of (co)variances for additive and permanent effects respectively. \mathbf{R}_o 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 a function of THI (MRRM) with the same effects as before but with a random effect for herd-year. Random covariates included the function of THI and for DIM they were modeled with linear splines using four knots at 5, 50, 200 and 305 DIM.

The (co)variance structure was:

$$V \begin{bmatrix} \mathbf{a} \\ \mathbf{p} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_o & & & \\ & \mathbf{I} \otimes \mathbf{P}_o & & \\ & & \mathbf{I} \otimes \mathbf{H}_o & \\ & & & \mathbf{I} \otimes \mathbf{R}_o \end{bmatrix}$$

where $\mathbf{G}_o = \text{var}(\mathbf{a})$, $\mathbf{P}_o = \text{var}(\mathbf{p})$ and $\mathbf{H}_o = \text{var}(\mathbf{h})$. All square matrices with dimension $n*(t+1)$ (n =parity, t =knots) corresponded to (co)variances for additive, permanent and herd-year effects respectively. For our case the matrices had a dimension of 15x15. The MRRM model was applied only to milk yield.

Analysis

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

RESULTS AND DISCUSSION

Estimates of variance components for univariate analyses of the first lactation milk, fat and protein yield are presented in Table 3-3. These estimates were within the range of those estimated for different regions of the U.S. (Freitas et al. 2006a) but higher than those previously reported for GA by Ravagnolo and Miszta (2000).

Table 3-4 presents parameters for a test-day model with random regression on THI for multiple parities. Phenotypic variances increase with parities for milk, fat and protein; the increase is 50-60% from first to second parity and 2-15% from second to third parity.

Non heat-stress additive genetic variances, hereinafter denoted by “generic”, increased by 30-40% from the first to second parity but slightly decreased in the third parity for milk and protein. Additive variance for heat stress increased approximately 100% from the first to the

second parity for milk, fat and protein. However, from second to third parity milk increased by 20%; and fat and protein increased approximately 100%. Genetic (co)variances between the generic additive and the heat stress component were negative for all cases, resulting in genetic correlations in the range of -0.30 to -0.50.

Figures 3-1, 3-2 and 3-3 show the posterior mean estimates and 95% HPD of the total additive variance as a function of THI for different lactations and milk fat and protein. A larger additive variance was observed for all parities and traits with higher values of THI but also with a higher SE. Patterns of the curves were similar across lactations but had larger increases for high THI.

Heritability estimates are presented in Figures 3-4, 3-5 and 3-6 for milk, fat and protein respectively. All estimates ranged from 0.10 to 0.24. For the first and second parity heritabilities first decreased and then increased with increasing THI. The decrease is due to a negative correlation between regular and heat stress components.

Correlations between lactations (Table 3-4) for generic additive effect (intercept) for milk, fat and protein were positive and high (greater than 0.84). More specifically, these correlations were 0.96 or higher between the second and third parity. Genetic correlations between lactations for additive heat tolerance were also high but lower than 0.80, indicating either differences in heat tolerances between multiple parities or a wider HPD.

Posterior means of additive (co)variance and genetic correlations for random regression of the model (knots and THI) are presented in Table 3-5, and the curves at different THI and DIM are shown in Figure 3-7. The additive variance for the first parity increases with DIM, whereas for the second and third parity the variances have a typical U-shape with higher values

at the extremes. On average, the generic additive variances for MRRM were higher in later parities, as in the MREP, despite the higher estimates at high DIM.

Negative correlations between the generic additive effect and heat stress were found for all lactations except at the beginning of the third parity (0.10). Differences in correlations were present at different stages of the lactation within and between parities. In the first parity the most negative correlation was around 50 DIM (-0.45) but for the later parities the most negative correlations were at DIM 200.

The additive genetic variances for heat stress were about half of the estimates from the repeatability model. This suggests that lactations are managed to avoid the maximum production during the hottest period and that MREP does not account for that timing. These components also have lower genetic correlations between different parities compared to estimates from the MREP model.

Curves for permanent and herd-year variances at different THI and DIM are shown in Figure 3-8 and Figure 3-9 respectively. Permanent variances were greater than additive and have a U-shape across DIM. Herd-year variances account for less variation during lactations except at the beginning of the lactations and somewhat at the end of the second and third parity. This is in agreement with studies that include the random herd-year curves to account for environmental variation due to herds (de Roos et al., 2004, Hammami et al., 2008).

Heritability estimates at different values of DIM and THI are presented in Figure 3-10. They ranged between 0.10 to 0.25, 0.13 to 0.28 and 0.08 to 0.25 for the first, second and third parity respectively. They were lower at the beginning of the lactation but increased with DIM and THI

CONCLUSIONS

Genetic parameters for heat tolerance were estimated for a multiple-parity test-day model with repeatability and random regression models. In both cases additive genetic effects for heat stress strongly increase with parity. The variances for heat tolerance from the random regression model were lower due to a better adjustment of the non-heat stress genetic additive variances across DIM, which in its absence resulted in inflated variances under the MREP.

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Table 3-1: Means and SD of milk yield, fat and protein in the first three lactations

Lactation	Milk (kg)		Fat (kg*100)		Protein (kg*100)	
	Mean	SD	Mean	SD	Mean	SD
1	27.5	7.0	94.8	27.7	85.7	20.4
2	31.6	9.4	109.3	36.3	97.5	26.3
3	33.0	10.1	114.8	39.5	100.7	28.1

Table 3-2: Number of test-day records, cows and herd-test-day classes per lactation

	Lactation		
	1	2	3
Test day records	350,623	160,262	74,834
Number of cows	38,608	17,549	8,210
Number of herd-test-day	16,467	13,043	10,156

Table 3-3: Variance components for the first lactation with the repeatability model

Parameter ¹	Milk (kg)	Fat (kg*100)	Protein (kg*100)
σ_{a1}^2	5.5	74.0	42.2
σ_{a1a2}	-0.178	-1.827	-1.302
σ_{a2}^2	0.028	0.219	0.174
σ_{p1}^2	12.0	133.0	101.0
σ_{p1p2}	-0.519	-6.345	-5.300
σ_{p1}^2	0.111	0.699	0.942
σ_e^2	13.1	310.0	127.8

¹ σ_{a1}^2 = variance for general additive effect; σ_{a2}^2 additive variance for heat tolerance

σ_{a1a2} = additive covariance between generic and heat tolerance effect

σ_{p1}^2 = permanent variance for generic effect; σ_{p2}^2 permanent variance for heat tolerance

σ_{p1p2} = permanent covariance between generic and heat tolerance effect

Table 3-4: Variance component estimates for the first, second, and third parities for milk, fat and protein using a multiple trait repeatability test-day model

Parameter ¹	Milk			Fat (kg*100)			Protein (kg*100)		
	1 ²	2	3	1	2	3	1	2	3
σ_{a1}^2	5.634	7.539	6.534	73.970	93.928	108.970	42.538	56.786	52.155
σ_{a2}^2	0.037	0.072	0.089	0.370	0.749	1.417	0.217	0.478	1.078
σ_{a1a2}	-0.209	-0.282	-0.358	-2.031	-2.401	-3.790	-1.318	-1.884	-3.742
σ_e^2	12.844	19.410	22.651	308.724	522.248	603.354	125.714	190.522	215.294
Corr a1 1		0.86	0.91		0.88	0.96		0.84	0.89
Corr a1 2			0.96			0.97			0.98
Corr a2 1		0.72	0.79		0.71	0.61		0.56	0.75
Corr a2 2			0.75			0.68			0.75
Corr a1a2	-0.46	-0.38	-0.47	-0.39	-0.39	-0.30	-0.43	-0.36	-0.50

¹ σ_{a1}^2 = variance for general additive effect; σ_{a2}^2 additive variance for heat tolerance

σ_{a1a2} = additive covariance between non heat stress and heat tolerance effect; σ_e^2 residual variance; Corr a1 non heat stress genetic correlations between lactations; Corr a2 heat stress genetic correlations between lactations, Corr a1a2 genetic correlations between non heat stress and heat tolerance effects within lactation

² Lactation number

Figure 3-1: Posterior means and 95% HPD intervals for additive variance for milk in the first, second and third parities using the repeatability model for different values of THI

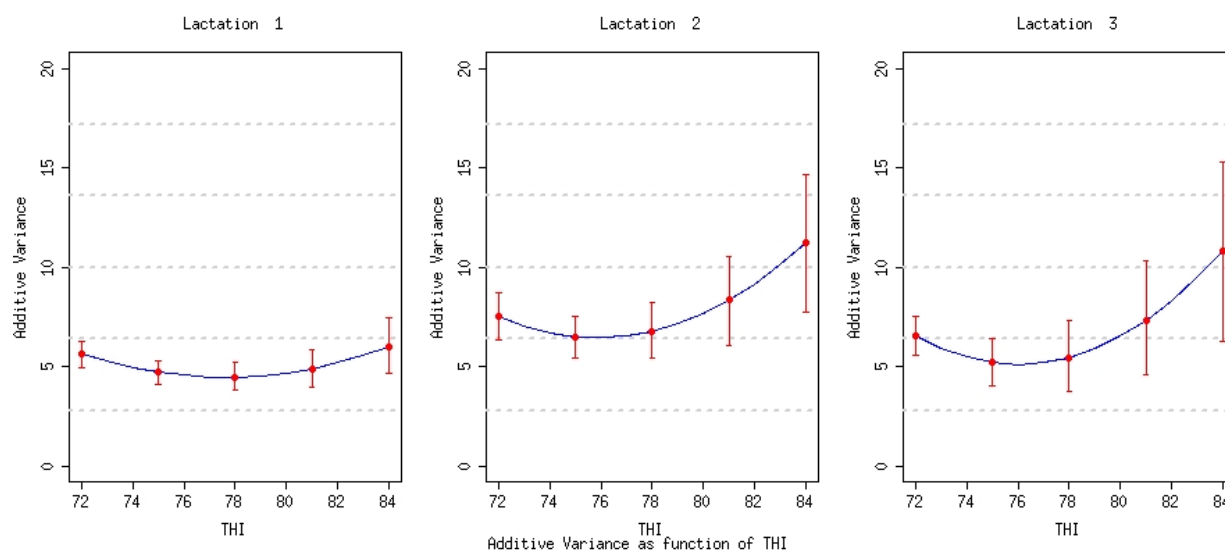


Figure 3-2: Posterior means and 95% HPD intervals for additive variance for fat in the first, second and third parities using the repeatability model for different values of THI

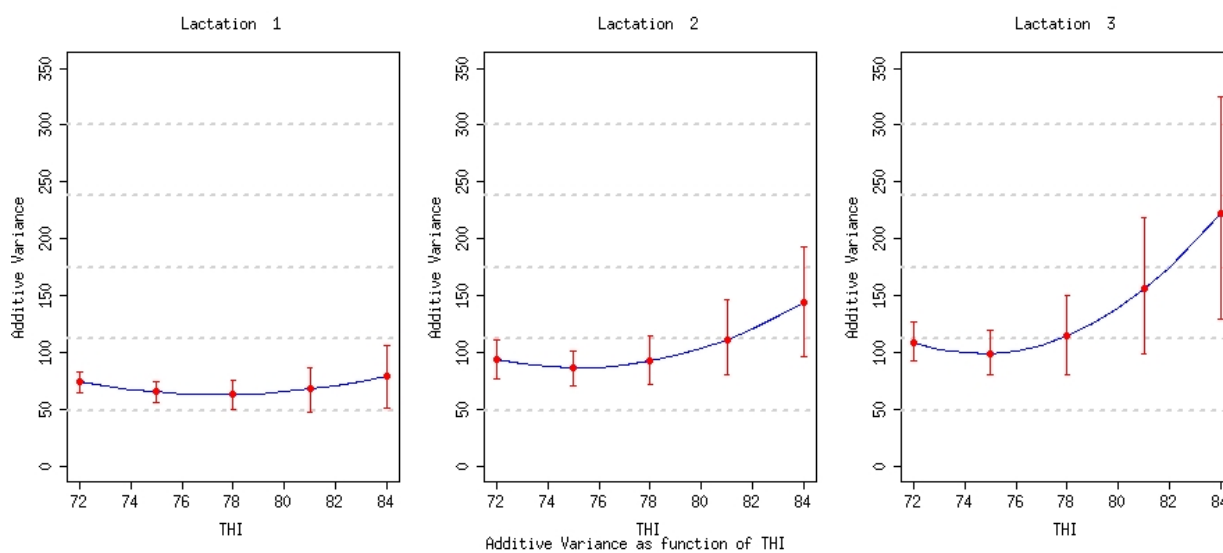


Figure 3-3: Posterior means and 95% HPD intervals for additive variance for protein in the first, second and third parities using the repeatability model for different values of THI

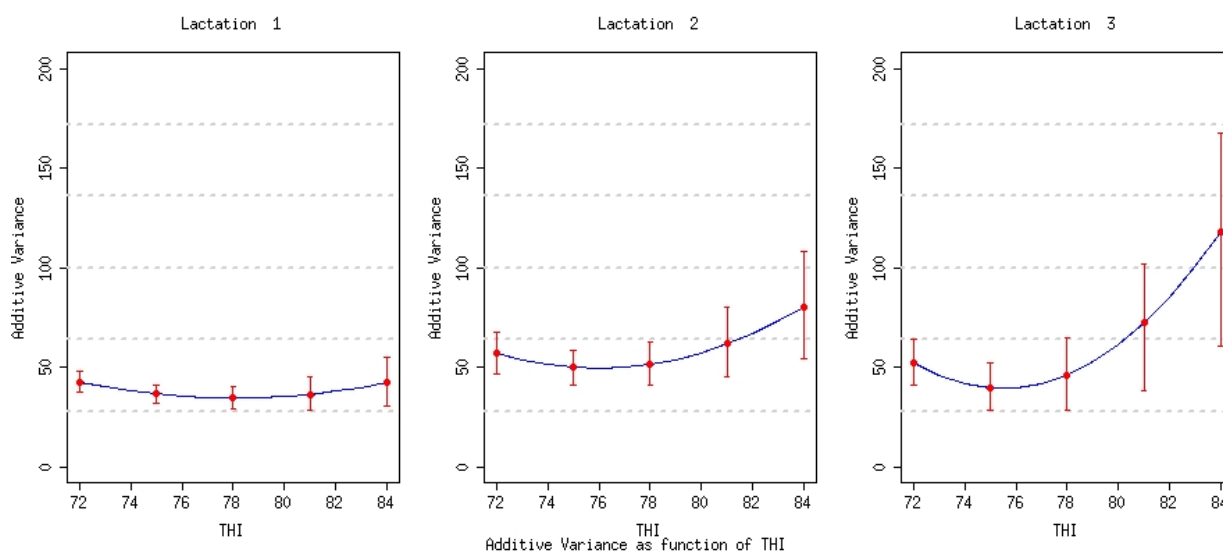


Figure 3-4: Posterior means and 95% HPD intervals for heritability estimates for milk in the first, second and third parities using the repeatability model for different values of THI

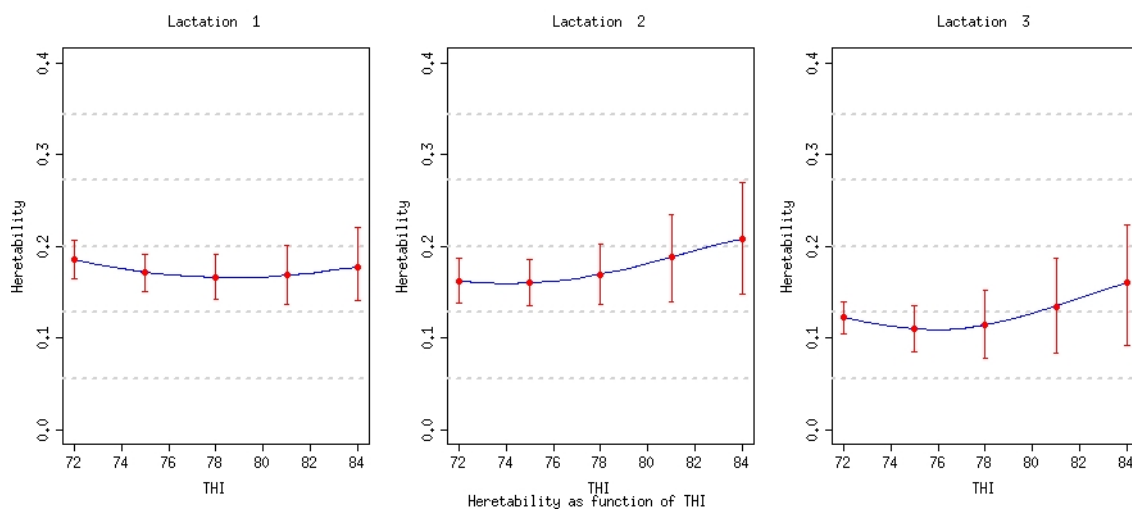


Figure 3-5: Posterior means and 95% HPD intervals for heritability estimates for fat in the first, second and third parities using the repeatability model for different values of THI

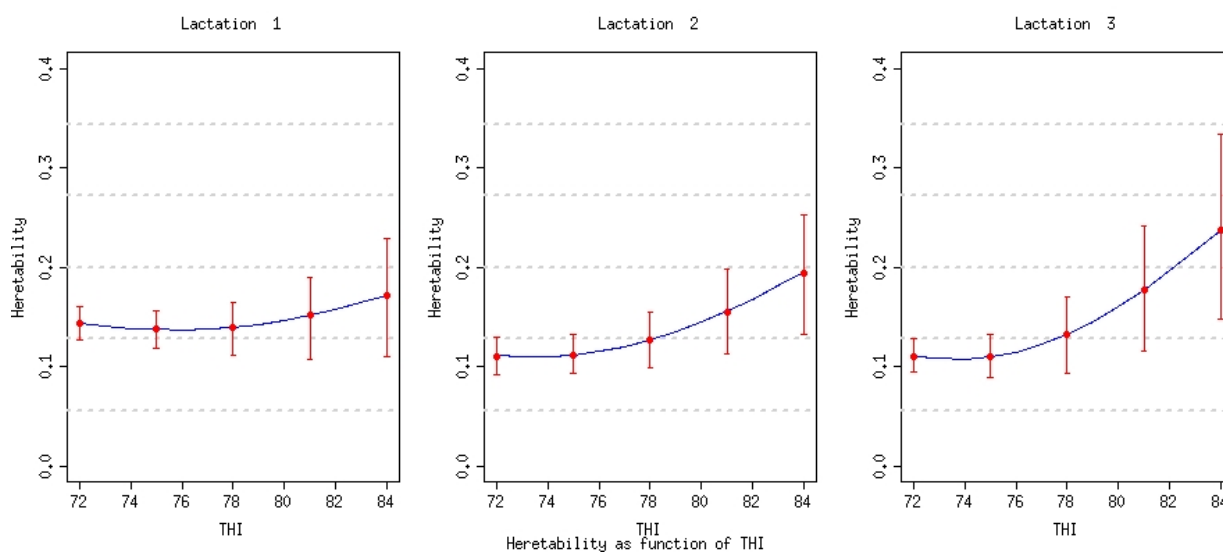


Figure 3-6: Posterior means and 95% HPD intervals for heritability estimates for protein in the first, second and third parities using repeatability model for different values of THI

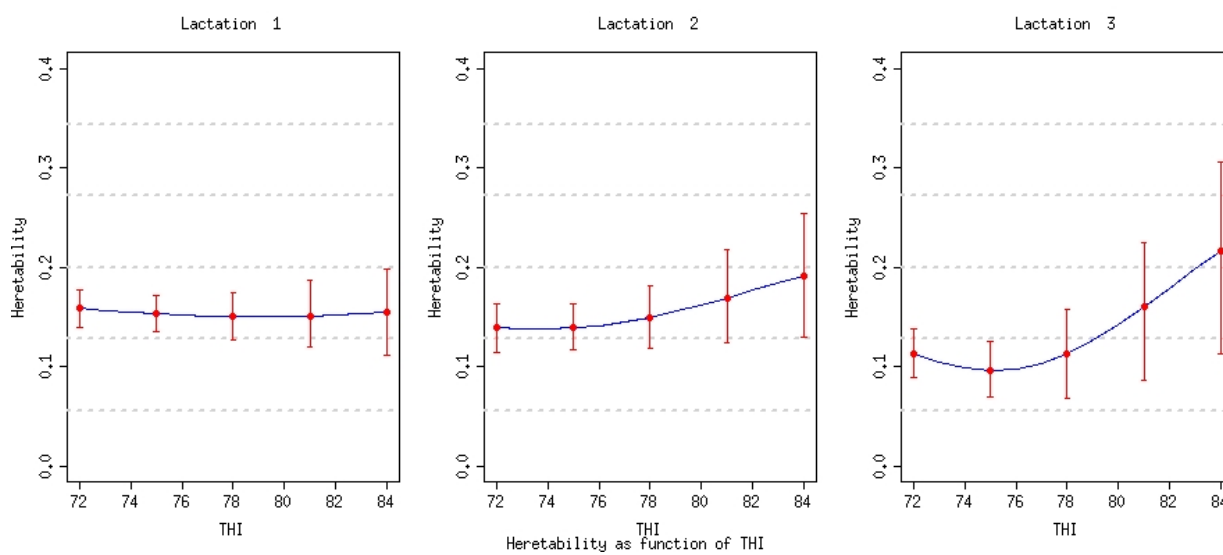


Table 3-5: Additive (co)variances and genetic correlations between knots and THI for milk in the first, second, and third parities

	Parity														
	First					Second					Third				
	5 ²	50	200	305	THI	5	50	200	305	THI	5	50	200	305	THI
5	3.96 ¹	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	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	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	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	0.02	-0.10	-0.18	-0.23	-0.30	0.04	0.06	-0.17	-0.34	-0.40	0.07

¹ variances on diagonal and bold, genetic correlations above diagonal, and co-variances below diagonal

² values correspond to the four knot position at DIM

Figure 3-7: Posterior means and 95% HPD intervals for additive variance for milk in the first, second and third parities using a random regression model at different values of THI

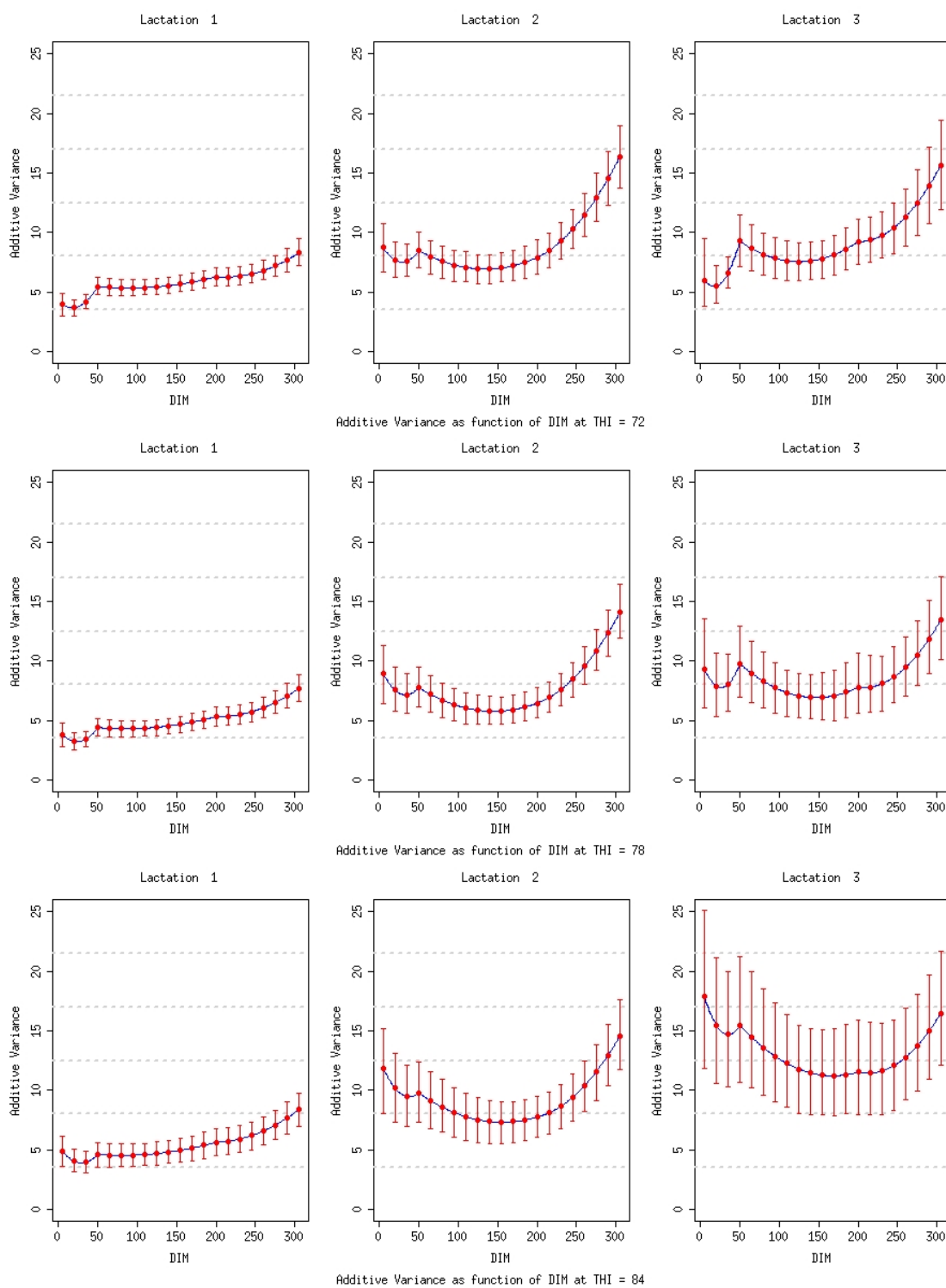


Figure 3-8: Posterior means and 95% HPD intervals for permanent variance for milk in the first, second and third parities using a random regression model at different values of THI

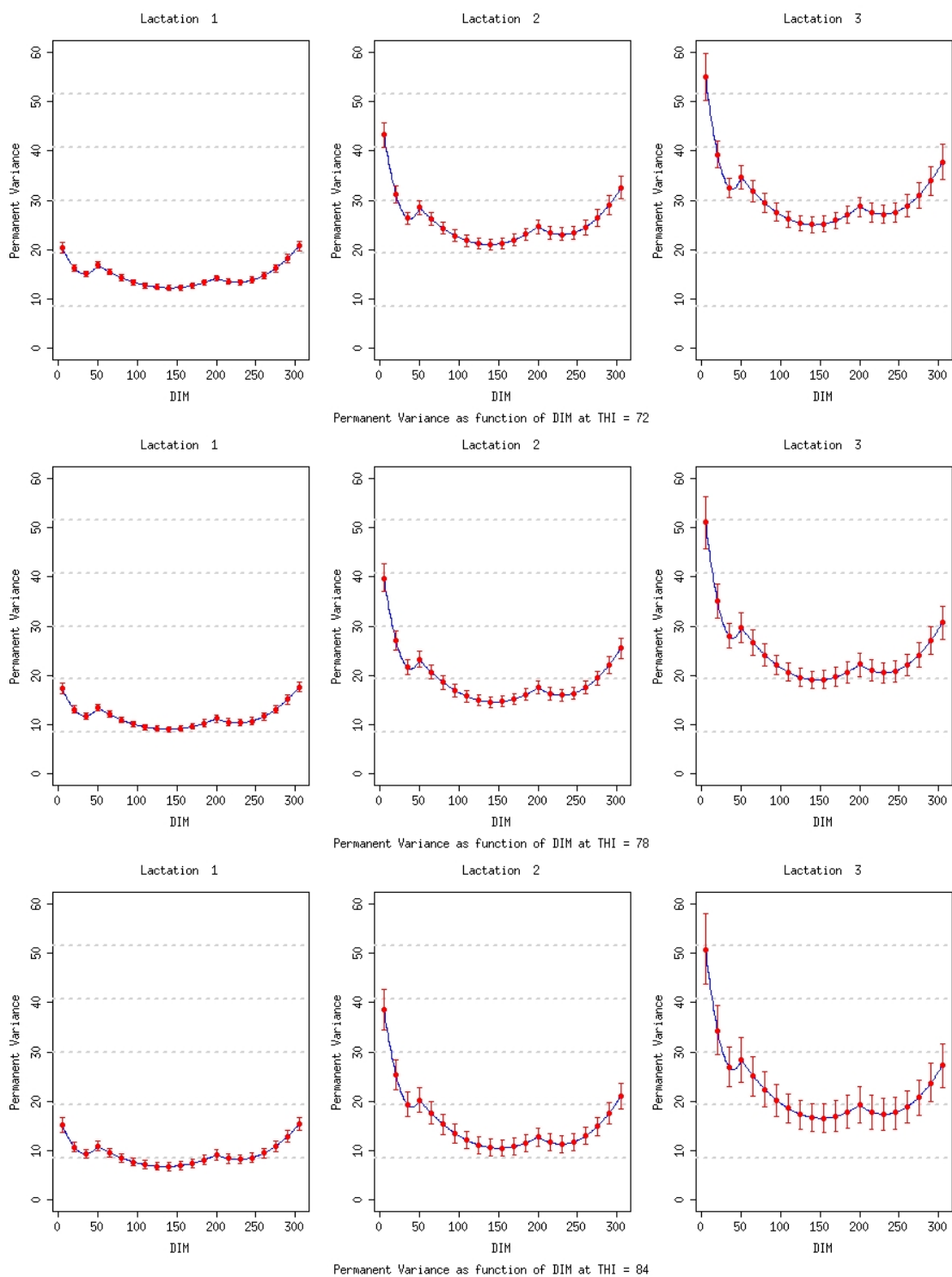


Figure 3-9: Posterior means and 95% HPD intervals for herd-year variance for milk in the first, second and third parities using a random regression model at different values of THI

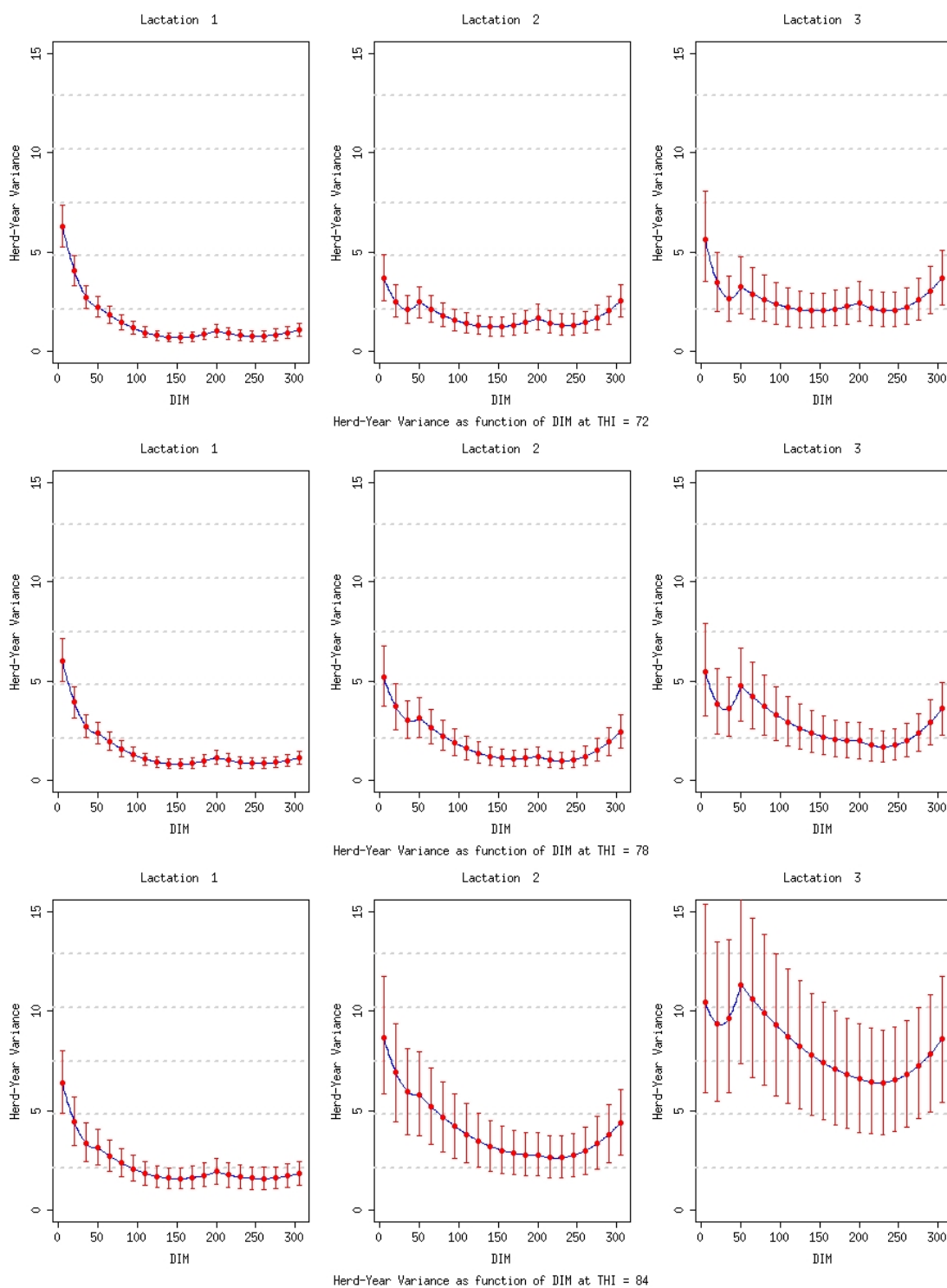
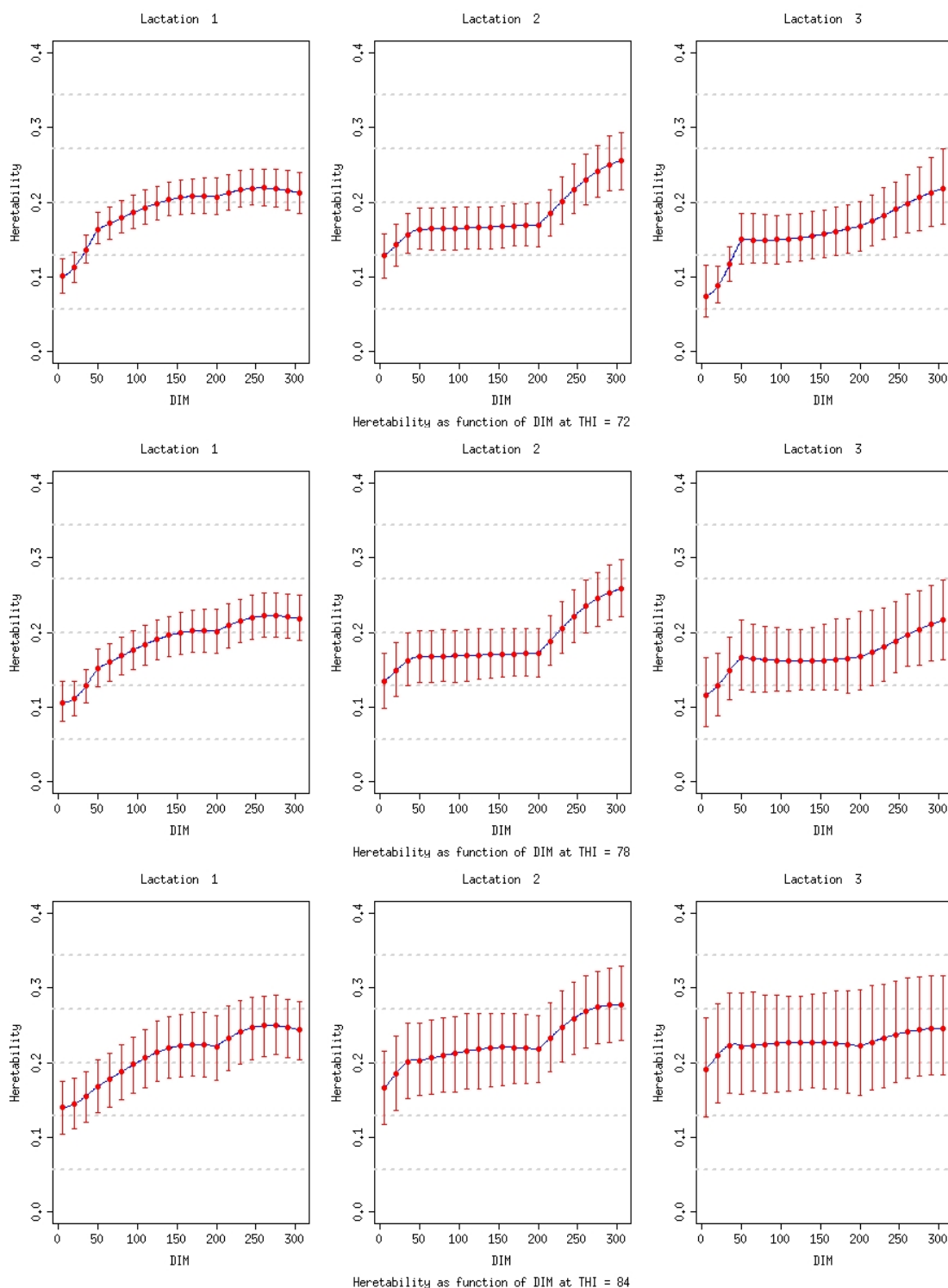


Figure 3-10: Posterior means and 95% HPD intervals for heritability estimates for the milk in first, second and third parities using a random regression model at different values of THI



CHAPTER 4

COMPUTING OPTIONS FOR MULTIPLE-TRAIT TEST-DAY RANDOM REGRESSION
MODELS WHILE ACCOUNTING FOR HEAT TOLERANCE²

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ABSTRACT

Data included 90,242,799 test day records from 5,402,484 Holsteins in first three parities. The total number of animals in the pedigree file was 9,326,754. Additionally, daily temperature humidity indexes (**THI**) from 202 weather stations were available. The fixed effects in the model included herd test day, age at calving, milking frequency and days in milk classes (**DIM**). Random effects were additive, permanent environment and herd-year. These effects were fit as random regressions. Covariates included linear splines with four knots at 5, 50, 200, and 305 DIM and a function of THI of the third day before the test day. THI were obtained from the closest weather station to the farm. The first three lactations were used as separate traits, resulting in 15 by 15 (co)variance matrices for each random effect. Mixed model equations were solved using an iteration on data program with a preconditioned conjugate gradient algorithm. Several preconditioners were used and included diagonal (**D**), block diagonal due to traits (**BT**) and block diagonal due to traits and correlated effects (**BTCORR**). One run included BT with a “diagonalized” model in which the random effects were reparameterized for diagonal (co)variance matrices among traits (**BTDIAG**). Memory requirements were 8.7 Gbytes for D, 10.4 Gbytes for BT and BTDIAG, and 24.3 Gbytes for BTCORR. Computing times (rounds) were 14 d (952) for D, 10.7 d (706) for BT, 7.7 d (494) for BTDIAG and 4.6 d (289) for BTCORR. The convergence pattern was strongly influenced by the choice of fixed effects. When sufficient memory is available, the option BTCORR is the fastest and simplest to implement; the next efficient method, BTDIAG, requires additional steps for diagonalization and back-diagonalization.

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-Ispuerto et al., 2007). Economic losses due to heat stress for the U.S. dairy industry are estimated to be between \$897 and \$1500 million dollars per year (St-Pierre et al., 2003). Different approaches are used to manage heat stress in dairy cattle including, cooling, shading and nutrition (West, 1999, Kadzere et al., 2002, West, 2003).

Misztal (1999) proposed a model to study the genetic component of heat stress in dairy cattle using performance data combined with public weather information. Existence of additive genetic variability for heat tolerance was shown to be important for milk, fat and protein production in first-parity cows (Ravagnolo and Misztal, 2000). A study by Aguilar et al. (2008) demonstrated that the effect of heat stress on production is greater in later parities.

A genetic evaluation for heat tolerance using the methodology proposed by Ravagnolo and Misztal (2000) was carried out for first-parity U.S. Holstein cows by Bohmanova et al. (2005). Estimated breeding values were calculated for approximately 10 million animals using a repeatability test-day model with a random regression on THI. Bulls with a higher heat tolerance had daughters with lower milk yield, higher content of milk solids, more robust bodies, better udders, longer productive lives and higher daughter pregnancy rates.

Large scale genetic evaluations are routinely performed by iterative methods using the preconditioned conjugate gradient algorithm (**PCG**). A critical point of the PCG algorithm is the preconditioner (Lidauer et al., 1999, Strandén and Lidauer, 1999, Tsuruta et al., 2001). Strandén et al. (2002) compared different preconditioners for fixed and random effects under single trait random regression models. Convergence was improved when the preconditioner included blocks

due to all of the fixed effects and with blocks due to all correlated effects for each animal. However, the memory requirements were increased. The diagonalization of the (co)variance matrix for random effects reduced the number of iterations without increasing memory requirements. Compared to Cholesky decomposition, eigenvalues decomposition of the (co)variance matrix for random effects showed a slightly better performance under PCG (Strandén et al., 2002).

The objective of this study is to compare different computing options for PCG algorithms for a large scale genetic evaluation using multiple-traits test-day random-regression models and accounting for heat tolerance.

MATERIAL AND METHODS

Data

TD records of U.S. Holsteins with the first three parity records between 1993 and 2004 were obtained from AIPL USDA. Edits required lactations with 2 or 3 milkings per day and at least 4 TD; the first TD < 75 DIM and TD between 5 and 305 DIM. Additional editing required the age at calving to be between 18 to 35, 28 to 49 and 40 to 63 months for the first, second and third parities respectively. Cows were also required to have a valid first lactation. The two data sets used were the national data (**ND**) corresponding to 9,326,754 cows and a subset of 38,608 cows from Georgia (**GA**). A summary of both datasets is presented in Table 4-1.

Additionally, the weather data were taken from 202 public weather stations. Hourly THI was calculated as proposed by Ravagnolo et al. (2000):

$$THI(t, h) = (1.8 \times T + 32) - (0.55 - 0.0055 \times RH) \times (1.8 \times T - 26) \quad (\text{NOAA, 1976})$$

where T is temperature in degrees Celsius, and RH is relative humidity in percentage. Herds were matched to the closest weather station and TD records were assigned the average daily THI of the third day before the TD. This 3 d lag was suggested in previous studies by Bohmanova et al. (2008).

A function of THI ($\varphi(thi)$) was created:

$$\varphi(THI) = \begin{cases} \text{if } THI \leq THI_{Threshold} & 0 \\ \text{if } THI > THI_{Threshold} & THI - THI_{Threshold} \end{cases}$$

where the value of the $THI_{Threshold}$ was set to 72 as in Ravagnolo et al. (2000).

Model

The following multiple trait random regression model was used for the genetic evaluation:

$$\begin{aligned} y_{ijklt} = & fixed_i \\ & + \sum_{q=1}^4 \alpha_q(dim) a_{qjt} + \varphi(thi) a_{5jt} \\ & + \sum_{q=1}^4 \alpha_q(dim) p_{qjt} + \varphi(thi) p_{5jt} \\ & + \sum_{q=1}^4 \alpha_q(dim) h_{qkt} + \varphi(thi) h_{5kt} + e_{ijklt} \end{aligned}$$

where the fixed effects included herd test day, age at calving, milking frequency and days in milk classes (DIM) and the random effects included additive (**a**), permanent environment (**p**) and herd-year (**h**). Random effects were fitted as random regression. Covariates included linear splines with four knots at 5, 50, 200 and 305 DIM and the function of THI. The first three lactations were used as separate traits.

The (co)variance structure was:

$$V \begin{bmatrix} \mathbf{a} \\ \mathbf{p} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_o & & & \\ & \mathbf{I} \otimes \mathbf{P}_o & & \\ & & \mathbf{I} \otimes \mathbf{H}_o & \\ & & & \mathbf{I} \otimes \mathbf{R}_o \end{bmatrix}$$

where \mathbf{G}_o , \mathbf{P}_o and \mathbf{H}_o were 15x15 (co)variance matrices for additive, permanent and herd-year effects respectively, and \mathbf{R}_o was a 3x3 diagonal matrix of residual variance corresponding to each trait. Genetics parameters were from a previous study (Aguilar et al., 2008).

Solutions for mixed model equations were computed using BLUP90IOD (Tsuruta et al., 2001). This program implements iteration on data with a preconditioned conjugated gradient algorithm. Several preconditioners were used: diagonal (**D**), block diagonal due to traits (**BT**) and block diagonal due to traits and correlated effects (**BTCORR**). BT runs were implemented with the regular (co)variance matrix and a “diagonalized” model in which the random effects were reparameterized for diagonal (co)variance matrices within traits (**BTDIAG**). The converge criterion (C) was based on the relative adjusted right-hand side and the iterations were stopped when $C < 10^{-12}$.

Diagonalization

(Co)variance matrices for a multiple trait random regression model can be diagonalized. Consider a single trait model, and let a random regression for a particular effect (e.g. random additive effect for animal j) be equal to $\sum_{i=1}^n \alpha_i a_{ij} = \boldsymbol{\alpha}' \mathbf{a}_j$ while it's (co)variance is $\text{var}(\mathbf{a}_j) = \mathbf{G}_0$, where $\boldsymbol{\alpha}$ is the vector of covariates and \mathbf{a}_j is the vector of animal effect j , both with dimension n (number of covariates). The (co)variance matrix \mathbf{G}_0 could be decomposed in eigenvectors (\mathbf{V}) and eigenvalues (\mathbf{D}): $\mathbf{G}_0 = \mathbf{V}\mathbf{D}\mathbf{V}'$

The random regression terms could be reparameterized as follows:

$$\boldsymbol{\alpha}'\mathbf{a}_j = \boldsymbol{\alpha}'\mathbf{V}\mathbf{V}'\mathbf{a}_j = \boldsymbol{\alpha}'^*\mathbf{a}_j^*$$

where: $\boldsymbol{\alpha}^* = \mathbf{V}'\boldsymbol{\alpha}$; $\mathbf{a}_j^* = \mathbf{V}'\mathbf{a}_j$ and $\text{var}(\mathbf{a}_j^*) = \mathbf{D}$ correspond to a diagonal matrix.

Now consider multiple trait random regression:

$$\sum_{i=1}^t \sum_{k=1}^n \alpha_{ik} a_{ikj} = \boldsymbol{\alpha}'\mathbf{a}_j,$$

where t is the number of traits and n the number of covariates.

The (co)variance matrix sorted by traits is as follows:

$$\text{var}(\mathbf{a}_j) = \mathbf{G}_0 = \begin{bmatrix} \mathbf{G}_{11} & \cdots & \mathbf{G}_{1t} \\ \vdots & \ddots & \vdots \\ \mathbf{G}_{t1} & \cdots & \mathbf{G}_{tt} \end{bmatrix}$$

where \mathbf{G}_{ii} is a (co)variance matrix of the n random regressions for the i^{th} trait of the j animal,

and $\mathbf{G}_{ii'}$ is the (co)variance matrix for n random regressions between i and i' traits for the j

animal. Furthermore \mathbf{G}_{ii} could be decomposed in eigenvectors (\mathbf{V}_{ii}) and eigenvalues (\mathbf{D}_{ii}):

$$\mathbf{G}_{ii} = \mathbf{V}_{ii}\mathbf{D}_{ii}\mathbf{V}_{ii}'$$

and the reparameterized random regression becomes:

$$\boldsymbol{\alpha}_i \mathbf{V}_{ii}' \mathbf{V}_{ii}' \mathbf{a}_{ii} = \boldsymbol{\alpha}_i^* \mathbf{a}_j^* \quad \text{for } i = 1, t$$

The (co)variance matrix structure for \mathbf{a}^* results in the following:

$$\begin{aligned}
 \text{var} \begin{pmatrix} a_1^* \\ \vdots \\ a_t^* \end{pmatrix} &= \text{var} \begin{pmatrix} V_{11}' a_1 \\ \vdots \\ V_{tt}' a_t \end{pmatrix} \\
 &= \begin{bmatrix} V_{11}' \text{var}(a_1) V_{11} & \cdots & V_{11}' \text{cov}(a_1, a_t) V_{tt} \\ \vdots & \ddots & \vdots \\ V_{tt}' \text{cov}(a_t, a_1) V_{11} & \cdots & V_{tt}' \text{var}(a_t) V_{tt} \end{bmatrix} \\
 &= \begin{bmatrix} V_{11}' V_{11} D_{11} V_{11}' V_{11} & \cdots & V_{11}' G_{1t} V_{tt} \\ \vdots & \ddots & \vdots \\ V_{tt}' G_{t1} V_{11} & \cdots & V_{tt}' V_{tt} D_{tt} V_{tt}' V_{tt} \end{bmatrix} \\
 &= \begin{bmatrix} D_{11} & \cdots & V_{11}' G_{1t} V_{tt} \\ \vdots & \ddots & \vdots \\ V_{tt}' G_{t1} V_{11} & \cdots & D_{tt} \end{bmatrix}
 \end{aligned}$$

Solutions after the transformation can be back transformed to the original scale by

$\mathbf{a}_{ij} = \mathbf{V}_i \mathbf{a}_{ij}^*$. This diagonalization also applies to the permanent and herd-year random effects.

RESULTS AND DISCUSSION

Table 4-2 shows the memory and time requirements to compute the solutions of the multiple-trait random regression model with the different preconditioners for the national data. The use of blocks increases memory requirements due to the storage of preconditioners. The maximum requirement corresponds to BTCORR, where storage for the preconditioner matrix (15x15, half stored) is needed for each level of the random effect (e.g. number of animals in the pedigree file) and is three times bigger than with the simple preconditioner (D).

The number of iterations required to reach convergence was considerably affected by the usage of block diagonal preconditioners. Using BT reduced the number of iterations compared

with D, but the reduction was bigger when random correlated effects and traits were considered as the preconditioner (BTCORR). Simulations using (co)variance matrices with different values for genetic correlations show that in scenarios with higher genetic correlations the use of a block diagonal preconditioner improves convergence. For random regression models with Legendre polynomials, which have lower correlations between covariates, a simpler diagonal preconditioner is necessary (Strandén et al., 2002). In our case, the reduction in the number of iterations of the random regression model could be related to the use of linear splines as a random regression function, which had intermediate to high genetic correlations between knots within and across parities.

The reparameterized model using a partial diagonalization for random correlated effects gives a compromise between memory and time requirements. It was not as efficient as BTCORR but had less than a half of the memory requirements. The memory requirements for BTDIAG are the same as that of the BT, and the number of iterations is reduced by 30%. Additional steps are required to implement this option for diagonalization and back-diagonalization of solutions to the original scale.

The convergence criterion for BTCORR (Figure 4-1) showed a high fluctuation compared with the other options. In order to study this behavior, different options were tested using the GA dataset. The options included the following models: 1) only the herd-test-day as the fixed effect, 2) herd-test-day and age as fixed effects and 3) the original model but with the whole block for all fixed effects in the preconditioner. In all these models, random effects were as in the original model and the preconditioner was BTCORR. Plots of convergence are in Figure 4-2. No fluctuations in convergence for BTCORR were present under the model with only one fixed effect; however, the inclusion of another fixed effect resembled the pattern with the full

model. Moreover, using the complete block for fixed effects as preconditioner eliminated such fluctuations, but such a model can not be implemented with the national data due to the large number of levels of fixed effects (herd-test-day). No benefit was found if the block for the fixed effects was for all effects except herd-test-day (results not shown).

CONCLUSIONS

A large scale genetic evaluation using a multiple-trait random-regression model accounting for heat tolerance can be run in a reasonable time. More time could be saved by optimizing the code and using parallel processing. The convergence criterion for BTCORR shows a high fluctuation that requires either a moving average or a strict stopping criterion. The convergence pattern is strongly influenced by the choice of fixed effects. When sufficient memory is available, the option BTCORR is the fastest and simplest to implement; the next efficient method, BTDIAG, requires additional steps for diagonalization and back-diagonalization

ACKNOWLEDGMENTS

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Table 4-1: Summary information for the national and Georgia data by lactations

	National			Georgia		
	1	2	3	1	2	3
Test day records	49,351,124	26,856,302	14,035,373	350,023	160,262	74,834
Number of Cows	5,402,484	2,932,915	1,537,959	38,608	17,549	8,210
Number Herd-Test day	2,603,783	2,153,285	1,749,619	16,467	13,043	10,156
Milk yield (kg)	29.5	34.6	36.2	27.5	31.6	33.0
Milk SD (kg)	7.3	9.9	10.7	7.0	7.0	10.1
Number of animals pedigree	9,326,754			68,096		

Table 4-2: Memory requirement, number of rounds and CPU time for genetic evaluation of national data using different preconditioners

	Preconditioner			
	D ¹	BT	BTDIAG	BTCORR
Memory (Gb)	8.7	10.4	10.4	24.3
Rounds	952	706	494	289
CPU time (hs)	336	257	186	110
Days	14	10.7	7.8	4.6

¹ D = Diagonal, BT = Block diagonal due to traits, BTDIAG = Block diagonal due to traits with “diagonalized” (co)variance matrix for random regression, BTCORR = Block diagonal due to trait and random regression

Figure 4-1: Convergence with different preconditioners for genetic evaluation using the national data

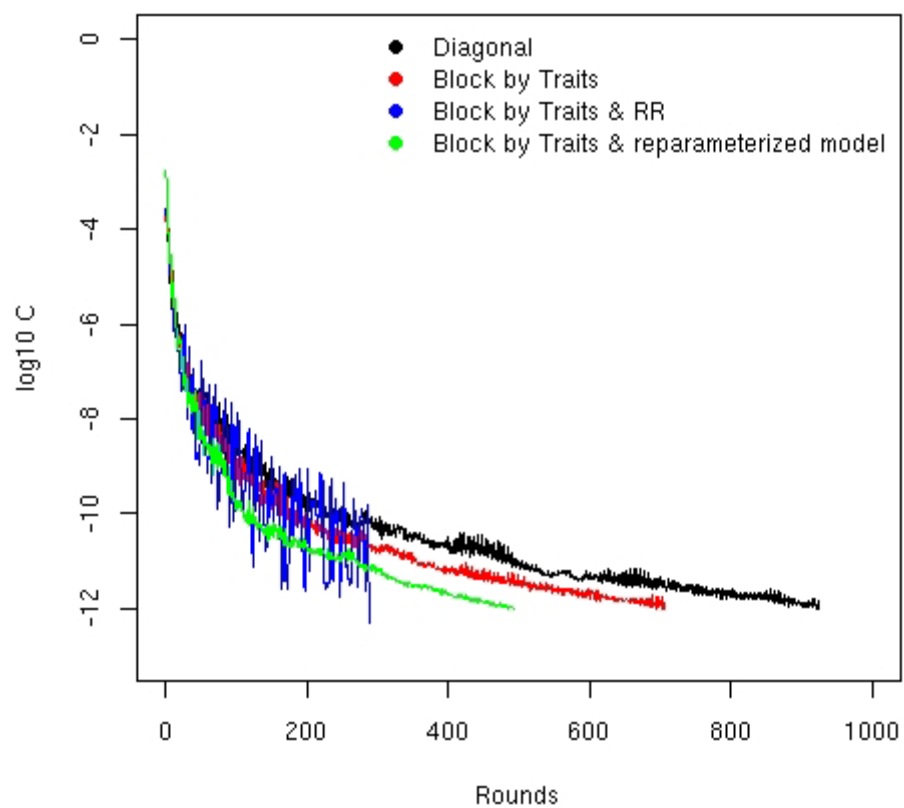
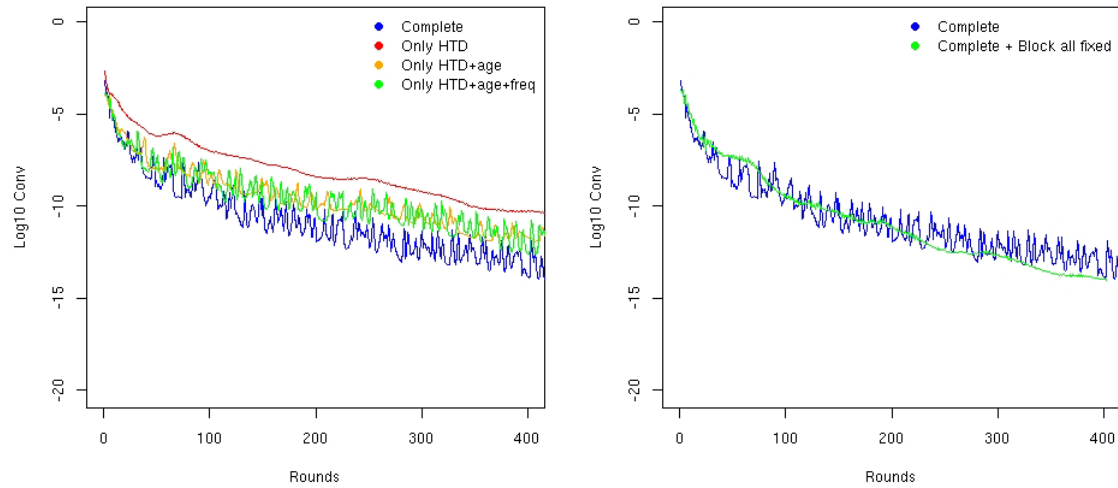


Figure 4-2: The influence of fixed effects on convergence with the preconditioner as block diagonal due to traits and correlated effects using GA data



CHAPTER 5

CONCLUSIONS

The additive genetic variance for heat tolerance increased with parity for milk production traits. It doubled from the first to second parity, and there was an additional increase from the second to the third parity. Genetic correlations for the heat stress effect between parities ranged from 0.56 to 0.79. The genetic correlations between regular and heat stress effects across parities and traits were between -0.30 and -0.47.

With the random regression model, the variances of the heat stress effect were about half of those obtained with the repeatability model. Under the repeatability model, the variances of the heat stress effect were inflated perhaps due to the timing of lactations to avoid the peak production during the heat stress periods.

The choice of preconditioners used in PCG algorithms to carry out the genetic evaluation strongly affected the convergence rate. Preconditioners based on blocks due to traits and random correlated effects were the fastest and simplest to implement when sufficient memory was available. The next most efficient method included block diagonal preconditioners where correlated random effects were reparameterized for diagonal (co)variance matrices among traits. Although the last option required less memory, additional steps for diagonalization and back-diagonalization are needed.